

# Journal of Vertebrate Paleontology

Publication details, including instructions for authors and subscription information: <u>http://www.tandfonline.com/loi/ujvp20</u>

# A new eilenodontine (Lepidosauria, Sphenodontidae) from the Lower Cretaceous of central Patagonia

Sebastian Apesteguia <sup>a</sup> & Jose L. Carballido <sup>b</sup>

<sup>a</sup> Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Fundación de Historia Natural 'Félix de Azara'-CEBBAD-, Universidad Maimónides, Hidalgo 775, Buenos Aires, Argentina

<sup>b</sup> CONICET, Museo Paleontológico 'Egidio Feruglio,', Av. Fontana 140, Trelew, Argentina, Published online: 04 Mar 2014.

To cite this article: Sebastian Apesteguia & Jose L. Carballido (2014) A new eilenodontine (Lepidosauria, Sphenodontidae) from the Lower Cretaceous of central Patagonia, Journal of Vertebrate Paleontology, 34:2, 303-317, DOI: <u>10.1080/02724634.2013.803974</u>

To link to this article: <u>http://dx.doi.org/10.1080/02724634.2013.803974</u>

## PLEASE SCROLL DOWN FOR ARTICLE

Taylor & Francis makes every effort to ensure the accuracy of all the information (the "Content") contained in the publications on our platform. However, Taylor & Francis, our agents, and our licensors make no representations or warranties whatsoever as to the accuracy, completeness, or suitability for any purpose of the Content. Any opinions and views expressed in this publication are the opinions and views of the authors, and are not the views of or endorsed by Taylor & Francis. The accuracy of the Content should not be relied upon and should be independently verified with primary sources of information. Taylor and Francis shall not be liable for any losses, actions, claims, proceedings, demands, costs, expenses, damages, and other liabilities whatsoever or howsoever caused arising directly or indirectly in connection with, in relation to or arising out of the use of the Content.

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden. Terms & Conditions of access and use can be found at <a href="http://www.tandfonline.com/page/terms-and-conditions">http://www.tandfonline.com/page/terms-and-conditions</a>

### A NEW EILENODONTINE (LEPIDOSAURIA, SPHENODONTIDAE) FROM THE LOWER CRETACEOUS OF CENTRAL PATAGONIA

#### SEBASTIAN APESTEGUIA<sup>\*,1</sup> and JOSE L. CARBALLIDO<sup>2</sup>

<sup>1</sup>Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Fundación de Historia Natural 'Félix de Azara'-CEBBAD-Universidad Maimónides, Hidalgo 775, Buenos Aires, Argentina, sebapesteguia@gmail.com; <sup>2</sup>CONICET, Museo Paleontológico 'Egidio Feruglio,' Av. Fontana 140, Trelew, Argentina, jcarballido@mef.org.ar

ABSTRACT—A new species of eilenodontine sphenodontian, *Priosphenodon minimus*, is described from a locality 400 km south of those that yield the northern Patagonian eilenodontines (the largest known terrestrial sphenodontians). The new species, represented by subadult specimens, is both the smallest known eilenodontine and the southernmost record of the group. *Pr. minimus* is characterized by a nearly vertical lateral process of the premaxilla; anteriorly extended frontals that lack the naso-prefrontal projections; a rounded frontal anterior process; a prefrontal that posteriorly embraces the nasal; a coronoid process of the dentary that is tall and with an anterior border that is vertical in medial view; strong anteromedial flanges on all teeth; uncommonly dense dental packing; and an anteriorly extended angular that reaches the midlength of the lower jaw. Differences from juvenile specimens of *Priosphenodon avelasi*, such as the interruption of the prefrontal-jugal contact, are marked. The holotype and associated material come from early Albian strata, and are therefore around 12 million years older than the northern Patagonian giant sphenodontians. The new species here described reveals that many of the characters used to diagnose *Kaikaifilusaurus calvoi* are widespread, so this taxon should be regarded as a nomen dubium. Therefore, the genus *Priosphenodon* and suggests that the new taxon represents an incidence of dwarfing. This discovery increases the monophyly of *Priosphenodon* and suggests that the new taxon represents an incidence of dwarfing. This biostratigraphic information on the terrestrial ecosystems of Patagonia.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

#### INTRODUCTION

The recognition of rhynchosaurs and trilophosaurs as archosauromorphs (Benton, 1985) and of *Clevosaurus* as carnivorous (Apesteguía, 2008) reduced the known diversity of terrestrial, strictly herbivorous rhynchocephalians to the Triassic *Pelecymala robusta* (Fraser, 1986), *Sphenotitan leyesi* (Martinez et al., 2013), and the Eilenodontinae. The latter group appears in the fossil record during the Jurassic: in particular, the earliest known representative comes from the Late Jurassic Morrison Formation (Rasmussen and Callison, 1981), followed by (in terms of both age and order of discovery) the Early Cretaceous Kootenai Formation (Throckmorton et al., 1981). The youngest and last known, but also best represented, are several forms from the early Late Cretaceous strata of Patagonia, Argentina.

In 1999, a field trip conducted by one of us (S.A.) under a project led by Fernando E. Novas (ANCP y T PID CT 01386) to outcrops of the Candeleros Formation (Neuquén Group, Río Limay Subgroup), considered as Cenomanian–Turonian in age (Leanza et al., 2004; Garrido, 2010), resulted in the discovery of an outstanding locality, named 'La Buitrera,' that preserves articulated skeletons of small- to medium-sized tetrapods (Apesteguía and Novas, 2003; Apesteguía, 2008). The main components of this fauna are opisthodontian rhynchocephalians. Recent exploration in Early Cretaceous strata from central Patagonia, Chubut Province (Fig. 1), resulted in the discovery of a new form. Here we describe this new taxon, which is closely related to the two large eilenodontines from the Candeleros Formation: *Kaikaifilusaurus calvoi* (Neuquén Province; Simón and

Kellner, 2003) and *Priosphenodon avelasi* (Río Negro Province; Apesteguía and Novas, 2003). The taxonomic status of these taxa and a revision of their diagnoses and validity are discussed here (also see Supplemental Data).

Institutional Abbreviations—FMNH, Field Museum of Natural History, Chicago, U.S.A.; LACM, Los Angeles County Museum, Los Angeles, U.S.A.; MPCA, Museo Provincial Carlos Ameghino, Río Negro, Argentina; MPCHv, Museo Ernesto Bachmann, El Chocón, Neuquén, Argentina; MPEF, Museo Paleontológico Egidio Feruglio, Trelew, Chubut, Argentina.

#### SYSTEMATIC PALEONTOLOGY

#### RHYNCHOCEPHALIA Günther, 1867 OPISTHODONTIA Apesteguía and Novas, 2003 EILENODONTINAE Rasmussen and Callison, 1981 *PRIOSPHENODON* Apesteguía and Novas, 2003

**Revised Diagnosis**—*Priosphenodon* differs from all other rhynchocephalians in the following combination of traits: welldeveloped and convex ascending process of the maxilla resulting in a robust preorbital region; hook-like end of the posterior process of the prefrontal embraces the nasal; suborbital fenestra hidden in ventral view; tall, leaf-shaped, densely packed reversed teeth (opisthodontian), with imbricated lingual and labial flanges that overlap the base of the preceding tooth in both lateral and medial views; ventromedially developed mentonian process of the jaw that is rounded in shape (i.e., devoid of a posterior hook-tip), and, accordingly, the dentary is strongly concave near the symphysis along the ventral margin; strong anterior

<sup>\*</sup>Corresponding author.



FIGURE 1. A, geographic map of Argentina and **B**, Chubut Province showing with a dashed line the southern limit of the Somun Cura-Cañadón Asfalto Basin. **C**, simplified geologic map of the area showing the 'Tres Cerros' locality (modified from Carballido et al., 2011; following Krause et al., unpub. data).

symphysial projections (spurs), with tips that leave deep marks on the buccal surface of the premaxilla.

**Type Species**—*Priosphenodon avelasi* Apesteguía and Novas, 2003.

Holotype—MPCA 300, partially articulated adult skeleton.

**Referred Material**—MPCA 301, a juvenile skeleton; MPCA 302, postcranial isolated remains; MPCA 303, a partially articulated adult skeleton.

**Locality and Horizon**—Upper layers of the Candeleros Formation (Cenomanian; Garrido, 2010), 'La Buitrera' Fossil Area, Cerro Policía, Río Negro Province, northwest Patagonia, Argentina.

#### PRIOSPHENODON MINIMUS, sp. nov. (Figs. 2-6)

**Etymology**—In reference to the small size of this species when compared with any other eilenodontine, especially in comparison with *Priosphenodon avelasi*.

**Holotype**—MPEF-PV 3166, represented by an almost complete skull with attached jaws. The left jaw was disarticulated for descriptive purposes.

**Referred Material**—MPEF-PV 3092, composed of around 20 partial bones from Huanimán Hill. They include partial jaws, maxillae, and palatines.

**Diagnosis**—In addition to its much smaller size, *Priosphenodon minimus* differs from the type species of *Priosphenodon* in the presence of the following unique autapomorphic traits: (1) maxilla with a facet for the dorsally expanded lateral process of the premaxilla close to the vertical (related to the shortening of the skull); (2) frontals anteriorly extended, and devoid of a nasoprefrontal projection; (3) rounded frontal anterior process; (4) prefrontal embraces the nasal posteriorly; (5) coronoid process of the dentary is much taller than that of *Priosphenodon avelasi*, with a straighter anterior border; (6) strong anteromedial flanges

on both maxillary and mandibular teeth; (7) unusually dense dental packing (greater than in any other eilenodontine); and (8) anterior-most extension of the angular reaches the middle of the jaw.

Locality and Horizon—The materials described herein were collected in rocks of the Chubut Group, central Patagonia, Chubut Province, Argentina (Fig. 1). The type specimen (MPEF-PV 3166) was collected from the Tres Cerros locality (Fig. 1), about 70 km northeast from Los Altares (Argentina), whereas the referred material (from the Huaniman locality) was collected 11 km northwest of the type locality. The type specimen and the referred material (which was concentrated in a single level) were found in the upper part of the La Paloma Member, just below its contact with the overlaying Cerro Castaño Member. The La Paloma Member is thought to have been deposited in an arid environment dominated by pyroclastic deposits with intercalated dune sediments, whereas the Cerro Castaño Member is composed mainly of fluvial and overbank deposits indicating a return to more humid conditions (Rauhut et al., 2003).

