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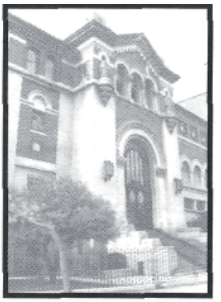

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HISTORIA EVOLUTIVA Y PALEOBIOGEOGRÁFICA DE LOS VERTEBRADOS DE AMÉRICA DEL SUR

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Rhynchocephalians: The least known South American Lepidosaurs

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Abstract: The history of Rhynchocephalia in South America is rich and complex. Although the Triassic forms were related to the global lineages, including clevosaurs and derived herbivorous forms, along Jurassic new lineages succeeded. These forms are closely related to other endemic Gondwanan species, all positioned southwards from the Central Gondwanan Desert. During the Cretaceous the presence of terrestrial and littoral rhynchocephalians, provided of a very derived dentition and large size, and belonging to at least three different lineages, shows that the clade diversity was still healthy. After K/Pg boundary at least two lineages survived in South America probably until the global cooling event at the Eocene–Oligocene boundary.

Key words: Rhynchocephalia, Gondwana, South America.

Resumen: Rhyncocéfalos: Los lepidosaurios sudamericanos menos conocidos. La historia de Rhynchocephalia en Sudamérica es rica y compleja. A pesar de que las formas Triásicas se encontraban relacionadas a linajes de distribución global, incluyendo clevosaurios y formas herbívoras derivadas; durante el Jurásico nuevos lonajes tienen éxito. Estas formas se encuentran cercanamente relacionadas a especies gondwánicas, todas ubicadas al sur del Desierto Central Gondwánico. Durante el Cretácico la presencia de rincocéfalos terrestres y litorales provistos con una dentición muy derivada y gran tamaño, y provenientes al menos a tres linajes diferentes, muestra que la diversidad del clado era aún saludable. Luego del límite K/P al menos dos linajes sobrevivieron en Sudamérica probablemente hasta el evento de enfriamiento global ocurrido en el límite Eoceno–Oligoceno.

Palabras clave: Rhynchocephalia, Gondwana, Sudamérica.

INTRODUCTION

Rhynchocephalians are today a single-genus clade restricted to some few islands around the New Zealand archipelago. However, during the Early Mesozoic, these lepidosaurs constituted frequent and successful Pangean elements in the terrestrial ecosystems. Originated around the Early Triassic, they originated at the same time that lizards, their sister taxa, and soon rhynchocephalians dispersed through all Pangea regions. By the Jurassic, they constituted a common group along the Jurassic of Laurasia and Gondwana, reaching a wide diversity of sizes, alimentation, as well as terrestrial and aquatic habitats.

By Early Cretaceous times, the lineage experienced a substantial decrease, mainly in the northern hemisphere, coincident in time with the Laurasian diversification of lizards. This made some researchers to propose that, in few words, rhynchocephalians became almost extinct by competence with lizards. The information we have today show that this was not necessarily true.

Actualy, the few lineages of Early Cretaceous rhynchocephalians experienced a remarkable diversification. Both pleurosaurs, sapheosaurs and basal opisthodontians developed aquatic specializations and, in some of them, also hypsodonty, ankylotecodonty and dental loss; whereas terrestrial forms developed dermal armors and an upgraded eupropaliny was developed in insectivorous and animalivorous "sphenodontines", the still poorly understood lineage that includes the extant *Sphenodon*. Other terrestrial forms, like homoeosaurines, developed long limbs

and a gigantic size, especially in the herbivorous eilenodontines, thus widening the dietary preferences of the group. Somehow, Laurasian rhynchocephalians aparently didn't reach Cretaceous times, except for eilenodontines and some marine forms that lived until the transition from Early to Late Cretaceous.

THE SOUTHERN HISTORY

After decades of scanty record, discoveries in the last two decades are depicting a new scenario for the history of South American rhynchocephalians. Some of these recent discoveries include forms from Triassic, Jurassic, Cretaceous and early Tertiary forms, demonstrating that the group survived the K/P event in South America. In this context, the extant composition of the South American lepidosaurian fauna is the result of a particularly complex history in which rhynchocephalians took a significant part. Along the Neogene, possibly after the demise of rhynchocephalians, lizards diversified and, together with snakes, outlined the extant austral lepidosaurian fauna.

The information about rhynchocephalians in the southern half of the world is patchier, but the findings in Faxinal de Soturno (Late Triassic, Rio Grande do Sul, Brazil), Balde de Leyes (Late Triassic, San Juan, Argentina), La Esquina (Late Triassic, La Rioja Province, Argentina), Pakisagudem (Early Jurassic, Andhra Pradesh, India), Cerro Cóndor (Middle Jurassic, Argentina), Annoual (Early Cretaceous, Morocco), La Buitrera (early Late Cretaceous, Argentina), Los Alamitos and Salitral de Santa Rosa (latest Cretaceous, Argentina), and Punta Peligro (Paleogene, Argentina), demonstrated that a very rich and highly informative history is yet to be told (Figure 1).

TRIASSIC: THE GLOBAL LINEAGES

After numerous findings of Triassic rhynchocephalians in North America, Europe (UK, Belgium, Germany), and China, southern fragmentary records arose in Madagascar (Flynn *et al.*, 1997, 1999), South Africa (Sues & Reisz, 1995), and Zimbabwe (Gow & Raath, 1977). Finally, the numerous findings about 1999 by José Bonaparte and Jorge Ferigolo teams in Rio Grande do Sul, Brazil, completed the expected Triassic global panorama.

