



# A basal sphenodontian (Lepidosauria) from the Jurassic of Patagonia: new insights on the phylogeny and biogeography of Gondwanan rhynchocephalians

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Herein we describe a new rhynchocephalian taxon from the Middle Jurassic of Patagonia, Argentina, representing the first Jurassic record of the group in South America. The new taxon, consisting of a complete dentary, is ascribed to Sphenodontia based on the presence of a 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. This allocation is reinforced by a phylogenetic analysis that places the new taxon in a basal position within a clade of sphenodontians that excludes *Diphydontosaurus* and *Planocephalosaurus*. Additionally, the new taxon clusters within a Gondwanan clade with the Indian *Godavarisaurus* from the Jurassic Kota Formation, sharing the presence of recurved and relatively large posterior successional teeth that are ribbed and bear a peculiar anterolingual groove. This sister-group relationship is intriguing from a palaeobiogeographical viewpoint, as it suggests some degree of endemism during the initial stages of the breakup of Pangaea. We also discuss the ontogenetic stage of the new taxon and provide insights on the evolution of successional dentition in rhynchocephalians.

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ADDITIONAL KEYWORDS: Argentina – Cañadón Asfalto – Central Gondwanan Desert – Gondwana – Middle Jurassic – ontogeny – palaeobiogeography – Rhynchocephalia – Sphenodontia – successional dentition.

## INTRODUCTION

Rhynchocephalia (Günther, 1867 *sensu* Gauthier, Estes & De Queiroz, 1988) is a clade of lizard-like reptiles that, together with Squamata, constitute the Lepidosauria (Carroll, 1977; Evans, 1984; Benton, 1985; Gauthier *et al.*, 1988). Rhynchocephalians are represented today by the sole genus *Sphenodon*, the 'tuatara', with only two species inhabiting several

islands around New Zealand (Daugherty *et al.*, 1990). The living rhynchocephalians are the remnants of a group that experienced a remarkable Mesozoic diversification, followed by a substantial reduction in the Late Cretaceous, believed by some authors (e.g. Carroll, 1985) to be related to the radiation of the Squamata.

The fossil record of rhynchocephalians dates back to the Late Triassic (Carnian) of North America (Sues & Olsen, 1990) and Europe (Fraser & Benton, 1989). Most other Triassic records are also from the northern landmasses, particularly North America (e.g. Sues &