The Chubut Group is a very thick sequence of sedimentary strata that is exposed extensively in Chubut Province. The geology of this group is not well known. The material described herein was found in the northern part of Chubut Province, which corresponds to the Somun Curá-Cañadón Asfalto Basin (Cortiñas, 1996; Fig. 1B). In this basin, the Chubut Group is divided into two formations, the Los Adobes Formation and the overlaying Cerro Barcino Formation (Codignotto et al., 1978; Figari and Courtade, 1993; Anselmi et al., 2004). Although different stratigraphic schemes have been proposed, most authors follow that of Codignotto et al. (1978), who divided Cerro Barcino formation into four subunits: the La Paloma, Cerro Castaño, Las Plumas, and Bayo Overo members. The base of the Chubut Group is considered to be late Valanginian–Hauterivian in age (see Rauhut et al., 2003). Nevertheless, on the basis of paleomagnetic data, Geuna et al. (2000) considered the base of this group as no older than Barremian, an age which is coincident with biostratigraphic information from charophytes and ostracods (Musacchio, 1972; Musacchio and Chebli, 1975). Recently, Llorens and Marveggio (2009) reported angiosperm palynomorphs from the lowermost member of the Los Adobes Formation (El Pajarito Member), indicating a lower Albian age for the base of the group. From this data we should expect a Cenomanian-Turonian age for the La Paloma Member fossils, but again, a lower Albian age for the La Paloma and Cerro Castaño members, was recently supported by radiometric data (Krause et al., unpub. data). Therefore, we ascribe an Albian age to the new taxon here described.

#### DESCRIPTION AND COMPARISIONS

Skull

The skull of *Priosphenodon minimus* is tall and narrow (Fig. 2), as in adult specimens of *Priosphenodon avelasi*, but unlike those

of juveniles of the latter species that have relatively wide skulls posteriorly. The antorbital region is shorter than in Pr. avelasi, as in other rhynchocephalians (e.g., Polysphenodon, Brachyrhinodon; Bonaparte and Sues, 2006). Conversely, the orbital region is large, as in most rhynchocephalians. The prefrontals are ornamented, a condition shared with Eilenodon robustus (LACM 120462) and Priosphenodon avelasi. The reduced extension of the rostrum in Pr. minimus seems to be related to the shortness of the maxilla and the absence of the anterior or premaxillary process of the maxilla, which is well developed in the marine form Palaeopleurosaurus and moderate in Pr. avelasi (S.A., pers. observ.). The convex nasal is well developed but short. Although the boundaries of the supratemporal fenestra of Pr. minimus are not preserved, a natural mold of the postorbital reveals the size and triangular shape of the fenestra, whose lateral border is straight and long, as in Pr. avelasi.

As in *Palaeopleurosaurus* and *Pr. avelasi*, and differing from most other rhynchocephalians, the lateral border of the fenestra is mainly formed by the postorbital, which is extended posteriorly. By contrast, the supratemporal fenestrae in *Sphenodon punctatus* are large and equidimensional (almost square), and in



FIGURE 2. *Priosphenodon minimus* holotype (MPEF-PV 3166) skull material in **A**, right lateral view; **B**, left lateral view; **C**, dorsal view; and **D**, ventral view. **E**, **F**, and **G** are reconstructions of those views. **Abbreviations: cho**, choana; **co.fa**, facet for coracoid; **d**, dentary; **ept**, ectopterygoid; **fo**, foramen; **jpt.fe**, interpterygoid fenestra; **j**, jugal; **md.fo**, mandibular foramen; **mx**, maxilla; **mx.as.pr**, maxillary ascending process; **mx.fo**, maxillary foramen; **mx.j.pr**, maxillary jugal process; **n**, nasal; **oc**, otoccipital complex; **pa**, palatine; **pala.pr**, palatal anterior process; **pal.vo.pr**, palatal vomerine process; **porb**, postorbital; **prfr**, prefrontal; **pt.a.pr**, pterygoid anterior process; **pt.m.pr**, pterygoid medial process; **pt.q.pr**, pterygoid quadrate process; **pt.r**, pterygoid ridge; **px**, premaxilla; **q**, quadrate; **rap**, retroarticular process; **sa**, surangular; **sd.d**, secondary dentine; **sq**, squamosal; **st.fe**, supratemporal fenestra. Scale bar equals 1 cm.

pleurosaurs they are relatively small and oval (Carroll, 1985a, 1985b; Carroll and Wild, 1994).

**Premaxilla**—The premaxilla of MPEF-PV 3166 is incomplete, but the preserved part of its maxillary process together with molds of the nasal processes allows description of this bone (Fig. 2B, C).

The maxillary process is well preserved. It clearly excludes the maxilla from the border of the nostril, as also occurs in *Pr. avelasi* and, convergently, in *Clevosaurus*, a feature with high adaptive value in the strengthening of the beak (Fraser, 1988; Jones, 2006). As in *Pr. avelasi* and *C. hudsoni*, the process does not contact the prefrontal. Whereas in adults of *Pr. avelasi* the space that separates the bones is minimal, in *Pr. minimus*, juveniles of *Pr. avelasi*, and *C. hudsoni* it is substantially larger.

Because the premaxilla overlaps the nasal and the distal part of the latter is not preserved, the following observations were made on the impressions in the sediment left by the bone and should be considered with caution. The impression left by the nasal process of the premaxilla tapers posteriorly, forming a sharp wedge that is bound by the anterior ends of the nasal. The shape of this articulation, although only partially preserved, sharply differs from the square distal end of the nasal process on the premaxilla of *Pr. avelasi.* 

**Maxilla**—The maxilla of MPEF-PV 3166 (Fig. 2B) is robust and tall. Its well-preserved ascending process is slightly inclined posteriorly, and shows a concave posterior or ocular side, and a convex anterior or narial side, a feature shared with *Pr. avelasi*. The maxilla is excluded from the narial border by the posterodorsal or maxillary process of the premaxilla.

The anterior or premaxillary process is almost absent in *Pr. minimus*, as also occurs in *Pr. avelasi* adults and juveniles (Apesteguía and Novas, 2003). Conversely, it is short but present in Clevosaurus (Fraser, 1988; Sues et al., 1994; Jones, 2006). In Sphenodon, the premaxillary process is clearly defined and forms a straight angle with respect to the ascendant process of the maxilla (S.A., pers. observ.). The premaxillary process is related to the development of the maxillary process of the premaxilla, and it is also well developed in Sigmala sigmala, the robust Pelecymala (Fraser, 1986), and some specimens assigned to Opisthias (LACM B5534, LACM MN-7959-13; S.A., pers. observ.). In the material assigned by Simpson (1926a) to Opisthias, although broken, the base of the anterior process is preserved. In materials from LACM assigned to Opisthias, the anterior process is well developed, but not as a defined process (i.e., forming a straight angle with respect to the ascendant process of the maxilla). The ascending process of Pr. minimus is slightly inclined posteriorly and, although relatively low, is well defined. This differs from the tall and vertical ascending processes present in Sigmala, Pelecymala, and Sphenodon, being more similar to that of Pr. avelasi and, secondarily, to those of Opisthias and C. hudsoni. The anterior or narial side of the ascending process is convex and forms an oblique, slightly concave line that descends to meet the dental line forming a small tip. Conversely, the posterior or ocular side is concave, as in Pr. avelasi. As noted above, the anterodorsal border of the ascending process is excluded from the narial margin by the posterodorsal or lateral process of the premaxilla. An oblique facet for the posterodorsal process of the premaxilla is present, as in juvenile specimens of Pr. avelasi (e.g., MPCA 302).

The lateral surface of the ascending process is not as convex as in *Pr. avelasi*, where it is inflated, making the preorbital region bulbous. The jugal process of the maxilla is short and tall, as in *Pr. avelasi*, a feature that seems to be related to the robust



FIGURE 3. *Priosphenodon minimus* holotype (MPEF-PV 3166) left dentary in **A**, medial view; **B**, lateral view; and **C**, dorsal view. **D**, reconstruction of the jaw in lateral view. **E**, **F**, **I**, referred material in lateral view; **G**, **H**, **J**, referred material in medial view; **K**, **L**, detail of well-preserved teeth of the referred material in lateral and occlusal views. **M**, **N**, dentary of a juvenile specimen from *Priosphenodon avelasi* from northern Patagonia (MPCA, unnumbered specimen). **Abbreviations: a**, angular; **d**, dentary; **co**, coronoid; **sa**, surangular. All scale bars equal 5 mm.



FIGURE 4. Comparisons between *Priosphen*odon avelasi of different ontogenetic stages and the *Pr. minimus* holotype. **A**, MPCA 312 (*Pr.* avelasi); **B**, MPCA 311 (*Pr. avelasi*); **C**, MPCA 324 (*Pr. avelasi*); **D**, MPCA 316 (*Pr. avelasi*); **E**, MPEF-PV 3166 (*Pr. minimus*); **F**, MPCA 301 (*Pr. avelasi*); **G**, MPEF-PV 3166 (*Pr. minimus*, reversed); **H**, **I**, MPCA 305 (*Pr. avelasi*) in lateral and medial views. Scale bar equals 10 mm.

construction of their skulls. The preserved 'lip' of secondary bone or 'bone of attachment,' projecting laterally over the posterior portion of the tooth row, is dorsoventrally high. Thus, the step that reaches the main part of the maxilla is much smoother than in other species. This step is more evident in the anterior part, directly underneath the ascending process. Dorsal to the secondary 'lip,' the dorsal edge of the maxilla is slightly concave, decreasing in height anteriorly.

The large anterior maxillary foramen, characteristic of rhynchocephalians, is located in the anterior region of the maxilla, toward the anterior side of the base of the ascending process. Although the anterior margin is broken, it is clear that the foramen is located in a teardrop-shaped fossa. Two other smaller, maxillary foramina are located along the side of the maxilla forming an arch. One of them is directly ventral to the prefrontal and the second is in the middle of the orbital region, close to the jugal contact. Whereas in *C. hudsoni* and both juveniles and adults of *Pr. avelasi* all foramina are positioned in a horizontal line that extends parallel to the tooth row (Fig. 4F), in *Pr. minimus* they are located in a dorsally concave line with respect to the tooth row (Fig. 4G). The suborbital fenestra, formed by the posteromedial region of the maxilla, is much reduced and almost obliterated, as in *Pr. avelasi*.

The maxillary dentition of *Pr. minimus* is similar to that of other species of *Priosphenodon*, with scale-shaped, closely packed teeth. The teeth embrace the preceding tooth with both lateral and medial flanges, and are invaded at their bases by additional hard tissues that were deposited during life, known as secondary bone (sensu Kieser et al., 2009). In *Pr. Minimus*, the teeth are much more acute and more vertically oriented with respect to those of *Pr. avelasi*, a condition that is here considered as autapomorphic and that is also present in the lower jaw (see below). Conversely, teeth of both juveniles and adults of *Pr. avelasi* and *K. calvoi* show a low, oblique apical tooth surface.

The teeth of Pr. minimus are large with respect to skull size but display a remarkable reduction in the middle of the jaw as a result of excessive wear. This is interpreted as additional evidence to support the adult or subadult stage of these individuals. Actually, the few well-preserved teeth are those located in the posterior part of the maxilla, the only place where new additional teeth arise in eilenodontines (Robinson, 1976; Foster, 2003). As in Pr. avelasi, the maxillary teeth are modified by wear to end in a strong labial cone visible laterally, from which arises a posteromedial flange, which is always strongly worn. In the most derived rhynchocephalians, posterior maxillary teeth bear posteromedial flanges that vary in size from small (e.g., Sphenodon, Palaeopleurosaurus, Pamizinsaurus) or medium-sized (e.g., Brachyrhinodon, Polysphenodon, Tingitana), to large (e.g., Clevosaurus, Homoeosaurus, Kallimodon), when compared with the size of the tooth as a whole. Priosphenodon spp. have well-developed posteromedial flanges (Fig. 4B). The holotype specimen of Pr.