Particularly, in South America, three Triassic territories trace the trails of rhynchocephalians in South America: the Caturrita Formation (Faxinal de Soturno, Rio Grande do Sul, Brazil), the Quebrada del Barro Formation (Marayes, San Juan Province, Argentina), and the Los Colorados Formation (La Esquina, La Rioja Province, Argentina).

Faxinal de Soturno

This locality provided abundant fossils deposited in a low-energy fluvial environment. As in other localities around the world, the presence of rhynchocephalians is associated to that of minute mammals or, in this case, brasilitherid cynodontians. Bonaparte and Sues (2004) correlated this assemblage with the Lower Coloradian faunal stage, even before the finding of Triassic rhynchocephalians in Argentina, and proposed an age correspondence to the early Norian of the European standard succession.

The only clade of rhynchocephalians found at the Caturrita Formation up to now are the clevosaurs, very probably a true clade extended all through Pangea. The global distribution of the Clevosauridae is particularly surprising for small terrestrial tetrapods, even for the times of Pangea, and paleoenvironmental maps are necessary to understand the ecological requirements of this clade.

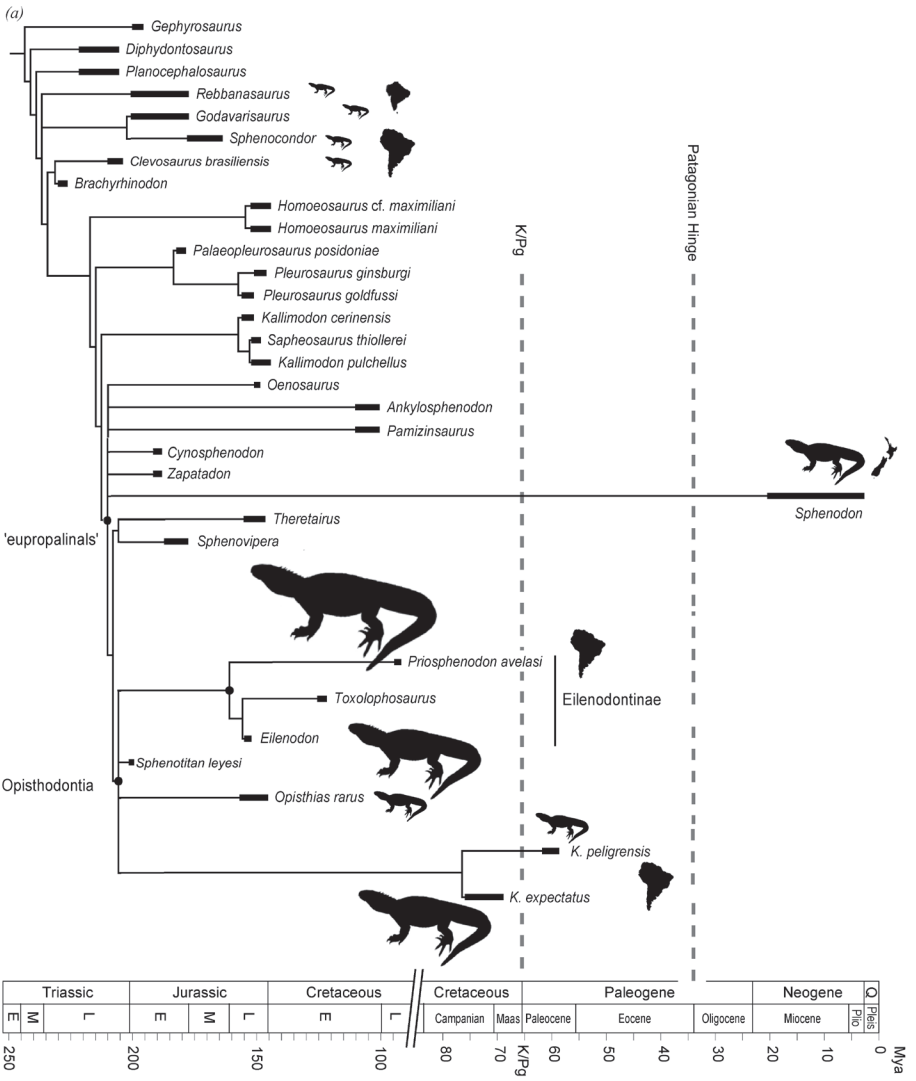

Figure 1. Time-tree of rhynchocephalians based on Apesteguía *et al.* (2014). Dotted lines indicate the K/Pg boundary, and the Patagonian Hinge, probable final extinction of rhynchocephalians in South America. Black silhouettes are only used for Gondwanan species and also indicate the relative size of the species.

Clevosaurids (from Clevosauridae Swinton, 1939) are small but stout rhynchocephalians with extraordinary strong beaks formed by the premaxilla, which extends two long nasal and maxillary processes framing the nostrils and excluding the maxilla from the margins of the external naris, especially by this long posterior process of the premaxilla (Fraser, 1988). They also share a distinct supratemporal and the suborbital fenestra enclosed only by the ectopterygoid and palatine, a derived trait when compared to *Gephyrosaurus* (Evans, 1980). Parietals form a rather straight posterior angle (Ferigolo, 2000).

Clevosaurus brasiliensis is integrated by several specimens. As in all clevosaurs

and also in derived opisthodontians (independently), the maxilla is fully excluded from the naris. It is noteworthy its high number of palatine and pterygoid teeth. Ferigolo considered as an important feature that its interpterygoid fenestra is positioned posteriorly respect to the series of pterygoid teeth. However, the shape and relations with the neighboring bones varies along ontogeny and the fenestra small and slightly closed posteriorly, plus the tooth wear, indicates that it is not a juvenile. The dentary shows a continuous wearing area, instead of precision bite marks, as also occurs in derived eupropalinal rhynchocephalians (i. e., *Opisthias*, *Sphenodon*).