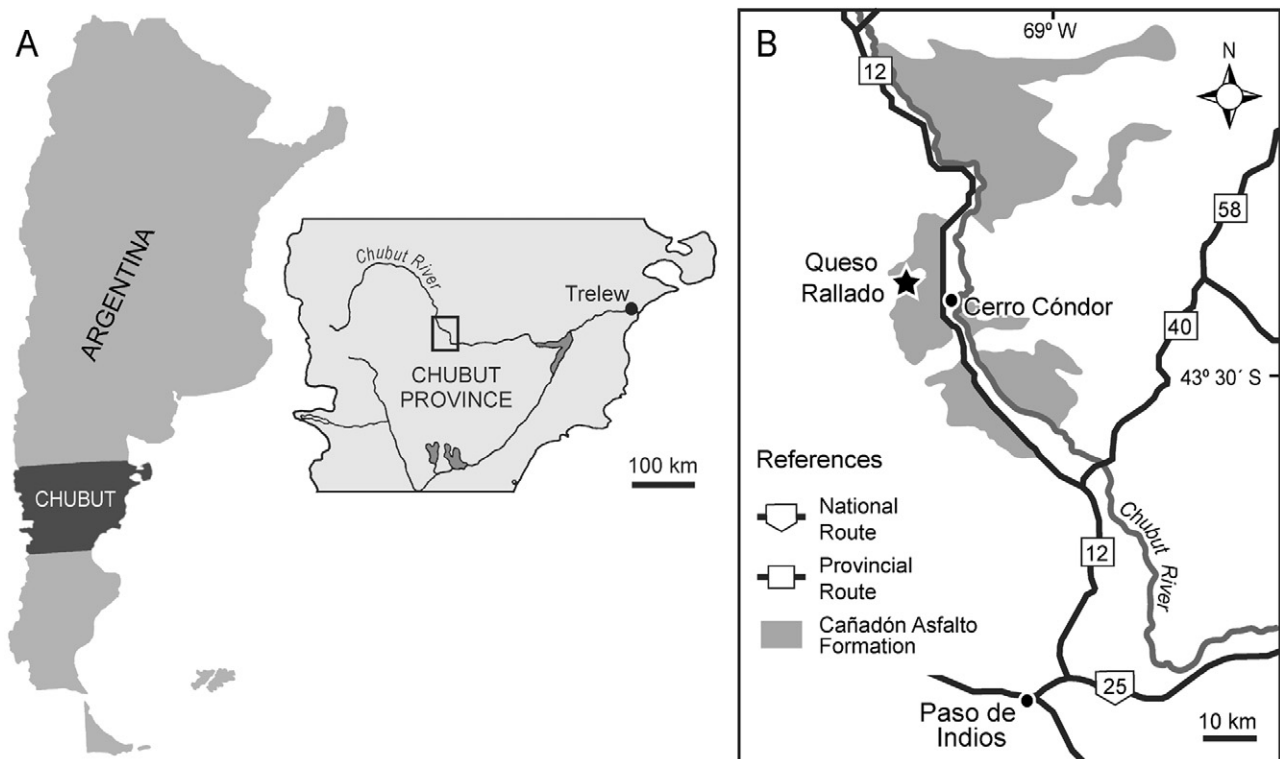
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Baird, 1993), the UK (e.g. Huene, 1910; Robinson, 1973; Fraser, 1982; Whiteside, 1986), Germany (e.g. Fraser & Benton, 1989), and China (Wu, 1994). Southern Triassic records include fragmentary material from Africa (Gow & Raath, 1977; Sues & Reisz, 1995) and well-preserved clefosaurus from Brazil (e.g. Ferigolo, 1999; Bonaparte & Sues, 2006). During the Early Jurassic rhynchocephalians continued to be abundant in northern regions including the UK (e.g. Evans, 1980), Mexico (e.g. Clark *et al.*, 1994; Reynoso, 1996, 1997, 2005), and China (Evans, 1992), whereas southern regions only include fragmentary remains from Zimbabwe (Gow & Raath, 1977), South Africa (Sues & Reisz, 1995), and India (Evans, Prasad & Manhas, 2001). The Middle and Late Jurassic record of the group was, up to now, restricted to the Northern Hemisphere, with no records from Gondwanan landmasses. This Laurasian record includes fragmentary material from the UK (Evans, 1992), France (e.g. Cocude-Michel, 1963), and the USA (e.g. Gilmore, 1909; Rasmussen & Callison, 1981), and well-preserved specimens from Mexico (e.g. Reynoso, 1996). Furthermore, the South American record of rhynchocephalians exhibits a time gap of more than 100 million years, from the Late Triassic (Norian) of Brazil (Caturrita Formation; Ferigolo, 1999) to the

early Late Cretaceous (Cenomanian) of Patagonia (Candeleros Formation; Apesteguía & Novas, 2003).

The Jurassic Cañadón Asfalto Formation of Chubut Province, Patagonia, Argentina (Fig. 1), has yielded the most taxonomically diverse Gondwanan biota of Middle Jurassic age (Escapa *et al.*, 2008; Pol, Rauhut & Becerra, 2011). This unit was intensively worked by Bonaparte (between 1978 and 1986), providing abundant remains of the eusauropods *Patagosaurus fariasi* Bonaparte, 1979, and *Volkheimeria chubutensis* Bonaparte, 1979, and the basal tetanuran *Piatnitzkysaurus floresi* Bonaparte, 1986, related to *Condoraptor currumili* Rauhut, 2005, from the same unit. In November 2000, Mr Pablo Puerta, technician at the 'Egidio Feruglio' Museum of Trelew (MEF), in the frame of a fieldtrip led by Dr Oliver Rauhut, discovered a mammalian jaw (Rauhut *et al.*, 2002) that prompted the intensive work of a small microvertebrate locality known as 'Queso Rallado' (Fig. 1). One of us (G. W. R.) and a MEF team intensively worked the locality during the last decade finding frogs, turtles (Sterli, 2008), dinosaurs (Pol *et al.*, 2011), pterosaurs, and mammals (Rougier *et al.*, 2007a, b; L. C. Gaetano & G. W. Rougier, 2011, unpubl. data).