*minimus* bears, on the left side, around 12 maxillary teeth. Although a short diastema was originally proposed as evidence for the maturity of the specimens (Apesteguía and Carballido, 2008), further preparation of the specimen has shown that a diastema is not present; therefore, we considered the specimen to be a subadult. As seen in juvenile specimens of *Pr. avelasi* (Apesteguía, 2008), there is no hatchling dentition in any ontogenetic stage for *Priosphenodon* spp. Therefore in *Priosphenodon*, only additional dentition is present, even in the earliest recorded ontogenetic stages, which is probably true for all eilenodontines.

**Nasal**—The nasal is represented mainly by a mold of the inner surface accompanied by a few bone fragments. Unlike the condition in basal rhynchocephalians, such as *Gephyrosaurus*, where the nasals are relatively narrow (Gauthier et al., 1988), the nasal of derived rhynchocephalians is wide and thick, forming a robust roof for the nasal cavity, as can be better seen in *Pr. avelasi* (Fig. 5B–E).

The lateral border of the nasal contacts the posterior surface of the maxillary process of the premaxilla. However, whereas in *Pr*.



FIGURE 5. *Priosphenodon minimus* holotype skull with details of the prefrontal compared with specimens of *Sphenodon punctatus* and *Priosphenodon avelasi* in different ontogenetic stages. **A**, *Sphenodon punctatus*; **B**, MPCA 324; **C**, MPCA 317; **D**, MPCA 305; **E**, MPCA unnumbered specimen; **F**, *Priosphenodon minimus* holotype skull; **G**, *Priosphenodon minimus* holotype with details of the prefrontal. **Abbreviations: cen.bas**, central basin; **fo**, foramen; **fr**, frontal; **fr.fa**, frontal facet; **fr.ina.pr**, frontal internasal process; **fr.n-prf.pr**, frontonasal prefrontal process; **j**, jugal; **mx**, maxilla; **n**, nasal; **n.fo**, nasal foramen; **prf**, prefrontal; **prf.fo**, prefrontal foramen; **prf.rug**, prefrontal rugosity; **prox.proc**, proximal process; **px**, premaxilla; **rug**, rugosity. All scale bars equal 10 mm.

*avelasi* the lateral boundary describes an oblique line that frames the lateral expansion of this bone, in *Pr. minimus* it extends almost parallel to the midline. The nasal also briefly contacts the maxilla, the prefrontal, and the frontal (not preserved). Anteriorly, the sharp anterior processes of the nasal (preserved as a mold) form the medial borders of the nostrils and embrace the molds of the nasal processes of the premaxilla.

The posterior portion of the nasal forms a tongue that overlaps the prefrontal, which bounds this portion laterally and medially. A small foramen is present posterior to an oblique ridge, where the posterolateral tongue enters the nasal main shaft. This foramen probably represents the external exit of the lateral ethmoid nerve, as present in *Ctenosaura pectinata* (Oelrich, 1956), and differs from the paired basins pierced by a dorsal foramen present in the center of the *Sphenodon* nasal (Fig. 5A) when viewed in lateral aspect. The nasal extends posteriorly with a straight path, as in *Pr. avelasi*. It enters as a sharp projection into a narrow concavity between the dorsal and medial processes of the prefrontal.

In dorsal view, the nasal meets the frontal anterior process posteriorly (as in the specimen MPCA 305 of *Pr. avelasi*) at the level of the posterior boundary of the maxillary ascending process. Although frontals are not preserved, the posterior boundary of the nasal mirrors the anterior shape of the frontal. In this respect, *Pr. minimus* differs from *Pr. avelasi*, because in the former the suture seam depicts a curved line, whereas in the latter the suture line tapers anteriorly to a sharp point (Fig. 5C–E). Additionally, in *Pr. minimus*, all the sutural contacts occur on the dorsal surface of the skull.

In *Pr. avelasi* (MPCA 305), there are two conspicuous ridges on the ventral side of the nasal: one runs obliquely along the bone and the other forms a medial ridge to meet its opposite along the midline of the skull and probably served as fixation point for a cartilaginous nasal septum (Whiteside, 1986). Of these, only the former, the oblique rugosity lying anterior and parallel to the sutural seam between the nasal and prefrontal, is preserved in *Pr. minimus*. In both species of *Priosphenodon*, this ridge is well developed and oriented at an oblique angle rather than parallel to the midline as in the basal forms *Gephyrosaurus* (Evans, 1980) and *Diphydontosaurus* (Whiteside, 1986:390).

Because a large part of the nasal was abraded in *Pr. minimus*, it is not possible to recognize its rugosity directly. However, there is a negative line in the mold, which might represent the impression of a crest.

**Prefrontal**—The prefrontal contacts the maxilla ventrolaterally, the frontal and nasal dorsomedially, and the jugal posteromedially. As in all eilenodontines, the prefrontal is large and its contact with the nasal is extensive. In *Pr. minimus*, the contact with the frontal is even more reduced than in *Pr. avelasi*. As the nasal overlaps the prefrontal posteriorly (as in some acrodont iguanians; K. Smith, pers. comm.), the prefrontal seems to bear a posterodorsal process that extends posteriorly along its margin with the nasal and frontal. This process, which tapers in *S. punctatus* (Fig. 5A) and juveniles of *Pr. avelasi* (Fig. 5E), appears to form a hook-like structure in adults of both *Pr. avelasi* (Fig. 5D) and *Pr. minimus* (Fig. 5F) that wraps around the nasal posterolateral end.

As in *Clevosaurus hudsoni* (Fraser, 1988), the prefrontal has a ventral process in the anterior region of the orbit that extends downwards in full contact with the maxilla (as in all rhynchocephalians, lacrimals are absent) until fitting in a palatine facet of the maxilla. As in *Sphenodon* (Fraser, 1988) and *Pr. avelasi*, a foramen for the nasolacrimal duct is located between the maxilla and the ventral process of the prefrontal. In the holotype of *Pr. minimus*, the prefrontal and the jugal are prevented from contacting each other by the maxilla (Fig. 2C), unlike the condition in the juvenile specimen of *Pr. avelasi* (MPCA 305; Fig. 4F).

As in other eilenodontines, such as *Eilenodon robustus* (LACM 120462) and *Pr. avelasi* (Fig. 5), the prefrontals are

markedly sculptured. As the surface was eroded, it is possible to observe the vascular cavities that filled the rugosities. In *Pr. avelasi*, three groups of rugosities (ventral, central, and upper) plus a small isolated rugosity or horn can be distinguished (Apesteguía, 2008); however, it is difficult to assess the correspondence of the cavities in *Pr. minimus* to the external rugosities of *Pr. avelasi*. The position of these cavities suggests that, from ventral to dorsal, the two preserved rugosities present in *Pr. avelasi*, whereas the other three cavities might correspond to the central group, and the two upper cavities could correspond to the upper group. The small isolated rugosity, or horn, of *Pr. avelasi* could be represented in *Pr. minimus* by the two uppermost cavities. However, more material is necessary to validate this assumption.

**Frontal**—Although preserved here as partial molds only, some details are still discernable. The most evident is the central constriction. The posterior part of the mold shows a notch that probably corresponds to the frontal half of the parietal foramen, located at the posterior border of the bone, as in other rhynchocephalians. Anteriorly, the frontals contact the nasals and prefrontals, and posteriorly the parietals. Other contacts are not evident in the material. Whereas in *Pr. minimus* there is only one projection between the nasals, in *Pr. avelasi* there are three in total, with another between the nasals and prefrontals, and a third after the prefrontals (Fig. 5C).

**Palatine**—Both palatines are well preserved and visible in ventral view in MPEF-PV 3166 (Fig. 2, 6). The palatine comprises three processes: the anteromedial vomerine process, the posterior pterygoid process, and the anterolateral maxillary process. The vomerine process is dorsal to the pterygoid and vomer, and thus hard to see in ventral view, but it is clearly visible in this specimen, bounding the posterior border of the choana or fenestra exochoanalis.

The maxillary process is not visible. The pterygoid process is posteromedially directed. The dentition extends along the entire length of the pterygoid process. In MPEF-PV 3166 and other eupropalinal rhynchocephalians, the pterygoid process is related to the development of the maxilla, with teeth following in the same direction as those of the maxillary dentition. This configuration was achieved in different ways in the two different forms of eupropalinal taxa, the sphenodontines and eilenodontines (Apesteguía, 2008).

The pterygoid process of the palatine in MPEF-PV 3166 has a robust sector that bears teeth and also projects medially toward the broad pterygoids. The palatine shelf in both *Pr. avelasi* and *Pr. minimus* is noteworthy in being quite narrow anteriorly, much more so than in any other terrestrial rhynchocephalian.

In basal lepidosauromorphs and basal members of Rhynchocephalia, such as *Gephyrosaurus* and *Diphydontosaurus*, the palatine teeth are arranged in several rows, a feature retained in *Planocephalosaurus*. In derived rhynchocephalians, a single tooth row is present. The palatine tooth row in *Pr. minimus* extends parallel to the maxillary tooth row. The ventral surface of the palatine shows a slight curvature, but this is always in a sagittal plane, as in all eupropalinal taxa (Apesteguía, 2008).

The palatine dentition is slightly different from the maxillary or dentary dentition, because it is less well developed and highly asymmetrical. In *Opisthias, Sphenodon*, and the taxa from the Middle Jurassic of England (Evans, 1992), the palatine dentition is distinctive, differing from that of *Clevosaurus, Polysphenodon*, *Brachyrhinodon*, and *Kallimodon* (Cocude-Michel, 1963) in the presence of small posterolateral flanges, which are also present in *Godavarisaurus* (Evans et al., 2001).

The palatine dentition in *Priosphenodon* spp. is formed by small teeth, which are less scale-shaped, wider, and more densely packed than those of the maxilla. The shape resembles that of the palatine teeth in *Opisthias* (LACM 120476) in having a single posterolabial flange that overlaps the anterior border of the



FIGURE 6. *Priosphenodon minimus* holotype skull in ventral view compared with specimens of *Priosphenodon avelasi* in different ontogenetic stages. **A**, MPCA 300; **B**, MPCA 301; **C**, MPCA 313; **D**, *Priosphenodon minimus* holotype skull detail of ventral surface; **E**, *Priosphenodon minimus* holotype skull in ventral view. Scale bar equals 10 mm for **A–C**, **E**; and 3 mm for **D**.

following tooth. An extensive overgrowth of secondary bone covers the bases of all teeth.

Seven well-preserved palatine teeth are present in *Pr. minimus*, but there is evidence of at least three more in the anterior region of the palatine. The teeth are like those of *Pr. avelasi*.

**Pterygoid**—This is the largest element in the sphenodontid palate. Of its originally triradiate structure, only the anterior (palatine) process is well preserved in the holotype. It is wide and anteromedially directed. The lateral or transverse process, which bears the pterygoid wing, is only preserved until approximately the level of the epipterygoid facet.