Additional important features are the absence of the anterior or premaxillary process of the maxilla (making a straight, vertical, anterior border of the maxilla and, consequently, a quadrate head in lateral view), a moderate development of the parietal table, much less-developed than in *Kallimodon*, and devoid of a sagittal ridge as that of *Priosphenodon avelasi*. The parietal foramen, as in *Clevosaurus hudsoni*, is fully positioned between the parietals, and slightly anterior respect to the half of the parietal length, whereas that of *P. avelasi* is in the limit with frontals.

The jugal needs and extra consideration since the specimen MCN-PV 2852 shows a closed lower temporal fenestra by means of an extended ventral process of the jugal, right as occurs in the extant *Sphenodon*, an adaptation linked to manage structural forces to get the stronger bites. The relative size of the basicranium and the size relations between pterygoids and palate bones modify substantially along ontogeny. This supports that the holotypical specimen is a juvenile, as also supported by the very large orbit size. (Figure 2)

Balde de Leyes

In recent years, a fully different rhynchocephalian was collected from the Late Triassic rocks of the Quebrada del Barro Formation, San Juan Province, Argentina. *Sphenotitan leyesi* (Martínez *et al.*, 2013) is represented by the partial skull of an adult individual, and abundant referred material (PVSJ 887 to 895) which makes this species the most abundant tetrapod on the site (about 50% of the findings). Additionally, a new very well preserved skull discovered in 2014 (PVSJ 900) provides extra information.

Sphenotitan bears a 100 mm, lightly built, triangular, posteriorly-wide skull, when compared to clevosaurs. It differs from other rhynchocephalians on long supratemporal fenestrae occupying over one-third of the skull length, large quadrate-quadratojugal foramen; maxilla with a straight orbital border and long and transversely wide posterior maxillary teeth organized in a dense dental packing (flanges partially cover the bases of preceding teeth).

The palatine bears large teeth restricted to the lateral margin, and located parallel enough to the maxilla (eupropalinal), despite some degree of curvature in the palatine. An additional small cluster of 15 conical teeth resemble the single isolated tooth present in the palatine of Clevosaurus, as observed by Martínez et al. (2015), suggesting in the latter an animalivorous feeding behavior. The anterior palatal shelf of the pterygoids bear four prominent rows of dozens of small teeth;

The deep and powerful lower jaw, dorsally curved retroarticular process, and the teeth wider and extremely packed, as in Priosphenodon minimus, devoid of dental regionalization, supports its inclusion among opisthodontians, a group of globally distributed rhynchocephalians with numerous gigantic members and characterized by 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 prooral fashion.

Sphenotitan shows numerous paedomorphical traits (long central region of the pterygoids and large quadrate foramen). This suggest that the gigantism reached by this species was not along a peramorphic developmental history (as in *Priosphenodon*)

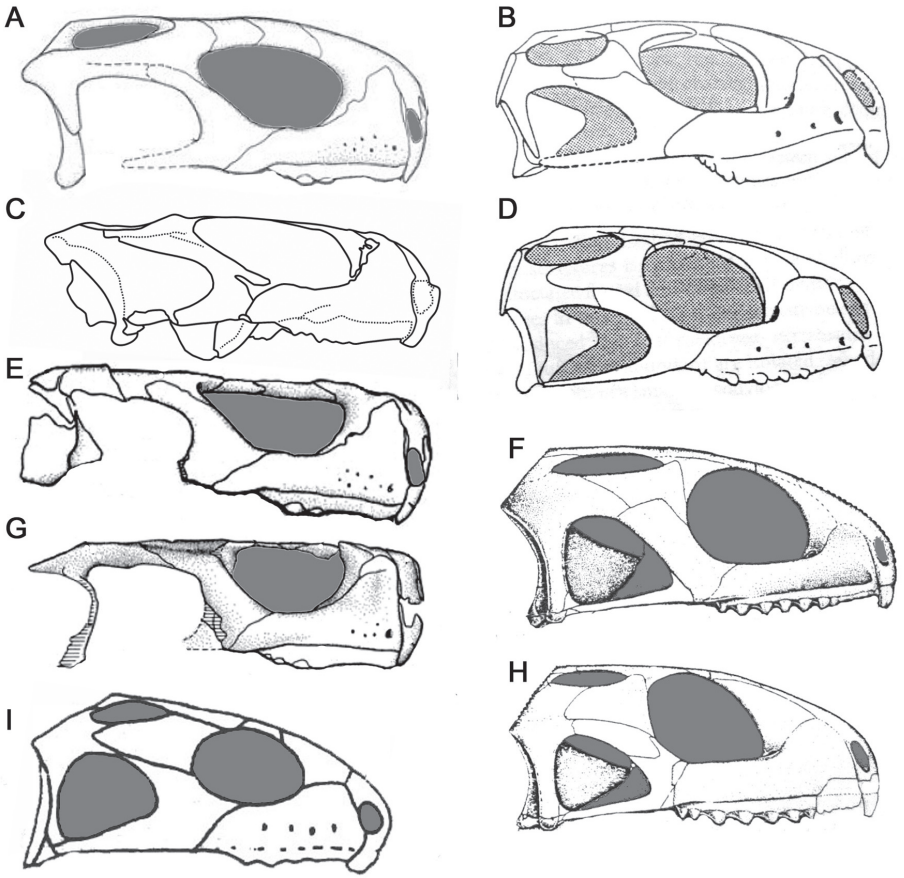

Figure 2. Comparison between clevosaurids. A, C, E, G, *Clevosaurus brasiliensis*; B, *C. bairdi*; D, *C. hudsoni*; F, *C. mcgilli*; H, *C. wangi*, and I, *Brachyrhinodon taylori*. Not to scale.

but as result of paedomorphic gigantism.With *Sphenotitan, "Clevosaurus" latidens* and *Pelecymala* (the last two very fragmentary) there are three known Triassic rhynchocephalians in the world well adapted to herbivory. Although its comparison with the small Triassic *Pelecymala* (Fraser, 1986) is necessary, such form very probably lacked the large fermentative spaces that size permitted in *Sphenotitan* and the eilenodontines. If all these taxa are related each other (as Martínez *et al.* 2013, 2015 propose), herbivory evolved or succeeded just once in the clade.