Herein we describe a new rhynchocephalian from the locality of Queso Rallado, near Cerro Condor



**Figure 1.** A, map of Argentina and Chubut Province indicating the study area where the new rhynchocephalian was found. B, close-up of the study area showing Queso Rallado locality, near Cerro Cándor village.

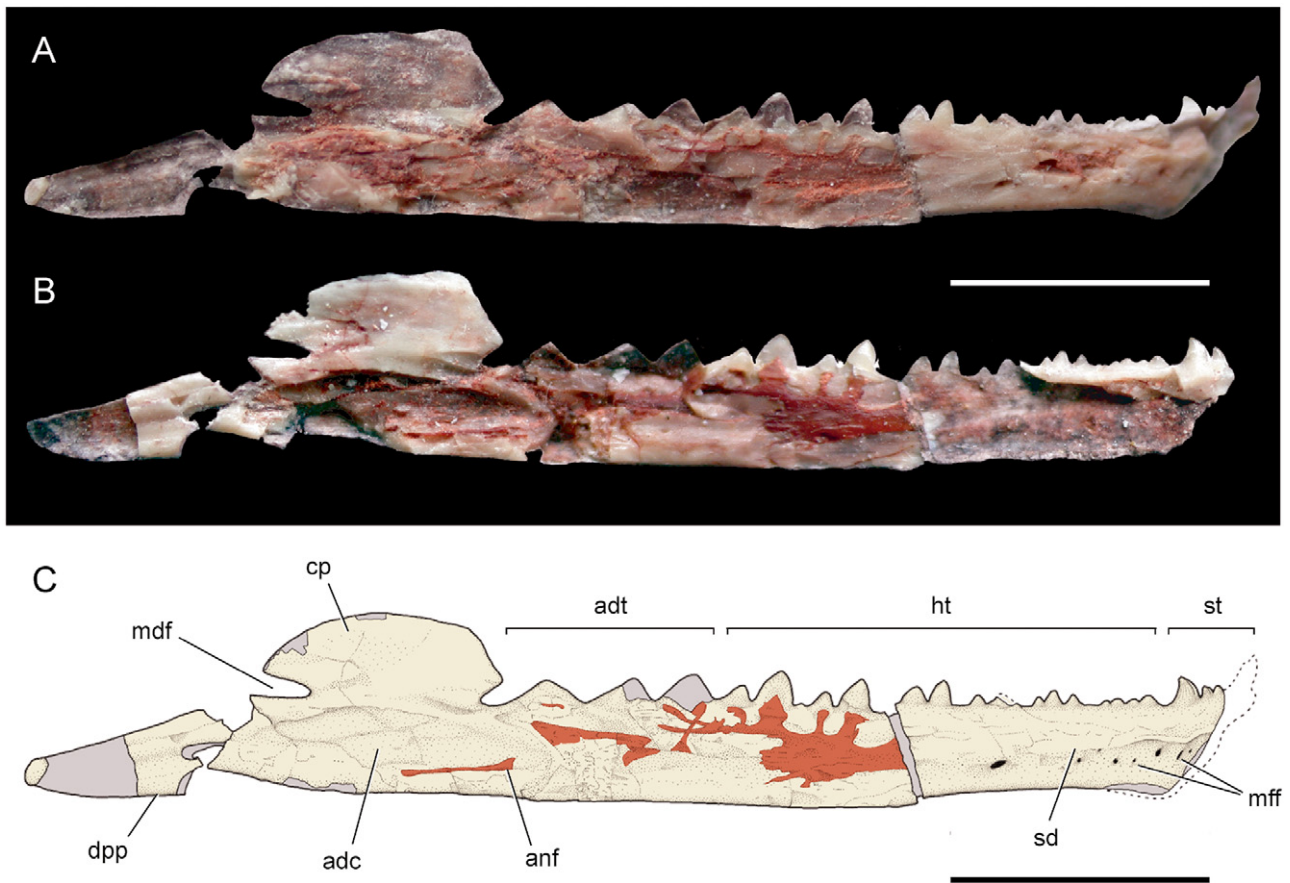
village (Fig. 1). The material described herein represents the first Jurassic rhynchocephalian from South America as well as the first of Middle Jurassic age from Gondwana, contributing to filling an extensive stratigraphical and morphological gap in the fossil record of the group.