The preserved part of the pterygoid contacts the vomer, palatine, and ectopterygoid. Contacts with the epipterygoid, basisphenoid (via its basipterygoid processes or trabeculae), and quadrate are not preserved in this material. When articulated, the pterygoids contribute to the palate, framing a triangular fenestra along the midline (the interpterygoid fenestra).

As in other rhynchocephalians, and especially the eupropalinal taxa, the pterygoids in *Pr. minimus* are excluded from the margins of the suborbital fenestra by the development of the palatines (Sues et al., 1994:character 32; Wu, 1994:character 35; Reynoso, 1996:character 18; Apesteguía and Novas, 2003:character 26). As in *Pr. avelasi*, the suborbital fenestra is only visible dorsally if the skull roof is removed, whereas in palatal view it is obliterated by the extensive development of the palatine and ectopterygoid.

The anterior (palatine) process is wide and rhomboidal in shape, and occupies more than half of the palatal roof. Together with its counterpart, they extend anteriorly to form an oval platform that reaches the vomers, but not the internal choanae. Departing from the central region of the pterygoid, on the ventral surface of the palatine process, two continuous crests run anteriorly on each side parallel to the tooth-bearing ridges as in basal forms such as *Diphydontosaurus avonis* (Whiteside, 1986:fig. 3) and *Planocephalosaurus robinsonae* (Fraser, 1982).

The transverse pterygoid process projects laterally and attaches to the ectopterygoid. It widens distally, ending as part of a flat, oval surface. Considering its position, it is possible that the pterygoid flange probably worked as a guide during jaw closure as in Sphenodon (Jones et al., 2012). The pterygoid wing size was used by Wu (2003) as evidence for the presence and importance of the M. pterygoideus atypicus, which originated on the wing and is involved in the anteroposterior movement of the lower jaw. The anterior part of the transverse pterygoid process articulates with the ectopterygoid by means of a complex joint that Whiteside (1986) regarded the strongest joint in the skull (at least in Diphydontosaurus), although Jones et al. (2011) suggested that several other joints in the skull roof might have been stronger. Actually, the anterior face of the pterygoid wing is formed, in part, by the ectopterygoid. The suture between the pterygoid and palatine is evidenced by a medial incision that defines a deep 'S' between both bones, as also observed in Pr. avelasi and Sphenodon (in which this feature becomes accentuated).

In non-eupropalinal taxa, the inward bowing of the palatine and its tooth row strongly restricts the pterygoid anteriorly. In eupropalinal taxa such as *Priosphenodon* and *Sphenodon*, where the palatine tooth row is straight and far from the pterygoids, the curvature of the palatine-pterygoid seam is still present, demonstrating the independence of the former feature and highlighting its possible utility in strengthening the palate.

The central part of the pterygoid is well preserved in ventral view and represents the area where the three pterygoid processes converge. The region extends from the articular recess for the palatine to the ventral process that posteriorly restricts the interpterygoid fenestra. In most rhynchocephalians, including *Priosphenodon*, this region is anteroposteriorly short and wide. Conversely, in sphenodontines (e.g., *S. punctatus*), it is elongated to reach about twice the minimal width between both pterygoids (Apesteguía, 2008).

In several lepidosaurs, the interpterygoid fenestra not only separates the pterygoids but also reaches the palatines. A fenestra separating only the pterygoids is a trait that separates rhynchocephalians from squamates (Apesteguía, 2008). In contrast to basal forms, but as in *Pr. avelasi*, the fenestra is restricted posteriorly by a small medial process, which is preserved only on one side and that is probably homologous to the ventral process of the pterygoid described by Bonaparte and Sues (2006).

In *Pr. avelasi*, the interpterygoid fenestra and the central pterygoid region are narrow throughout ontogeny (Fig. 6A–E; Apesteguía, 2008). However, in a juvenile specimen of *Pr. avelasi* (which is the same size as the holotype of *Pr. minimus*; Fig. 6C), the fenestra is as wide as the total width of both the pterygoid anterior processes, whereas in the adults of *Pr. avelasi* the width of the fenestra is less than a single palatine (Fig. 6A), as in *Pr. minimus* (Fig. 6D, E). The occurrence of a wide interpterygoid fenestra in adults of *Sphenodon punctatus* therefore represents the retention of a juvenile trait. Only the base of the quadrate pterygoid process was preserved.

**Ectopterygoid**—The ectopterygoids are poorly preserved and are visible as small and angled bones that form the posterolateral border of the suborbital fenestra. As in *Pr. avelasi*, the ectopterygoids of MPEF-PV 3166 are curved bars, wedged between the palatines and pterygoids.

The lateral process of the ectopterygoid is not preserved. The medial ectopterygoid process has an anterior and a posterior pterygoid branch. The pterygopalatine or anterior branch bears two facets embracing both the pterygoid and the palatine, and gives extra strength to the pterygoid wings, whereas the posterior pterygoid branch is reduced. As in Pr. avelasi, ectopterygoids of Pr. minimus are uncommon. Whereas in Squamata and relatively basal rhynchocephalians (e.g., Clevosaurus hudsoni) the ectopterygoids extend posteromedially from the maxilla-jugal contact to the pterygoid-palatine contact, describing an oblique line, in Priosphenodon the pterygoids are transversely developed at  $90^{\circ}$  with respect to the main axis of the skull. Therefore, the maxilla and palatine are tightly attached posteriorly by the ectopterygoid, hiding the suborbital fenestra in ventral view. This feature is unique to Priosphenodon among rhynchocephalians (Apesteguía and Novas, 2003).

**Squamosal**—The squamosal is poorly preserved and represented by only a short sliver of bone in the upper and posterior part of the skull. The preserved part is the dorsal region. It is thick and horizontally positioned over a lappet of bone that represents the otoccipital complex. The squamosal forms the posterior corner of the skull roof (Romer, 1956) and the posterolateral border of the right supratemporal fenestra.

**Otoccipital Complex**—This structure, formed by the fusion of the opistothic and exoccipital (Estes et al., 1988), is present in lepidosaurs but not basal lepidosauromorphs (Maisch and Matzke, 2006). Although the anterior boundary with the prootic is not preserved, a portion of the dorsomedial boundary with the supraoccipital is present. Posterolaterally, the complex contacts the quadrate, of which only fragments remain.

#### Lower Jaw

The lower jaw of *Pr. minimus* is deep, especially the dentary, as in all eilenodontines. The ratio between the tooth maximum height and the height of the jaw below it (Fraser, 1988; Apesteguía and Novas, 2003; Säilä, 2005) is about one-third in *Pr. minimus*, differing from closely related species such as *Pr. avelasi* and *E. robustus*. The splenial, as in most rhynchocephalians, does not ossify, leaving a wide, open Meckelian canal that widens posteriorly.

**Dentary**—The dentary is the largest bone of the jaw. In basal forms, such as *Gephyrosaurus* and *Diphydontosaurus*, the dentary is long and gracile, suggesting an insectivorous diet (Whiteside, 1986), and terminates in a small, oval symphysis, divided by a deep sulcus. More derived rhynchocephalians developed a deeper and shorter jaw (see Reynoso, 2005), with a prominent coronoid process, in association with the development of propalinal movements and the processing of harder food items.

In *Priosphenodon*, the dentary is deep, as in other eilenodontines, with the tallest point ventral to the coronoid process. This condition is commonly associated with small tooth size, but this is not the case in *Pr. minimus*, in which the teeth are tall. The dentary depth can be measured as a ratio between the precoronoid maximum height divided by the total length (Apesteguía, 2008). In *Pr. minimus* this ratio is about 0.27, whereas in *Pr. avelasi* (MPCA 300) it is 0.216. Although the length of the dentary from the symphysis to the posterior process of the dentary is about 97 mm in the holotype, it reaches 110 mm in the largest measured dentary of *Pr. avelasi*. In the holotype of *Pr. minimus*, the preserved part of the dentary reaches 29.27 mm in length, but it lacks the symphysis and the posterior process.

The dorsal border of the dentary, which bears the dentition, extends anteriorly and straight from the coronoid process (Fig. 3) and then curves dorsally to reach the symphysial region at a height equivalent to the coronoid apex. In dorsal view, the dental line slowly turns laterally from the coronoid process towards the anterior tip of the dentary. However, the very intense wear exhibited by this specimen does not allow measurement of the orientation of the entire tooth rows, because most of these are not preserved. In the holotype, as the symphysis does not preserve the shape of the mentonian process, the symphysial recess or the symphysial spur cannot be described. The secondary bone follows the dental line. Its ventral extent is bounded by a wellmarked sulcus that extends from the symphysial recess to end between the fourth to seventh preserved teeth (in Pr. avelasi it ends between the sixth and tenth teeth). Toward its end, the secondary dentition platform curves upwards, disappearing close to the base of the teeth.

The medial side of dentary is divided by the Meckelian groove, which gets deeper posteriorly. The proximodorsal half of the dentary has been eroded by contact with food and the palatine and maxillary dentitions. Anteriorly, it has a well-developed edentulous border. Despite the intense wear, these teeth do not belong to the hatchling series, which is absent in eilenodontines such as *Toxolophosaurus* and *Pr. avelasi* (Apesteguía and Novas, 2003).

Although a diastema is not present posterior to the last tooth in any of the preserved jaws, the extreme wear observed in the dentary teeth, especially in the referred specimens (MPEF-PV 3092; Fig. 6), indicates that these individuals had reached an advanced ontogenetic stage, but had not yet attained their maximum size.

The platform that bears the teeth is curved and its borders climb to the base of the penultimate tooth (as in *Pr. avelasi*). A subtle platform, developed in a deeper level, frames the deepest part of the Meckelian groove dorsally. Posteriorly, the platform climbs to constitute the base of the facet for the coronoid bone (as seen in the disarticulated bones in MPEF-PV 3166). The lower platform continues anteriorly with a ventral curvature to form the postsymphysial lamina (Apesteguía, 2008). As is characteristic of other eilenodontines, some species of *Opisthias* (Apesteguía, 2008), and *Sphenocondor* (Apesteguía et al., 2012), the coronoid prominence is low. However, it is relatively taller in *Pr. minimus* than in *Pr. avelasi*.

The coronoid region is formed by the dentary, the coronoid (medially), and the surangular (laterally). In most sphenodontians (except the basal form *Gephyrosaurus*), the coronoid eminence is high. In *Pr. minimus*, as in other eilenodontines (Apesteguía and Novas, 2003), it is square and low in profile. Posterior to the coronoid region, the dentary descends gradually following an oblique line leading to the mandibular foramen (for the mandibular artery; O'Donoghue, 1920). In medial view, this foramen is limited anteriorly by the coronoid bone, posteriorly by the surangular (only a very small fragment is preserved), and the prearticular ventrally (Fig. 3). Whereas in *Pr. avelasi* the prearticular height under the foramen is close to half of the coronoid height, in *Pr. minimus* the prearticular is much shallower and the coronoid is relatively taller. The posterior process of the dentary was not preserved.