Jurassic: the increasing differences

Jurassic rhynchocephalians are also abundant in northern continents, whereas southern regions only include fragmentary remains from India (Evans *et al.*, 2001), Zimbabwe (Gow & Raath, 1977), and South Africa (Sues & Reisz, 1995). Middle and Late Jurassic rocks provided almost no records for Gondwanan landmasses. Apesteguía *et al.* (2012) reported a new form from Cerro Cóndor (Argentina) as Middle to Late Jurassic. Interestingly, this form, known as *Sphenocondor*, shows that after its initial Pangaean diversification, rhynchocephalians radiated in two distinct, geographically separated lineages (i.e., Euramerican and South-Gondwanan), thus diversifying and replacing the early forms (e.g., clevosaurs).

Cerro Cóndor

Sphenocondor (Apesteguía *et al.*, 2012) represents the first Jurassic record of the group from South America and the first of Middle to Late Jurassic age for Gondwana, thus contributing to fill an extensive stratigraphical and morphological gap in the fossil record of the group. At the time of its publication, *Sphenocondor* was composed only by a complete dentary, considered as a rhynchocephalian after the deep and wide Meckelian groove, long posterior process, well-developed coronoid process, and acrodont teeth showing dental regionalization including successional, alternate hatchling, and additional series. *Sphenocondor* differentiates from other rhynchocephalians by the following combination of features: slender lower jaw with a low and squared coronoid process; dentary posterior process as long as the base of the coronoid process; adductor fossa centered under the coronoid process; at least two strongly recurved and profusely striated successional teeth with no separation between them (differing from *Theretairus* and *Sphenovipera*) and with an anterior flange marked by a wide canal; alternate hatchling dentition organized in three groups of different size and showing a slight basal constriction; unadorned additional teeth; two dentine types organized in a radiating pattern.

Perhaps the most interesting aspect of *Sphenocondor* is result of the phylogenetic analysis. *Sphenocondor* resulted as relatively basal form within Rhynchocephalia, clustered with the Indian *Godavarisaurus* from the Jurassic Kota Formation. This result suggests the existence of an endemic Southern Gondwanan clade of rhynchocephalians, as also seen in other tetrapods like eusauropods (e.g., Bonaparte, 1986; Remes *et al.*, 2010) and chelid turtles (Leanza *et al.*, 2004). This not only reflects an increasing endemism in agreement with the breakup of Pangaea, but also palaeoclimatic constraints. The restriction of the Jurassic Euramerican and South Gondwanan forms to the Dry Subtropical (winter wet) climatic belt, right southwards from the extensive Central Gondwanan Desert (CGD), suggest the latter as an effective barrier for the dispersal of some groups of terrestrial organisms, isolating southern Gondwana from the equatorial region and Laurasia during Jurassic times. Actually, Early Jurassic Pangaean distributions were replaced by Mid to Late Jurassic partial endemisms.

Cretaceous: the uniqueness

The Cretaceous is the richest source of evidence for South American rhynchocephalians. *Priosphenodon* represented the first Late Cretaceous rhynchocephalian worldwide and contributed to fill an extensive stratigraphical and morphological gap in the fossil record of the group. However, 17 years after its finding and 13 after its publication, we know many more Late Cretaceous species and sites.

Only some few lineages remained present in northern continents during the Early Cretaceous. On one hand, the decrease coincides in time with the Laurasian diversification of lizards, but on the other hand the few lineages of Early Cretaceous rhynchocephalians experienced a remarkable diversification. Particularly, different lineages of aquatic rhynchocephalians resulted abundant and successful, like pleurosaurs, sapheosaurs, and aquatic opisthodontians. The specializations are numerous and in dentition include hypsodonty, ankylotecodonty, and dental loss.

For terrestrial forms, there are some few lineages, the homoeosaurines, which developed long limbs, and two belonging to the crown, showing an upgraded eupropaliny: the sphenodontines and the terrestrial opisthodontians, including eilenodontines. In the sphenodontines a dermal armor appeared and also gigantism in the peri-Antarctic forms, whereas gigantic size and herbivorism was preserved in eilenodontines. Laurasian rhynchocephalians apparently didn't survived after Early Cretaceous times.

Figure 3. Articulated skeleton of a juvenile specimen of *Priosphenodon avelasi*. The La Buitrera Paleontological Area, also known as "The Patagonian Gobi" is one of the better sites for the study of micro and mesovertebrates in South America.

Concerning the record in South America, is surprising that despite the intense work done in Araripe, and the finding of lizards there, no rhynchocephalians have been recorded yet. On the other side, Early Late Cretaceous rocks of Río Negro, Neuquén and Chubut provinces provided abundant remains of eilenodontine rhynchocephalians, demonstrating their importance as component of the Late Cretaceous terrestrial ecosystems in South America and possibly Gondwana. Furthermore, the finding in Late Campanian units from Patagonia, such as the Los Alamitos and Allen Formations, of other lineages of basal opisthodontians as well as sphenodontines prove that different rhynchocephalians were present and healthy in North Patagonia, but also probably along the southern strip of Gondwanan continents, at least until the very end of the Mesozoic. After that, they were probably affected by either the K/P extinction.