#### MATERIAL AND METHODS

The material consists of a nearly complete dentary preserved in two slabs as part (Fig. 2A) and counterpart (Fig. 2B). Both parts were digitally superimposed and considered as one specimen for descriptive and comparative purposes (Fig. 2C), unless stated otherwise. Photographs were taken using a Nikon Coolpix 990 digital camera and measurements were taken from digital images using IMAGE J (Abramoff, Magalhaes & Ram, 2004).

Anatomical terminology mainly follows that of Harrison (1901) and Romer (1956) with additional terms from Apesteguía (2008). We refer to the dentary and the dentition in general using standard anatomical orientation terms (anterior/posterior; dorsal/ventral; lateral/medial); the tooth orientation terminology (labial/lingual; mesial/distal; basal/apical) of Smith & Dodson (2003) is used when referring to particular teeth.

The presence of 'caniniform' successional teeth in rhynchocephalians has been considered of great systematic value by some authors (e.g. Gauthier *et al.*, 1988; Reynoso, 1996, 2003). However, the precise homology between these 'caniniform' teeth and other successional remains uncertain in fossil taxa. Therefore, we use herein the term 'caniniform' as a functionally defined morphological concept, free of homology assumptions (Vogt, Bartolomaeus & Giribet, 2010); accordingly, the term appears in



**Figure 2.** *Sphenocendor gracilis* gen. et sp. nov., holotype (MPEF-PV 2358), right dentary. A, general view of dentary in slab A. B, general view of dentary in slab B (reversed). C, partial restoration combining part and counterpart. Dotted line depicts the symphyseal region preserved as an impression in slab A. Abbreviations: adc, adductor fossa; adt, additional teeth; anf, angular facet; cp, coronoid process; dpp, dentary posterior process; ht, hatchling teeth; mdf, mandibular foramen; mff, mental foramina; sd, secondary bone; st, successional teeth. Scale bars = 5 mm.

quotes throughout the text. This way, a ‘caniniform’ is any successional tooth in the anterior region of the dental line that detaches and remains substantially larger than adjacent teeth.

The name Rhynchocephalia Günther (1867) was originally erected for the genus *Sphenodon* and the Triassic rhynchosaurs were included later (Nopsca, 1928; Romer, 1956), although subsequent work removed the latter forms from the group (Benton, 1985; Evans, 1988). Consequently, in spite of the former link of rhynchosaurs to rhynchocephalians and the misleading name similarity, Estes (1983) then proposed Sphenodontida to encompass *Sphenodon* and allies. Known taxa and hypotheses of inter-relationships within the group have considerably increased since then and, hence, the contents of different suprageneric taxa vary accordingly. The more widespread uses of the names Rhynchocephalia, Sphenodontia, and its vernacular derivatives (e.g. Reynoso, 1996; Evans *et al.*, 2001) are followed and employed here.

The methodology employed in the phylogenetic analysis is detailed under the corresponding heading (see Phylogenetic analysis).

#### SYSTEMATIC PALAEOLOGY

LEPIDOSAURIA DUMERIL ET BIBRON, 1839  
(*SENSU* EVANS, 1984)

RHYNCHOCEPHALIA GÜNTHER, 1867  
(*SENSU* GAUTHIER *ET AL.*, 1988)

SPHENODONTIA WILLISTON, 1925  
(*SENSU* BENTON, 1985)

#### *SPHENOCONDOR* GEN. NOV.

*Type species: Sphenocondor gracilis* sp. nov.

*Diagnosis:* As for type and only known species.

*Etymology:* ‘Spheno’ refers to the Sphenodontia, and ‘condor’ is after the nearby village of Cerro Cóndor, Chubut Province, Argentina.

#### *SPHENOCONDOR GRACILIS* SP. NOV.

*Etymology:* The specific epithet ‘gracilis’ refers to the slenderness of the jaw.

*Holotype:* MPEF-PV 2358, a single dentary preserved in two slabs as part (A) and counterpart (B).