Eilenodontines do not exhibit dental regionalization at any post-hatchling ontogenetic stage (Apesteguía and Novas, 2003; Apesteguía, 2008). Teeth are numerous, uniform in shape, and lateromedially wide. However, whereas in all eilenodontines the maxillary teeth have well-developed posteromedial flanges, the teeth of the lower jaw have an important development of both anteromedial and anterolateral flanges; thus, both lingual and labial flanges hide the base of the anterior tooth in lateral view. This arrangement is due to the position of the teeth and is presumably functionally related. Tooth size increases posteriorly, with larger teeth being the most recently added. Their tips point anteriorly and are densely packed to form a continuous saw-like structure. Secondary bone overgrowths are present on the base of every tooth. The intense wear is a consequence of eupropaliny (Apesteguía and Novas, 2003) and is heterogeneous. Wear is especially well developed on the anterior teeth, whereas in the last three teeth (the last erupted) it is considerably less developed. A subtle groove extends along the midline of the mandibular teeth, but more specimens are necessary in order to verify this feature

**Surangular**—Only a small part of this bone is preserved in MPEF-PV 3166. It occupies a large part of the posterior region of the jaw, between the coronoid and the articular, contributing to the dorsal middle region of the jaw and the posterior boundary of the mandibular foramen. In *Pr. minimus*, it is only preserved as the posterior border of the mandibular foramen. In this specimen, the foramen is not fully visible but covered with a fragment of broken bone. Besides its participation in the posterior border of the foramen, a small process of the surangular also forms a small part of the ventral border, thus differing from *Pr. avelasi*. Additionally, the surangular bounds the prearticular and thus contributes the anterior border of the adductor fossa (Romer, 1956).

**Angular**—The angular is a long, scale-shaped bone that is widely exposed on the medial side of the jaw. The bone passes under the coronoid to partially cover the posterior region of the Meckelian groove. Anteriorly, it contacts the dentary and helps to form the floor of the Meckelian groove. The angular in *Pr. minimus* is unusually long, reaching anteriorly the middle of the jaw, a point considerably further anterior than in *Pr. avelasi* or any other species. The posterior extent of the angular cannot be evaluated, but, as in *Pr. avelasi*, it probably had a posterodorsal limit that reached the prearticular to form an elevated angular-prearticular ridge.

**Prearticular**—The prearticular forms the posterior end of the jaw and is widely exposed medially. Anteriorly, it articulates with the dentary and coronoid, the latter being partially covered by the anterolingual process of the prearticular. Dorsally, the prearticular articulates with the surangular. Its posterior region and the retroarticular process are not preserved.

**Coronoid**—The coronoid is located immediately posterior to the tooth row. It is mainly exposed in medial view and covers most of the coronoid process of the dentary. Its dorsal process is taller than any other part of the jaw. The labial process, epidentary rugosity, and anterodorsal prominence (Apesteguía, 2008) are not well enough preserved to be evaluated here. Posteriorly and laterally, the coronoid is overlapped by the thin dorsal margin of the anterolateral process of the surangular. Medially, the anterior part of the coronoid articulates with the dentary and covers a substantial part of the last tooth. As in various different diapsids such as araeoscelidians and younginiforms (Gow, 1975; Reisz, 1981; Gauthier, 1984), the coronoids of Priosphenodon spp. are remarkably low with respect to both jaw height and tooth height (Apesteguía and Novas, 2003). However, in Pr. minimus, it is relatively much taller than in Pr. avelasi, and its anterior border is straighter.

#### PRIOSPHENODON MINIMUS AND THE VALIDITY OF KAIKAIFILUSAURUS

In January 1999, several articulated skeletons of an eilenodontine rhynchocephalian were found in the Canderleros Formation of Río Negro Province. The discovery was communicated in several meeting abstracts (e.g., Novas et al., 1999; Apesteguía et al., 2001; Apesteguía, 2002). In 2002, a different team found two fragmentary dentaries in the Canderleros Formation of Neuquén Province and communicated this at the XVIII Congresso Brasileiro de Paleontologia, in Brazilia (Simón and Kellner, 2002:280-281). Within a few days of each other, Apesteguía and Novas submitted a paper describing the Río Negro taxon (Pr. avelasi Apesteguía and Novas, 2003), whereas Simón and Kellner submitted a paper on their material (Kaikaifilusaurus calvoi Simón and Kellner, 2003) to a different journal. The latter paper was published 2 months before the former. These taxa not only were collected from the same formation, but also share a number of derived characters, which prompted Martinelli and Forasiepi (2004) and Albino (2007) to regard them as synonymous, with the latter author referring both taxa to the same species. Because the binomen K. calvoi was published earlier than Pr. avelasi, the latter taxon was regarded as a junior subjective synonym of the former.

No new material has been reported for *K. calvoi*, which is known only from the original material. In contrast, *Pr. avelasi* is known from numerous specimens representing different ontogenetic stages (Apesteguía and Novas, 2003). An extensive description of *Pr. avelasi* is in preparation, but lies outside the scope of this contribution. Nevertheless, several details of this new material are provided herein to allow comparisons between *Pr. minimus* and adult and juvenile specimens of *Pr. avelasi*. The discovery of *Pr. minimus*, which shares many derived character states with both *K. calvoi* and *Pr. avelasi*, has provided new information on the potential synonymies among these taxa and prompted a taxonomic revision of the Patagonian eilenodontines.

Five autapomorphic characters of the dentary were proposed as diagnositic of *K. calvoi* by Simón and Kellner (2003):

(1) A marked dorsoventral symphysial expansion on the medial surface. This expansion results from the addition of two different characters, the 'symphysial spur' (Apesteguía, 2008) or 'spout-like symphysial region' (Simón and Kellner, 2003), and the 'mentonian process' (Apesteguía, 2008). A hook-like development of the symphysis is typical in some rhynchocephalians, but it is particularly rounded in *K. calvoi* and *Pr. avelasi*.

Reynoso (2003), working on *Cynosphenodon huizachalen*sis, recognized that these peculiar rhynchocephalian symphysial structures are the result of differential growth rates in certain parts of the dentary. Under Reynoso's scheme, fast dorsal growth increases the distance between the caniniform (when present) and the symphysial spur, whereas slower ventral growth leads to a separation between the anteroventral end of the symphysis and the dentary diaphysis. Simultaneously, this differential growth amplifies the morphological differences, changing the direction of the spur and contributing to the creation of a ventral hook or mentonian process, and also leads to the anterior-most tip of the symphysis extending more anteriorly, so that it develops a characteristic angle with the long axis of the dentary. Reynoso (2003) demonstrated that the angle at which the anterior margin of the symphysis departs from the vertical varies with age, but that it is relatively constant in adults. The discovery of the specimen LACM 135644 (loc. 6174), a juvenile of Eilenodon robustus, permitted the recognition of a smaller and equally rounded mentonian process (see below) for that genus. A similar small process is present in Opisthias rarus (LACM 120467), but the region was not preserved in MPEF-PV 3166.

In summary, the dorsoventral symphysial expansion is the result of two independent features that vary ontogenetically (see below). A dorsal expansion is widely distributed among rhychocephalians, whereas the ventral expansion is well developed in *K. calvoi* and *Pr. avelasi*, and reduced in *E. robustus* (this features in unknown in MPEF-PV 3166).

- (2) An anterodorsally oriented edentulous ridge. This feature is widespread in adult eupropalinal rhynchocephalians, including Sphenodon. In derived sphenodontids, teeth are strongly worn against the double palatine and maxillary tooth rows, which are commonly reduced in adult forms to a sharp osseous border. Wear of the anterior dentary series, particularly hatchling teeth, produces this sharp border. Some rhynchocephalians have few teeth (e.g., Clevosaurus) and the edentulous ridge appears very early in ontogeny. Furthermore, the faster dorsal growth proposed by Reynoso (2003) extends this region forward to form the symphysial spur that fits into facets on the posterior surface of the premaxillary beak. The persistence of an anterior successional tooth at the end of this spur has not yet been demonstrated. In summary, the presence of an edentulous ridge is a product of the ontogenetic stage of the specimen, as also observed in other eupropalinal rhynchocephalians, and cannot, therefore, represent an autapomorphy. A similar feature is also present in herbivorous agamids such as Uromastyx (Robinson, 1976), forming part of a morphofunctional complex associated with herbivory and acrodonty.
- (3) A short, anteroposteriorly oriented symphysial shelf. A symphysial shelf is widely distributed, but is especially common in opisthodontians. Whereas in Toxolophorosaurus cloudi it is wide and forms a true spout-like structure (S.A., pers. observ.), in most taxa it forms a well-developed spur. A symphysial shelf can also be seen in specimens assigned to Opisthias (e.g., LACM 135516 and 120467), the former specimen possessing a caniniform, but the latter too worn for the presence/absence of a caniniform to be determined. The symphysial shelf is also present in the holotype of Pr. avelasi (where it is horizontal) and in K. calvoi, where it is oblique. Simón and Kellner (2003) stated that this feature was absent in Toxolophosaurus and unknown in Eilenodon. However, the 'shelf' of Simón and Kellner (2003) is essentially an incipient version of the 'spout-like structure' described by Throckmorton et al. (1981) for Toxolophosaurus. In Eilenodon, the spur has a truncated shape (S.A., pers. observ.), as in Priosphenodon. Although this character is not well preserved in MPEF-PV 3166, it is present in the referred material from Huanimán (MPEF-PV 3092).
- (4) A pronounced gap between the coronoid process and the last tooth. This feature varies through ontogeny. Simón and Kellner (2003) stated that this feature was absent in Sphenodontinae, but present in *Tingitana* and *Pamizinsaurus*. However,

when sphenodontians reach maturation and the last additional tooth erupts, the lower jaw still experiences a few millimeters of growth, generating a small diastema (Reynoso, 2005). The diastema characterizes senescent individuals of most rhychocephalian species, as is evident from its presence in *Clevosaurus* (Fraser, 1988), for example.

(5) Ventral margin of the dentary close to the symphysis strongly concave. This character is also present in *Pr. avelasi, Eilenodon* (LACM 135644), and *Sphenodon* to some extent (M. E. H. Jones, pers. comm.). This character is strongly developed in the holotype specimen of *K. calvoi*. In *Pr. avelasi*, the development of this feature is variable, a difference that could be interpreted as species differentiation, but also as result of population variability or sexual dimorphism. For the moment, this character is considered as polymorphic in *Pr. avelasi*. This anatomical region is unfortunately absent in all known specimens of *Pr. minimus*.

This survey demonstrates that the five characters proposed in the original diagnosis of *K. calvoi* have a more widespread distribution, and therefore do not represent unique autapomorphic traits for this taxon. Most of the diagnostic features of *K. calvoi* are in fact shared with *Pr. avelasi* and *Pr. minimus*, indicating that all these forms share a close relationship. However, with good skull material, both *Pr. avelasi* and *Pr. minimus* are sufficiently well preserved to demonstrate that they are separate taxa (see above). *K. calvoi* cannot be morphologically differentiated from *Pr. avelasi* (Apesteguía and Novas, 2003) or *Pr. minimus* (except for the small size of the latter). Moreover, the material originally referred to *K. calvoi* does not possess any autapomorphic characters and this taxon is regarded as a nomen dubium.