La Buitrera

The last 50 m of the Candeleros Formation at the La Buitrera Paleontological Area form marvelous outcrops exposed almost continuously along 40km, as considered from El Pueblito (S) to La Escondida (N), passing along the Cerro Policía, La Buitrera site, El Loro, and Cerro Bandera. The abundant 3D, articulated fossil vertebrates are preserved in old dune fields alternated with fluvial and lacustrine deposits, that permitted the preservation of hundreds of specimens of *Priosphenodon avelasi* (Apesteguía & Novas, 2003), the abundant-most species of this area (Figure 3).

Priosphenodon avelasi is a very large, 1.5 m long eilenodontine rhynchocephalian. Actually, is the biggest in the world, with a skull that reaches 15 cm in length. Its powerful lower jaws and lateromedially wide teeth, upgraded the eupropaliny already developed by the group. *Priosphenodon avelasi* shows a dorsoventral expansion of the jugal that almost closes the infratemporal fenestra, thus contributing to resist the

anterior torsion force of the quadrate condiles, allowing a very strong ortal closure and also a very precise propalinal movement. For some few years *Priosphenodon avelasi* was considered as junior synonym of *Kaikaifilusaurus calvoi* Simon & Kellner 2003. However, the latter was known after two isolated and very fragmentary dentaries which, once the clade was better known (e.g., with the discovery of *Priosphenodon minimus* Apesteguía & Carballido, 2014) resulted insufficient to diagnose a new species.

Priosphenodon avelasi is diagnosed for: a single, sharp, beak-like structure on the rostral end of the skull; bulging nasals; frontals rostrally straight; jugals dorsoventrally deep; suborbital fenestrae closed by transversely oriented ectopterygoids; maxillary and palatine tooth rows elongate, straight and in parallel; palatal roof narrow; teeth closely packed, with imbricate labial and lingual flanges; no caniniform teeth and no dental regionalization; and square, distally expanded unguals.

The radiation of eilenodontines occurred before or during Jurassic times (Apesteguía, 2008), before the spread of Neopangea. The group rapidly acquired large size what successfully accompanied an herbivorous diet (Throckmorton *et al.*, 1981) in which larger individuals, increased resistance to climatic variation, storage capacity during adverse times, and for fermentative and detoxication spaces.

Concerning gigantism among rhynchocephalians, it occurred several times. In aquatic forms like pleurosaurs (e.g., *Pleurosaurus*) and basal opisthodontians (i.e., *Ankylosphenodon*), gigantism improved hydrodynamics and thermal stability. In *Priosphenodon avelasi* is considered as result of its peramorphic-managed evolution, evident in the small size of the interpterygoid region, the small quadrate-quadratojugal foramen and the overall excess of ornamentation in cranial bones.

If *Priosphenodon* lived in an arid area with abundant dunes surrounding a playa-lake area and it fed on plants ¿how can be so abundant and so big? ¿the plants that they used as food were so abundant? ¿or they were toxic or saline?

The anatomical peculiarities of *Priosphenodon avelasi* suggest a high specialization in the processing of plant material. The shape and size of the flat skull table, a cutting anterior beak that improves the clean cut of hard vegetation, well-developed adductore musculature, tall and robust jaw, wide teeth with low crowns and propalinal movement are features that make *Priosphenodon* skull superficially similar to caviomorph rodents. Despite the impossibility to strictly compare a mammal with an ectothermal reptile, they may have had some overlapping in the adaptative zones. Furthermore, it is necessary to consider too that these eilenodontines were abundant, gregarious reptiles that lived in subterraneous caves probably excavated with their powerful beaks and hoofed claws (Apesteguía, 2008).

Tres Cerros - Huanimán

Priosphenodon minimus (Apesteguía & Carballido, 2014) is a small form in a lineage of giants. Its tall and narrow skull only reaches 23 mm in length, with a short antorbital region and a well-developed orbitary region. Prefrontals are profusely ornamented, an eilenodontine condition. The large orbits arise suspects of a juvenile condition, but the relative size of the interpterygoid and infratemporal fenestrae, the quadrate size, the length of the pterygoid central region (Apesteguía, 2008), as well as the intense teeth wearing support an adult condition for the *P. minimus* holotype specimen. Furthermore, extra support is provided by the abundant additional material collected in the Huaniman Hill, which is exactly the same size.

Is *Priosphenodon minimus* an early and still small eilenodontine or is a secondarily reduced form? The phylogenetic precision is not sharp enough to define it and, in any case, P. minimus results more derived than the substantially larger *Eilenodon* and *Toxolophosaurus*. In herbivorism size matters, since it is used for the development

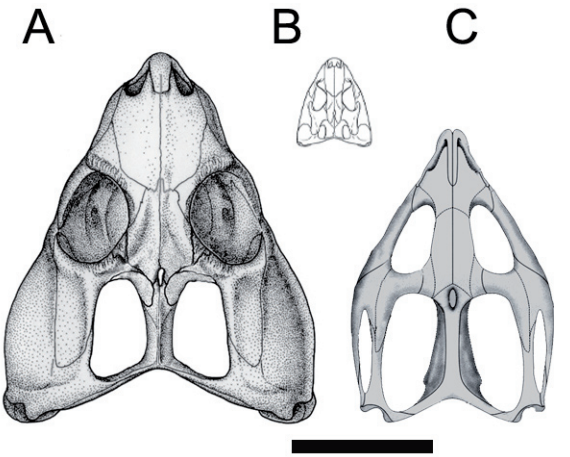

Figure 4. Comparison between adult specimens of the Cretaceous eilenodontines A, *Priosphenodon avelasi*; B, *P. minimus*, and the Triassic basal opisthodontian C, *Sphenotitan leyesi*. Scale bar is 50 mm.

of fermentative spaces. Actually, their cut and grinding dentition and eupropalinal processing of food prompts an obligated herbivory for the lineage, and makes a small size a poorly desirable condition. The small size of *P. minimus* suggests their survival in a stress zone, where volcanism and other factors did not permitted the presence of larger species as those from northern Patagonia (Figure 4).