#### PHYLOGENETIC RELATIONSHIPS

To evaluate the monophyly of *Priosphenodon* and its relationships with other sphenodontians, the new species was incorporated into the data matrix of Apesteguía et al. (2012), which includes 27 terminal taxa and 72 characters. Character 66 of Apesteguía et al. (2012), which is related to skull size, was not included in the analysis but was optimized as a continuous character to assess size evolution among sphenodontians (see below), and a further state wad added to character 58 (teeth with large anterolateral flanges that exceed the precedent tooth; see Supplemental Data).

Character scores for *Pr. minimus* and skull sizes used are listed in Appendix 1.

The analysis was conducted using TNT version 1.1 (Goloboff et al., 2008a, 2008b). A heuristic search was performed with 1000 replicates of Wagner trees (with random addition sequences) followed by tree bisection and reconnection (TBR) branch swapping (saving 10 trees per replicate). This analysis found 72 most parsimonious trees (MPTs) of 185 steps each (consistency index = 0.54; retention index = 0.72). The optimal score was obtained in 40% of the replicates.

As also carried out by Apesteguía et al. (2012), a reduced strict consensus (Wilkinson, 1994) was obtained through the posteriori deletion of the unstable taxon *Pamizinsaurus*. The reduced strict consensus tree (Fig. 4) does not greatly differ from that obtained by Apesteguía et al. (2012), with the exception of inclusion of *Pr. minimus* and an unresolved relationship between *Sapheosaurus* and *Kallimodon* (node I of Apesteguía et al., 2012). *Priosphenodon* was obtained as a monophyletic group (Fig. 7), but with low Bremer support. Nevertheless, this low support is due to uncertainly in the position of *Toxolophosaurus* whose relationships vary in those trees one step longer than the MPTs.



FIGURE 7. Reduced strict consensus tree obtained after the a posteriori elimination of *Pamizinsaurus*. Numbers above the nodes indicate Bremer support values. For the reconstruction of the size evolution in Sphenodontia, the length of the skull was used as a proxy (measured between the premaxilla and the quadrate; see Supplemental Data).

#### DISCUSSION

#### The Adult Stage of Priosphenodon minimus, sp. nov.

Although frequently overlooked, rhynchocephalians change substantially during ontogeny (Rieppel, 1992; Jones, 2008), especially in the relative size of the interpterygoid and infratemporal fenestrae (Robinson, 1976), quadrate size, the length of the pterygoid central region (Apesteguía 2008), as well as in the dental series, which is composed of hatchling, additional, and successional teeth (e.g., Howes and Swinnerton, 1901; Robinson, 1976; Whiteside, 1986; Reynoso, 1997, 2003).

Juvenile specimens of *Pr. minimus* are currently unknown. The adult status of the holotype is evident from the small size of its interpterygoid fenestra. With the exception of the paedomorphic 'sphenodontines', which retain a large fenestra in adults (Apesteguía, 2008), other rhynchocephalians experience a substantial reduction of the fenestra during development life, as occurs in *Pr. avelasi*. In *Pr. minimus* (Fig. 6D, E) and adults of *Pr. avelasi*, the width of the fenestra is less than that of a single palatine (Fig. 6A). Conversely, in a juvenile specimen of *Pr. avelasi* (which is the same size as the holotype of *Pr. minimus*; Fig. 6C), the fenestra width is equal to the total width of both pterygoid anterior processes. This is a useful feature for determining relative ages in lineages other than 'sphenodontines' and supports the adult status of the *Pr. minimus* holotype.

Additionally, the strong tooth wear observed in all specimens of *Pr. minimus* (which is much more severe than in any other species of *Priosphenodon*) suggests that they are all at least subadults. The main ontogenetically variable feature in rhychocephalians is the shape of the supratemporal fenestra, which changes, as the parietal crest develops, from oval- to 'D'-shaped in adult specimens of eupropalinal rhynchocephalians. By contrast, *Homoeosaurus* possesses a euriparietal condition, with the parietals forming a wide table between the supratemporal fenestrae that is devoid of a sagittal crest. Another common allometric change is evident in the postorbitals, which expand anteroposteriorly during growth, as in *Sphenodon* (Jones, 2008:fig. 8). In addition, both the interpterygoid fenestra and the pterygoid central region narrow during growth. The retention of a wide interpterygoid region in adults of *S. punctatus* is considered to be a paedomorphic trait (Apesteguía, 2008).

The prefrontal of juvenile specimens of *Priosphenodon* (Fig. 5E) bears a tapering posterodorsal process that extends posteriorly along the limit with the nasal and frontal. Conversely, in adult specimens of *Pr. avelasi* (Fig. 5D) and *Pr. minimus* (Fig. 5F), the nasal overlaps the prefrontal and forms a hook-like structure in dorsal view that embraces the nasal posterior end.

#### **The Eilenodontine Radiation**

Based on its sister group, eilenodontines evolved from a group of opisthodontians during the Early Jurassic (Apesteguía et al., 2012:fig. 6). Therefore, the group should have been able to disperse widely before the breakup of Neopangaea, allowing them to reach areas of North and South America. The group rapidly acquired large size and adopted an herbivorous diet (Throckmorton et al., 1981). The earliest *Eilenodon* has a skull length of around 109 mm; that of *Toxolophosaurus* is ca. 60 mm; and that of *Pr. avelasi* is ca. 150 mm. Although the small Triassic sphenodontid *Pelecymala* (Fraser, 1986) was also probably herbivorous, its small size (skull length estimated at 30 mm) suggests a different digestive strategy from that of eilenodontines, as well as the Late Triassic *Sphenotitan leyesi* (Martínez et al., 2012).

Whereas small body size in temperate to cold climates allowed lepidosaurs to exploit an herbivorous lifestyle (Espinoza et al., 2004), herbivory in eilenodontines was related to gigantism and the warm, dry climate in which they lived (Apesteguía, 2008). Both species of *Priosphenodon* lived in relatively arid environments. The Candeleros Formation was deposited in the interdune deposits of the endorheic system of the Picún Leufu Basin (Garrido, 2010), and the La Paloma Member, of the Cerro Barcino Formation, represents dunes and pyroclastic deposits (Rauhut et al., 2013).

To evaluate trends of size evolution within Rhynchocephalia, skull length (measured between the premaxilla and the quadrate) was optimized as a continuous character in TNT (Goloboff et al., 2008a, 2008b). Increments in the size can be observed, with opisthodontians representing the largest taxa known (Fig. 7). The inclusion of Pr. minimus in this group indicates at least one event of dwarfism in Opisthodontia (Fig. 7). The presence of such a dwarf, as part of a lineage of giants, in which size was important for the development of fermentative digestion, is not easy to explain. The highly specialized dentitions of eilenodontines, with wide and low, flanged crowns positioned in a tall and robust dentary, indicate obligate herbivory (Throckmorton et al., 1981). These dental features promoted enhanced eupropalinal processing of food, which is characteristic of this lineage. Small body size would presumably have been disadvantageous for a specialized herbivore living in these environments (Espinoza et al., 2004).

Espinoza et al. (2004) studied the ecophysiological rules that control the evolution of herbivory in iguanids and other squamates. They found that the acquisition of herbivory is frequent in lineages of large size that live in hot, dry areas like islands and deserts, where insects are not abundant. Body size is one of the main features promoting herbivory, and an herbivorous lizard generally has a minimum snout-vent length of 150 mm (Pough, 1973) and is >100 g in weight (Espinoza et al., 2004). An interesting exception to this general rule is the Liolaemidae, a family of small lizards from temperate-cold climates, which are all <100 g in weight. Under these climatic conditions, they are subject to ecophysiological constraints, and a high body temperature of about 35-40°C is necessary for the efficient processing and fermentation of vegetal matter (Cooper and Vitt, 2002; Espinoza et al., 2004). However, Espinoza et al. (2004) proposed that these herbivorous lizards could live in cold climates due to their small size, because their low thermal inertia would permit rapid warming when conditions were favorable, a strategy that would be untenable for larger lizard taxa. Although the climatic conditions in which Pr. minimus lived are not entirely known, they certainly lived several hundred kilometers south of any other known eilenodontine, so it is possible that the climate that they experience was cooler than that enjoyed by their more northerly relatives.

As noted above, *Pr. minimus* can be easily differentiated from adult and juvenile specimens of *Pr. avelasi*, and regarded as a separate species. Nevertheless, the available specimens of *Pr. minimus* appear to be subadults. Some characters shared by *Pr. minimus* and juveniles of *Pr. avelasi* are here regarded as a product of the heterochronic evolution that drove *Pr. minimus* to a dwarf condition. Heterochronic processes are usually claimed to be responsible for dwarfing events (e.g., Gould, 1977; Alberch et al., 1979; Benton et al., 2010). Such processes have been postulated to occur even in derived forms within clades of large terrestrial animals such as sauropod dinosaurs (Jianu and Weishampel, 1999; Salgado, 1999; Benton et al., 2010; Stein et al., 2010) and elephants (Raia et al., 2003).

The small size of Pr. minimus plus the severe wear of their teeth are in accordance with the highly volcanic environment in which they lived (Cortiñas, 1996). Although eilenodontines were probably ectothermic, their anatomical peculiarities suggest a high degree of specialization for the processing of plant material. The shape and size of the flat skull table, a sharp beak that is vertically inclined or slightly procumbent in its anterior part improving both the excavation (Agrawal, 1967) and cutting of vegetation, as well as the well-developed adductor musculature, tall and robust jaw, wide teeth with low crowns, and propalinal movement are features that make Priosphenodon skulls superficially similar to those of some fossorial rodents (e.g., Marmota himalayana, Rhizomys cinereus) or allodontid multituberculates (e.g., Ctenacodon) (Simpson, 1926b; Agrawal, 1967). Despite the problems associated with comparing mammals and ectothermic reptiles, they may have had some overlap in their adaptive zones. Furthermore, eilenodontines appear to have been abundant gregarious reptiles that lived in burrows that were excavated by their powerful beaks and hoofed claws (Apesteguía, 2008).

#### CONCLUSIONS

The new species of *Priosphenodon* provides a greater understanding of the eilenodontine radiation. However, because Pr. minimus appears to be a dwarf species, it also demonstrates a greater diversity of body sizes and ecotypes amongst eilenodontines (Apesteguía, 2002). It adds a further example to the surprising diversity of Cretaceous Patagonian sphenodontians as a whole, which includes highly peramorphic eilenodontines and paedomorphic 'sphenodontines' living in the seasonally cold-temperate peri-Antarctic regions of Cretaceous Patagonia (Apesteguía and Jones, 2011), as well as probable aquatic taxa related to opisthodontians (Apesteguía et al., 2012). Specialized herbivorous reptiles have strict ecological requirements that open possibilities for their use as paleoenvironmental indicators. Being the southernmost eilenodontine, Pr. minimus provides some climatological evidence for this latitude. Because eilenodontines were present in both the early Late Cretaceous of the Neuquén Basin and the late Early Cretaceous Cañadón

Asfalto-Somuncura Basin, in strata that are considered as deposited under arid conditions, eilenodontines demonstrate their potential utility as bioenvironmental markers for different basins in southern South America.

#### ACKNOWLEDGMENTS

We would like to thank those who participated in the field trip that found the holotype, especially L. Canesa and M. Caffa. P. Puerta and O. Rauhut found the referred material and gave it to us for its publication. In addition, we particularly thank L. Reiner and P. Puerta for their preparation of the material, E. Ruigómez for access to material, and J. A. González for illustrations. D. Pol and M. Jones are thanked for comments and suggestions. The editors, J. Müller and P. Barrett, provided helpful comments and suggestions that greatly improved the manuscript. This work was funded by grants from the Jurassic Foundation PICT 0378 (to J. L. C.) 'Dinosaurs and other fossil remains from the Early Cretaceous of central Patagonia' (to D. Pol and G. Cladera), and 'Dinosaurs and other fossil remains from the Early Cretaceous of central Patagonia' (to J. Carballido and D. Pol) and by the Fundación Egidio Feruglio.

#### LITERATURE CITED

- Agrawal, V. C. 1967. Skull adaptations in fossorial rodents. Mammalia 31:300–312.
- Albino, A. 2007. Lepidosauromorpha; pp. 87–115 in Z. Gasparini, L. Salgado, and R. A. Coria (eds.), Patagonian Mesozoic Reptiles. Indiana University Press, Bloomington, Indiana.
- Alberch, P., S. J. Gould, G. F. Oster, and D. B. Walke. 1979. Size and shape in ontogeny and phylogeny. Paleobiology 5:296–317.
- Anselmi, G., M. T. Gamba, and J. L. Panza. 2004. Hoja Geológica 4369–IV, Los Altares, Provincia del Chubut. Instituto de Geología y Recursos Minerales, Servicio Geológico Minero Argentino Boletin 313, 98 pp.
- Apesteguía, S. 2002. Eilenodontinos: esfenodontes gigantes del Jurásico y Cretácico de ambas Américas. In Actas VIII Congreso Argentino de Paleontología y Bioestratigrafía, Corrientes, Argentina, Oct 7–10th 2002, Vol. 1. p. 22. Universidad Nacional del Nordeste and Centro de Ecología Aplicada del Litoral (Eds.). Available in The Polyglot Paleontologist: http://www.paleoglot. org/files/Apest.02a.pdf.
- Apesteguía, S. 2008. Esfenodontes (Reptilia, Lepidosauria) del Cretácico Superior de Patagonia: anatomía y filogenia. Ph.D. dissertation, Universidad Nacional de La Plata, La Plata, Argentina, 535 pp. Available at http://sedici.unlp.edu.ar/handle/10915/4405.
- Apesteguía, S., and J. L. Carballido. 2008. A new sphenodontid (Lepidosauria) from the Cretaceous of Chubut Province and the distribution of the eilenodontines. III Congreso Latinoamericano de Paleontología de Vertebrados, Neuquén, 22–25 September 2008. Actas 1:17.
- Apesteguía, S., and M. E. H. Jones. 2011. A Late Cretaceous "tuatara" (Lepidosauria: Sphenodontinae) from South America. Cretaceous Research 34:154–160.
- Apesteguía, S., and F. E. Novas. 2003. Large Cretaceous sphenodontian from Patagonia provides insight into lepidosaur evolution in Gondwana. Nature 425:609–612.
- Apesteguía, S., R. O. Gómez, and G. W. Rougier. 2012. A basal sphenodontian (Lepidosauria) from the Jurassic of Patagonia: new insights on the phylogeny and biogeography of Gondwanan rhynchocephalians. Zoological Journal of the Linnean Society 166:342–360.
- Apesteguía, S., S. De Valais, J. A. González, P. A. Gallina, and F. L. Agnolín. 2001. The tetrapod fauna of 'La Buitrera,' new locality from the basal Late Cretaceous of North Patagonia, Argentina. Journal of Vertebrate Paleontology 21(3, Supplement):29A.
- Benton, M. J. 1985. Classification and phylogeny of the diapsid reptiles. Zoological Journal of the Linnean Society 84:97–164.
- Benton, M. J., Z. Csiki, D. Grigorescu, R. Redelstorff, P. M. Sander, K. Stein, and D. B. Weishampel. 2010. Dinosaurs and the island rule: the dwarfed dinosaurs from Hateg Island. Palaeogeography, Palaeoclimatology, Palaeoecology 293:438–454.
- Bonaparte, J. F., and H.-D. Sues. 2006. A new species of *Clevosaurus* (Lepidosauria: Rhynchocephalia) from the Upper Triassic of Rio Grande do Sul, Brazil. Palaeontology 49:917–923.

- Carballido, J. L., D. Pol, I. Cerda, and L. Salgado. 2011. The osteology of *Chubutisaurus insignis* del Corro, 1975 (Dinosauria: Neosauropoda) from the 'middle' Cretaceous of Central Patagonia, Argentina. Journal of Vertebrate Paleontology 31:93–110.
- Carroll, R. L. 1985a. A pleurosaur from the Lower Jurassic and the taxonomic position of the Sphenodontida. Paleontographica, Abteilung A 189:1–28.
- Carroll, R. L. 1985b. Evolutionary constraints in aquatic diapsid reptiles. Special Papers in Paleontology 33:145–155.
- Carroll, R. L., and R. Wild. 1994. Marine members of the Sphenodontia; pp. 70–83 in N. C. Fraser and H.-D. Sues (eds.), In the Shadow of the Dinosaurs: Early Mesozoic Tetrapods. Cambridge University Press, Cambridge (U.K.) and New York.
- Cocude-Michel, M. 1963. Les rhynchocephales et les sauriens de calcaires lithographiques (Jurassique supérieur) d'Europe occidentale. Nouvelles Archives du Muséum d'Histoire Naturelle de Lyon 7:1– 187.
- Codignotto, J. F., J. Nullo, J. Panza, and C. Proserpio. 1978. Estratigrafía del Grupo Chubut entre Paso de Indios y Las Plumas, provincia del Chubut, Argentina. VII Congreso Geológico Argentino. Actas 1, 471–480.
- Cooper, W. E., and L. J. Vitt. 2002. Distribution, extent, and evolution of plant consumption by lizards. Journal of Zoology 257:353–366.
- Cortiñas, J. S. 1996. La cuenca de Somuncura–Cañadón Asfalto: sus límites, ciclo evolutivo del relleno sedimentario y posibilidades exploratorias. XIII Congreso Geológico Argentino y III Congreso de Exploración de Hidrocarburos, Buenos Aires, 13–18 October 1996. Actas 1:147–163.
- Espinoza, R. E., J. J. Wiens, and C. R. Tracy. 2004. Recurrent evolution of herbivory in small, cold-climate lizards: breaking the ecophysiological rules of reptilian herbivory. Proceedings of the National Academy of Sciences of the United States of America 101:16819–16824.
- Estes, R., K. de Queiroz, and J. Gauthier. 1988. Phylogenetic relationships within Squamata; pp. 119–281 in R. Estes and G. Pregill (eds.), Phylogenetic Relationships of the Lizard Families: Essays Commemorating Charles L. Camp. Stanford University Press, Stanford, California.
- Evans, S. E. 1980. The skull of a new eosuchian reptile from the Lower Jurassic of South Wales. Zoological Journal of the Linnean Society 70:203–264.
- Evans, S. E. 1992. A sphenodontian (Reptilia: Lepidosauria) from the Middle Jurassic of England. Neues Jahrbuch für Mineralogie, Geologie und Palaeontologie Mittelhungen 8:449–457.
  Evans, S. E., G. V. R. Prasad, and B. K. Manhas. 2001. Rhyncho-
- Evans, S. E., G. V. R. Prasad, and B. K. Manhas. 2001. Rhynchocephalians (Diapsida: Lepidosauria) from the Jurassic Kota Formation of India. Journal of the Linnean Society 133:309–334.
- Figari, E. G., and S. F. Courtade. 1993. Evolución tectosedimentaria de la Cuenca de Cañadón Asfalto, Chubut. XII Congreso Geológico Argentino y II Congreso de Exploración de Hidrocarburos, Mendoza, 10–15 October 1993. Actas 1:66–77.
- Foster, J. R. 2003. New specimens of *Eilenodon* (Reptilia: Sphenodontia) from the Morrison Formation (Upper Jurassic) of Colorado and Utah. Brigham Young University Geology Studies 47:17–22.
- Fraser, N. C. 1982. A new rhynchocephalian from the British Upper Trias. Palaeontology 25:709–725.
- Fraser, N. C. 1986. New Triassic sphenodontids from south-west England and a review of their classification. Palaeontology 29:165–186.
- Fraser, N. C. 1988. The osteology and relationships of *Clevosaurus* (Reptilia: Sphenodontida). Philosophical Transactions of the Royal Society of London, Series B 321:125–178.
- Garrido, A. C. 2010. Estratigrafía del Grupo Neuquén, Cretácico Superior de la Cuenca Neuquina (Argentina): nueva propuesta de ordenamiento litoestratigráfico. Revista del Museo Argentino de Ciencias Naturales 12:121–177.
- Gauthier, J. 1984. A cladistic analysis of the higher categories of the Diapsida. Ph.D. dissertation, University of California, Berkeley, California, 564 pp.
- Gauthier, J., R. Estes, and K. De Queiroz. 1988. A phylogenetic analysis of the Lepidosauromorpha; pp. 15–98 in R. Estes and G. Pregill (eds.), Phylogenetic Relationships of the Lizard Families: Essays Commemorating Charles M. Camp. Stanford University Press, Stanford, California.
- Geuna, S. E., R. Somoza, H. Vizán, E. G. Figari, and C. A. Rinaldi. 2000. Paleomagnetism of Jurassic and Cretaceous rocks in central Patago-

nia: a key to constrain the timing of rotations during the breakup of southwestern Gondwana. Earth and Planetary Science Letters 181:145–160.