Cerro Tortuga, Salitral de Santa Rosa

The rhynchocephalian material from the Allen Formation and equivalents is relatively abundant. The better known material includes *Lamarquesaurus cabazai* (Apesteguía & Rougier, 2007), the specimen MACN-PV RN 1062 (Martinelli & Forasiepi, 2004; Apesteguía & Jones, 2011), and *Kawasphenodon expectatus*, from the Los Alamitos Formation (Apesteguía, 2005).

Lamarquesaurus, from Cerro Tortuga, is known after a right maxilla with a total length estimated in 45 mm (the preserved part is 36 mm long), devoid of ascending and premaxillary processes. It exhibits additional teeth separated by wide spaces; strongly concave maxilla; anterolingual flanges and shallow lateral ridges in maxillary teeth; labial border splits in two portions; antorbital region of the labial border deeply furrowed; and deep concavities in the maxillary dentina over the third and fifth tooth positions (the last three characters are possibly uniquely derived features). Its separated teeth and wear facets indicating a precise ortal bite make clear that it is not an eilenodontine.

Cerro Bonaparte, Salitral de Santa Rosa

Another maxilla was published originally by Martinelli and Forasiepi (2004) and reinterpreted by Apesteguía and Jones (2011). The specimen MACN-PV RN 1062 bear teeth identical to those of *S. punctatus*, and does possess a large tooth that may represent a caniniform as found on the maxilla of *Cy. huizachalensis* (Reynoso, 1996) and *S. punctatus*. The material represents the only member of Sphenodontinae known for South America but given the partial nature of the material we are unable to refer it to a specific genus or erect a new genus. An interesting aspect is that the size of this maxilla suggests that Patagonian sphenodontines were already large by Late

Cretaceous times. Its large size (shared with the extant *S. punctatus*) may be related to peri-Antarctic adaptations, related to cold-temperate climates or high latitudes. Additionally, the feeding adaptations of sphenodontines (i.e., stabbing first palatine tooth, powerful bite) that allow predation on large insects and small vertebrates are also likely to be useful for life in cool environments (Apesteguía, 2008; Evans & Jones, 2010). Sphenodontines developed an eupropalinal movement independently from that of eilenodontines, as a combinatión of skull stranghtening by closing of lower temporal fenestra and a lenghtening and straightening of palatines. Though climatic conditions on Antarctica and peri-Antarctic regions during the Cretaceous were not necessarily cold, the ability of *S. punctatus* to remain active during low temperatures is considered as an ancient trait (Bogert, 1953) that might reflect this high latitude ancestry (Apesteguía, 2008).

Sphenodontine rhynchocephalians continued living successfully in southern continents, especially in high latitude zones, after its total disappearing from the rest of the world. Laurasian small vertebrates that entered South America during the Campanian appear to have been delayed in reaching southernmost latitudes until at least the early Paleocene (Goin *et al.*, 2008). This may be due to a combination of climate and the well-developed three epeiric seas that flooded Patagonia and the center of the continent from north to south (Urien *et al.*, 1995).

Los Alamitos

The littoral Los Alamitos Formation provided a 11 cm long lower jaw, holotype of *Kawasphenodon expectatus* (Apesteguía, 2005). The material have few, large additional teeth when compared to jaw height, with a marked trend to an edentulous condition. Teeth are square-based, anteriorly inclined teeth and the few precise striae resembling opisthodontians. Well-developed double wearing is clearly present in other more fragmentary specimens and anteroposteriorly elongated marks from maxillary teeth are evident over the labial secondary dentine, demonstrating long propalinal movements.

Though the general morphology of the lower jaw and its almost edentule condition resemble clevosaurs and *Sapheosaurus*, *Kawasphenodon* is part of the large radiation of the basal Opisthodontia. The tooth shape and the littoral nature of the Los Alamitos Formation, with a mixture of marine and terrestrial taxa, suggest the possibility of aquatic rhynchocephalians populating the littoral lagoons. However, the fragmentary nature of the remains evidences some degree of transport of the bones. The moderate taxonomic and ecological diversity of these Late Campanian sphenodontids from North Patagonia, perhaps extended along Greater Gondwana, illustrates their healthy survival in South America at least until the very end of the Mesozoic. After that, southern rhynchocephalians were affected by either the K/P extinction or the latest Cretaceous North America-South America connection, with the arrival of northern lizards which changed the local balance between sphenodontians and the non-abundant pre-Campanian Gondwanan lizards.