- Goloboff, P. A., S. Farris, and K. Nixon. 2008a. TNT (Tree Analysis Using New Technology) (Will Henning Society edition). Program and documentation available at www.Zmuc.Dk/Public/Phylogeny/Tnt. Accessed October 22, 2012.
- Goloboff, P. A., S. Farris, and K. Nixon. 2008b. TNT, a free program for phylogenetic analysis. Cladistics 24:774–786.
- Gould, S. J. 1977. Ontogeny and Phylogeny. Belknap Press, Cambridge, Massachusetts. 501 pp.
- Gow, C. E. 1975. The morphology and relationships of *Youngina capensis* Broom and *Prolacerta broomi* Parrington. Palaeontologia africana 18:89–131.
- Günther, A. 1867. Contribution to the anatomy of *Hatteria (Rhyncho-cephalus*, Owen). Philosophical Transactions of the Royal Society of London 157:595–629.
- Howes, G. B., and H. H. Swinnerton. 1901. On the development of the skeleton of the tuatara, *Sphenodon punctatus*; with remarks on the egg, hatching, and on the hatched young. Transactions of the Zoological Society of London 16:1–74.
- Jianu, Č. M., and Ď. B. Weishampel. 1999. The smallest of the largest: a new look at possible dwarfing in sauropod dinosaurs. Geologie en Mijnbouw 78:335–343.
- Jones, M. E. H. 2006. The Early Jurassic *Clevosaurus* from China (Diapsida: Lepidosauria). New Mexico Museum of Natural History and Science Bulletin 37:548–562.
- Jones, M. E. H. 2008. Skull shape and feeding strategy in *Sphenodon* and other Rhynchocephalia (Diapsida: Lepidosauria). Journal of Morphology 269:945–966.
- Jones, M. E. H., N. Curtis, M. J. Fagan, P. O'Higgins, and S. E. Evans. 2011. Hard tissue anatomy of the cranial joints in *Sphenodon* (Rhynchocephalia): sutures, kinesis, and skull mechanics. Palaeontologia Electronica 14(2):17A. http://palaeo-electronica. org/2011\_2/251/index.html.
- Jones, M. E. H., P. O'Higgins, M. J. Fagan, S. E. Evans, and N. Curtis. 2012. Shearing mechanics and the influence of a flexible symphysis during oral food processing in *Sphenodon* (Lepidosauria: Rhynchocephalia). Anatomical Record 295:1075–1091.
- Kieser, J. A., T. Tkatchenkoa, C. Dean, M. E. H. Jones, W. Duncan, and N. J. Nelson. 2009. Microstructure of dental hard tissues and bone in the tuatara dentary, *Sphenodon punctatus* (Diapsida: Lepidosauria: Rhynchocephalia); pp. 80–85 in T. Koppe, G. Meyer, and K. W. Alt (eds.), Comparative Dental Morphology. S. Karger Publishing, London.
- Leanza, H. A., S. Apesteguía, F. E. Novas, and M. S. de la Fuente. 2004. Cretaceous terrestrial beds from the Neuquén Basin (Argentina) and their tetrapod assemblages. Cretaceous Research 25:1–96.
- Llorens, M., and N. Marveggio. 2009. Palinoflora de la Formación Los Adobes (Cretácico) y su implicancia en la edad del Grupo Chubut. XVI Simposio Argentino de Paleobotánica y Palinología, Mar del Plata, Argentina. 6–9 December 2009. Actas 1:49.
- Maisch, M. W., and A. T. Matzke. 2006. The braincase of *Phanto-mosaurus neubigi* (Sander, 1997), an unusual ichthyosaur from the Middle Triassic of Germany. Journal of Vertebrate Paleontology 26:598–607.
- Martinelli, A. G., and A. M. Forasiepi. 2004. Late Cretaceous vertebrates from Bajo de Santa Rosa (Allen Formation), Río Negro Province, Argentina, with the description of a new sauropod dinosaur (Titanosauridae). Revista del Museo Argentino de Ciencias Naturales, n. s. 6:257–305.
- Martínez, R. N., C. Apaldetti, C. E. Colombi, A. Praderio, E. Fernández, P. Santi Malnis, G. A. Correa, D. Abelin, and O. Alcober. 2013. A new sphenodontian (Lepidosauria: Rhynchocephalia) from the Late Triassic of Argentina and the early origin of the herbivore opisthodontians. Proc. R. Soc. B 2013 280, 20132057.
- Musacchio, E. A. 1972. Charophytas del Cretácico inferior en sedimentitas Chubutenses al este de la Herrería, Chubut. Ameghiniana 9:354–356.
- Musacchio, E. A., and G. Chebli. 1975. Ostrácodos no marinos y carófitos del Cretácico Inferior en las Provincias del Chubut y Neuquén en Argentina. Revista de la Asociación Paleontológica Argentina 12:70–96.
- Novas, F. E., S. Apesteguía, D. Pol, S. de Valais, A. M. Forasiepi, H. A. Leanza, J. A. Gonzáles, and A. Haro. 1999. Primer registro de

Lepidosaurios Esfenodontes para el Cretácico Superior. Ameghiniana 36:16R.

- O'Donoghue, C. H. 1920. The blood vascular system of the tuatara, *Sphenodon punctatus*. Philosophical Transactions of the Royal Society of London, Series B 210:175–252.
- Oelrich, T. M. 1956. The anatomy of the head of *Ctenosaura pectinata* (Iguanidae). Miscellaneous Publications of the Museum of Zoology, University of Michigan 94:3–122.
- Pough, F. H. 1973. Lizard energetics and diet. Ecology 54:837-844.
- Raia, P., C. Barbera, and M. Conte. 2003. The fast life of a dwarfed giant. Evolutionary Ecology 17:293–312.
- Rasmussen, T. E., and G. Callison. 1981. A new herbivorous sphenodontid (Rhynchocephalia: Reptilia) from the Jurassic of Colorado. Journal of Paleontology 55:1109–1116.
- Rauhut, O. W. M., G. Cladera, P. Vickers-Rich, and T. H. Rich. 2003. Dinosaur remains from the Lower Cretaceous of the Chubut Group, Argentina. Cretaceous Research 24:487–497.
- Reisz, R. R. 1981. A diapsid reptile from the Pennsylvanian of Kansas. University of Kansas University of Kansas, Publications of the Museum of Natural History 7:1–74.
- Reynoso, V. H. 1996. A Middle Jurassic Sphenodon-like sphenodontian (Diapsida: Lepidosauria) from Huizachal Canyon, Tamaulipas, México. Journal of Vertebrate Paleontology 17:52–59.
- Reynoso, V. H. 1997. A "beaded" sphenodontian (Diapsida: Lepidosauria) from the Early Cretaceous of central Mexico. Journal of Vertebrate Paleontology 17:52–59.
- Reynoso, V. H. 2003. Growth patterns and ontogenetic variation of the teeth and jaws of the Middle Jurassic sphenodontian *Cynosphenodon huizachalensis* (Reptilia: Rhynchocephalia). Canadian Journal of Earth Sciences 40:609–619.
- Reynoso, V. H. 2005. Possible evidence of a venom apparatus in a Middle Jurassic sphenodontian from the Huizachal red beds of Tamaulipas, México. Journal of Vertebrate Paleontology 25:646–654.
- Rieppel, O. 1992. The skull in a hatchling of *Sphenodon punctatus*. Journal of Herpetology 26:80–84.
- Robinson, P. L. 1976. How Sphenodon and Uromastix grow their teeth and use them; pp. 43–64 in A. d'A. Bellairs and C. B. Cox (eds.), Morphology and Biology of Reptiles. Academic Press, London.
- Romer, A. S. 1956. Osteology of the Reptiles. University of Chicago Press, Chicago, Illinois, 772 pp.
- Säilä, L. K. 2005. A new species of the sphenodontian reptile *Clevosaurus* from the Lower Jurassic of South Wales. Palaeontology 48:817–831.
- Salgado, L. 1999. The evolution of the Diplodocimorpha (Dinosauria; Sauropoda): a developmental model. Ameghiniana 36:203–216
- Simón, M. E., and A. W. A. Kellner. 2002. The first eilenodontin sphenodontid (Lepidosauria, Rhynchocephalia) from South America. XVIII Congresso Brasileiro de Paleontologia, Brasília, Brazil, 13–18 June 2002. Actas 1:280–281.
- Simón, M. E., and A. W. A. Kellner. 2003. New sphenodontid (Lepidosauria, Rhynchocephalia, Eilenodontinae) from the Candeleros Formation, Cenomanian of Patagonia, Argentina. Boletim Museu Nacional, Nova Série, Geologia, Rio de Janeiro 68:1–12.
- Simpson, G. G. 1926a. American terrestrial Rhynchocephalia. American Journal of Science 5:12–16.
- Simpson, G. G. 1926b. Mesozoic Mammalia. IV. The multituberculates as living animals. American Journal of Science 63:228–250.
- Stein, K., Z. Csiki, K. Curry-Rogers, D. B. Weishampel, R. Redelstorff, J. Carballido, and P. M. Sander. 2010. Small body size and extreme cortical bone remodeling indicate phyletic dwarfism in *Magyarosaurus dacus* (Sauropoda: Titanosauria). Proceedings of the National Academy of Sciences of the United States of America 107:9258–9263.
- Sues, H.-D., J. M. Clark, and F. A. Jenkins Jr. 1994. A review of the Early Jurassic tetrapods from the Glen Canyon Group of the American Southwest; pp. 284–294 in N. C. Fraser and H.-D. Sues (eds.), In the Shadow of the Dinosaurs: Early Mesozoic Tetrapods. Cambridge University Press, Cambridge (U.K.) and New York.

- Throckmorton, G. S., J. A. Hopson, and P. Parks. 1981. A redescription of *Toxolophosaurus cloudi* Olson, a Lower Cretaceous herbivorous sphenodontid reptile. Journal of Paleontology 55:586– 597.
- Whiteside, D. I. 1986. The head skeleton of the Rhaetian sphenodontid Diphydontosaurus avonis gen. et sp. nov. and the modernizing of a living fossil. Philosophical Transactions of the Royal Society of London, Series B 312:379–430.
- Wilkinson, M. 1994. Common cladistic information and its consensus representation: reduced Adams and reduced cladistic consensus trees and profiles. Systematic Biology 43:343–368.
- Wu, X.-C. 1994. Late Triassic-Early Jurassic sphenodontians (*Clevosaurus*) from China and the phylogeny of the Sphenodontida; pp. 38–69 in N. C. Fraser and H.-D. Sues (eds.), In the Shadow of the Dinosaurs: Early Mesozoic Tetrapods. Cambridge University Press, Cambridge (U.K.) and New York.
- Wu, X.-C. 2003. Functional morphology of the temporal region in the Rhynchocephalia. Canadian Journal of Earth Sciences 40:589–607.

Submitted March 24, 2012; revisions received April 17, 2013; accepted May 4, 2013.

Handling editor: Johannes Müller.

APPENDIX 1. Character scores used for *Priosphenodon minimus* as incorporated into the data matrix of Apesteguía et al. (2012), with the exclusion of the character 66 (related to skull size).

#### Priosphenodon minimus

#### 11???1111?1??0?1????1220????01122??11?02?213012??212103 121?????2????0

As proxy for species size, we used the length between the premaxilla and the quadrate. The measurements used are provided below (in mm), and were mapped on the phylogeny as a continuous character. An \* indicates estimated values for incomplete skulls.

Youngina	60
Pristidactylus	
Gephyrosaurus	30
Diphydontosaurus	15
Planocephalosaurus	20
Rebbanasaurus	15*
Godavarisaurus	15*
Homoeosaurus	24
Palaeopleurosaurus	57
Brachyrhinodon	21–24
Clev. hudsoni	39
Kallimodon	30-38
Sapheosaurus	41
Pamizinsaurus	16
Zapatadon	11.3
Sphenodon	58
Cynosphenodon	29
Ópisthias	41.5*
Toxolophosaurus	60
Eilenodon	109
Ankylosphenodon	82.5
Sphenocondor	28
Sphenovipera	20.5
Theretairus	20*
Kawasphenodon	$110^{*}$
Priosphenodon avelasi	125
Priosphenodon minimus	23*