TERTIARY: BORDERING THE EXTINCTION

Punta Peligro

Lower Tertiary rocks of Chubut Province, central Patagonia, Argentina, provided remains of a smaller species of *Kawasphenodon*, demonstrating their survival in South America to the K/Pg extinction event. *Kawasphenodon peligrensis* (Apesteguía *et al.*, 2014) differs from *K. expectatus*, and from all other rhynchocephalians in several traits, but it is also substantially smaller (about 1/3 the size of *K. expectatus*). Its dentition can be associate to a grinding and shredding mode of food reduction and, coupled

with a large body size, to an herbivorous diet in eilenodontines (Throckmorton *et al.*, 1981; Apesteguía & Novas, 2003). In this regard, their dietary habits were probably omnivorous. *K. peligrensis* is markedly smaller than many of their close relatives. Body size optimized as a continuous character in the Rhynchocephalian phylogeny developed indicate that both the small size of *K. peligrensis* and the gigantism of *K. expectatus* are apomorphic respect to a plesiomorphic mid-size condition in opisthodontians.

At least two separate lineages of eupropalinal rhynchocephalians survived the end-Cretaceous mass extinction event in southern continents; the sphenodontines and the opisthodontians. Augé and Rage (2006) reported a possible rhynchocephalian for the Palaeocene of Morocco, but the specimen is too fragmentary to make a confident identification. Furthermore, Apesteguía (2012) recognized a possible fragment of an eilenodontine jaw from the Maastrichtian of Spain, but more material and a better preservation is necessary to confirm this observation.

Like large 'madtsoiid' snakes and terrestrial sebecid crocodyliforms, rhynchocephalians probably endured in Patagonia until the global cooling event at the Eocene–Oligocene boundary (Zachos *et al.*, 2001), also considered as the 'Patagonian Hinge' (Goin *et al.*, 2010).

The co-existence of lizards and rhynchocephalians in time and regions took place in South America along 200 million years, and thus it is no sense to say that lizards extinguished rhynchocephalians, even when considering different lineages. They probably occupied different adaptative zones (Apesteguía & Gómez, 2010). Although lizards also eventually replaced rhynchocephalians in most parts of the southern hemisphere (Zug *et al.*, 2001), for reasons that are unclear (Jones, 2006; Evans & Jones, 2010), it occurred much less dramatically than previously thought. Furthermore, when they are together, like in the Cretaceous of South America, they are remarkably different, thus giving support to the idea of niche partitioning.

Opisthodontians, which global record dates back to the Late Triassic, constituted a successful lineage that survived in Patagonia (e.g., Apesteguía & Novas, 2003; Apesteguía, 2005) when most other rhynchocephalian lineages apparently became extinct in other parts of the world (e.g., Evans & Jones, 2010).

The discovery of sphenodontines in the Late Cretaceous of South America suggests that sphenodontines are likely to be recovered too from the Jurassic of South America, but also perhaps from early to mid-Cenozoic deposits as well.

REFERENCES

Apesteguía, S. 2005. A late Campanian sphenodontid (Reptilia, Diapsida) from northern Patagonia. *Comptes Rendus Palevol* 4: 663-669.

Apesteguía, S. 2008. Esfenodontes (Reptilia, Lepidosauria) del Cretácico Superior de Patagonia: Anatomía y Filogenia. Unpublished PhD Thesis, Universidad Nacional de la Plata, Argentina, 535 pp. Available at: http://sedici.unlp.edu.ar/handle/10915/ 4405.

Apesteguía, S. & J.L. Carballido. 2014. A new Eilenodontine (Lepidosauria: Sphenodontidae) from the Lower Cretaceous of Central Patagonia. *Journal of Vertebrate Paleontology* 34: 303-317.

Apesteguía, S. & M.E.H. Jones. 2012. A Late Cretaceous "tuatara" (Lepidosauria: Sphenodontinae) from South America. *Cretaceous Research* 34: 154-160.

Apesteguía, S. & F.E. Novas. 2003 Large Cretaceous sphenodontian from Patagonia provides insight into lepidosaur evolution in Gondwana. *Nature* 425: 609-612.

Apesteguía, S. & G.W. Rougier. 2007 A late Campanian sphenodontid maxilla from northern Patagonia. *American Museum Novitates* 3581: 1-11.

Apesteguía, S., R.O. Gómez, & 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. 2012. The youngest European sphenodontian? A possible Late Campanian eilenodontine from the Baske Country. En (Royo Torres, R., Gascó, F. y Alcalá, L., Eds.) Libro de Abstracts del 10th Annual Meeting of the European Association of Vertebrate Paleontologists. Teruel (2012), 20: 11-14.

Apesteguía, S. & R.O. Gómez. 2011. Sphenodontians: New insights on the least known south american lepidosaurs. XI Congreso Argentino de Herpetología. Buenos Aires. Octubre de 2011. Libro de resúmenes.

Apesteguía, S., R.O. Gómez & G.W. Rougier. 2014. The youngest South American rhynchocephalian, a survivor of the K/Pg extinction. Proceedings of the Royal Society B 2014 vol. 281, N° 1792, 20140811.

Augé, M. & J-C. Rage. 2006. Herpetofaunas from the upper Paleocene and lower Eocene of Morocco. Annales du Paléontologie 92: 235-253.

Bogert, C.M. 1953. The tuatara: why is it a lone survivor? Scientific Monthly 76: 163-170.

Bonaparte, J.F. 1986. History of the terrestrial Cretaceous vertebrates of Gondwana. 4th Congreso Argentino de Paleontología y Bioestratigrafía (Mendoza), Actas 4: 6395.

Bonaparte, J. F. & 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.

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. & M.E.H. Jones. 2010 The origin, early history and diversification of lepidosauromorph reptiles. In: S. Bandyopadhyay (ed.) *New Aspects of Mesozoic Biodiversity, 132*, pp. 27-44. Berlin: Springer.

Evans, S. E., G.V.R. Prasad & B.K. Manhas. 2001. Rhynchocephalians (Diapsida: Lepidosauria) from the Jurassic Kota Formation of India. *Journal of the Linnean Society* 133: 309-334.

Ferigolo, J. 2000. Esfenodontídeos do Neo-Triássico/?Jurássico do Estado do Rio Grande do Sul, Brasil. In: Holz M, & L.F. De Ros (eds.) Paleontologia do Rio Grande do Sul: CIGO/UFRGS pp.236-245.

Flynn, J.J., J.M. Parrish, W. Simpson, L. Razafimanantsoa, R. Andriatompohavana & A. Totovolahy. 1997. New Triassic and Jurassic vertebrates from Madagascar. *Journal of Vertebrate Paleontology* 17: 46A.

Flynn, J. J., J.M. Parrish, B. Rakotosamimanana, W.F. Simpson, R.L. Whatley, & A.R. Wyss. 1999. A Triassic fauna from Madagascar, including early dinosaurs. *Science* 286: 763-765.

Fraser, N. C. 1988. The osteology and relationships of *Clevosaurus* (Reptilia: Sphenodontida). *Philosophical Transactions of the Royal Society* B 321:125-178.

Goin, F.J., J.N. Gelfo, L. Chornogubsky, M.O. Woodburne, & T. Martin. 2008. Origins, radiations, and distribution of South American mammals: from greenhouse to icehouse worlds. In: Patterson, B.D., & Costa, L.P. (Eds.), Bones, Clones, and Biomes: an 80-Million-Year History of Recent Neotropical Mammals. University of Chicago Press, Chicago, IL.

Goin FJ, M.A. Abello, & L. Chornogubsky. 2010. Middle Tertiary marsupials from central Patagonia (early Oligocene of Gran Barranca): understanding South America's Grande Coupure. In: R.H. Madden (ed.) *The paleontology of Gran Barranca: evolution and environmental change through the Middle Cenozoic of Patagonia*, pp. 69-105. Cambridge: Cambridge University Press.

Gow, C.E. & M.A. Raath. 1977. Fossil vertebrate studies in Rhodesia: Sphenodontid remains from the Upper Trias of Rhodesia. *Paleontologia Africana* 20: 121-122

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. 2009. Dentary tooth shape in *Sphenodon* and its fossil relatives (Diapsida: Lepidosauria: Rhynchocephalia). In: T. Koppe, G. Meyer, & K.W. Alt (eds.) *Interdisciplinary Dental Morphology. Frontiers in Oral Biology 13* , pp. 9-15. Greifswald: Karger.

Leanza, H. A., S. Apesteguía, F. E. Novas, & M.S. de la Fuente. 2004. Cretaceous terrestrial beds from the Neuquén basin (Argentina) and their tetrapod assemblages. *Cretaceous Research* 25: 1-96.

Martinelli, A.G. & A.M. Forasiepi. 2004. Late Cretaceous vertebrates from the Bajo de Santa Rosa (Allen formation), Río Negro, Argentina, with the description of a new sauropod dinosaur (Titanosauridae). *Revista del Museo Argentino de Ciencias Naturales* 6: 257-305.

Martínez, R.N., C. Apaldetti, C.E. Colombi, A. Praderio, E. Fernandez, P.S. Malnis, G.A. Correa, D. Abelin, & O. Alcober. 2013. A new sphenodontian (Lepidosauria: Rhynchocephalia) from the

Late Triassic of Argentina and the early origin of the herbivore opisthodontians. *Proceedings of The Royal Society* B 280: 20132057 http://dx.doi.org/10.1098/rspb.2013.2057

Martínez, R.N., C. Apaldetti, G.Correa, C.E. Colombi, E. Fernández, P. Santi Malnis, A. Praderio, D. Abelín, L.G. Benegas, A. Aguilar-Cameo, & O.A. Alcober. 2015. A New Late Triassic Vertebrate Assemblage from Northwestern Argentina. *Ameghiniana* 52(4): 379-390.

Remes, K., F. Ortega, I. Fierro, U. Joger, R. Kosma, *et al*. 2009. A New Basal Sauropod Dinosaur from the Middle Jurassic of Niger and the Early Evolution of Sauropoda. *PLoS ONE* 4(9): e6924. doi:10.1371/journal.pone.0006924

Reynoso, V. H. 1996. A Middle Jurassic Sphenodon-like sphenodontian (Diapsida: Lepidosauria) from Huizachal Canyon, Tamaulipas, México. *Journal of Vertebrate Paleontology* 17: 52-59.

Simón, M. E. & 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.

Sues, H.D. & R.R. Reisz. 1995. First record of the Early Mesozoic sphenodontian *Clevosaurus* (Lepidosauria: Rhynchocephalia) from the southern hemisphere. *Journal of Paleontology* 69: 123-126.

Throckmorton, G.S., J.A. Hopson, & P. Parks. 1981 A redescription of *Toxolophosaurus cloudi* Olson, a Lower Cretaceous herbivorous sphenodontian reptile. *Journal of Paleontology* 55: 586-597.

Urien, C.M., J.J. Zambrano, & M.R. Yrigoyen. 1995 Pretroleum basins of southern South America. In: Tankard, A.J., R. Suarez, & H.J. Welsink (eds.), *Petroleum Basins of South America. American Association of Petroleum Geologists Memoir* 62: 63-77.

Zachos, J, M. Pagani, L. Sloan, E. Thomas, & K. Billups. 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* 292: 686-693.

Zug, G.R.; L.J. Vitt, & J.P. Caldwell. 2001. Herpetology - An Introductory Biology of Amphibians and Reptiles. 2. ed. San Diego: Academic Press, 2001. 630 pp.