*Locality and horizon:* Queso Rallado locality, about 2.3 km north-west of Cerro Cóndor village, 360 km west from Trelew, Chubut Province, Argentina (Fig. 1). The bearing beds consist of silicified mudstones within series of mudstones and limestones

that are part of the Lower Member of the Cañadón Asfalto Formation (Rougier *et al.*, 2007b) and that were deposited in a lacustrine carbonate environment (Figari, Courtade & Constantini, 1996). The age of this unit has usually been considered as Callovian (Proserpio, 1987) or Callovian–Oxfordian (e.g. Tasch & Volkheimer, 1970; Musacchio, Beros & Pujana, 1990; Figari & Courtade, 1993; Page *et al.*, 1999; Silva Nieto *et al.*, 2002; Cabaleri *et al.*, 2010). However, recent radiometric data (Cuneo & Bowring, 2010) suggest that it might be older (beginning its deposition in the Toarcian). Despite some difficulty in establishing precise correlations between the Queso Rallado Quarry and the dated beds, the age of the fossils is almost certainly Middle Jurassic.

*Diagnosis:* Small sphenodontian rhynchocephalian differing from all other rhynchocephalians in having 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; 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; unadorned additional teeth; two dentine types organized in a radiating pattern; symphysis anterodorsally projected; adductor fossa centred under the coronoid process; and alternate hatchling dentition organized in three groups of different size and showing a slight basal constriction. These last three characters constitute autapomorphic features.

#### DESCRIPTION AND TAXONOMIC COMPARISONS

##### *Dentary*

The lower jaw is very slender and, as in basal forms (e.g. *Diphydontosaurus avonis* Whiteside, 1986), the dentary represents about 90% of the total length of the jaw. The height of the dentary varies along the jaw (Table 1), from 2 mm in the precoronoid region to 3.72 mm at the level of the coronoid process. The dental margin of the dentary is about 15.9 mm from the symphysis to the anterior part of the coronoid process, and can be divided into successional, hatchling, and additional regions, based on the dentition (Fig. 2). The presence of a deep and wide Meckelian groove on the medial side of the mandible is only evident in the posterior part of slab B (Fig. 2B). The lateral surface of the dentary, as preserved in slab A (Fig. 2A), shows development of secondary bone (secondary dentine of Fraser, 1986) below the tooth row (at least on the anterior portion of the dentary). This feature has been regarded as a character of derived rhynchocephalians, being absent in basal taxa such

**Table 1.** Measurements (in mm) of the holotype of *Sphenocondor gracilis* gen. et sp. nov. (MPEF-PV 2358)

Measurements	Value
Total length of dentary	24.96
Total length of jaw (estimated)	26.4
Maximum height of jaw at symphysis	2.5
Minimum height of jaw (anteriorly)	1.42
Height of jaw at coronoid process	3.72
Length of coronoid process at base	4.53
Length of coronoid process at top	3.07
Height of coronoid process	1.73
Length of posterior process	5.29
Height of last successional tooth	0.54
Length of adductor fossa	5.82
Height of adductor fossa	1.18

as *Gephyrosaurus* and *Diphydontosaurus* (Fraser, 1988; Jones, 2006; Jones *et al.*, 2009).

The ventral margin of the dentary is rather straight as in basal rhynchocephalians and some derived forms such as *Cynosphenodon huizachalensis* Reynoso, 1996 and 'Sphenodontid B' from the Early Cretaceous beds of Anoual, Morocco (Evans & Sigogneau-Russell, 1997).

The symphyseal region is badly damaged, but a large and pointed fragment is evident in slab A (Fig. 2A). This fragment might represent part of a large successional tooth or a symphyseal spur (crowned or not by a symphyseal tooth), although its poor preservation prevents us from confirming its identity. A symphyseal spur occurs in *Sphenodon*, *Sphenovipera*, *Cynosphenodon*, *Rebbanasaurus* (Evans *et al.*, 2001; Reynoso, 2005; Fig. 4F), the Kirtlington sphenodontid, and the sphenodontians LACM 135616 and LACM 1335531 from the Morrison Formation (S. A., pers. observ.). The region that often bears a mental process is not preserved.

The coronoid process is low and squared, more developed than in *Diphydontosaurus* and similar in height to those of *Planocephalosaurus* (Fraser, 1982), *Sphenodon*, and eilenodontines (including *Kaikaiiflusaurus*; Apesteguía & Novas, 2003; Apesteguía, 2008). In this aspect, it clearly differs from *Clevosaurus* (Fraser, 1988) and *Ankylosphenodon* (Reynoso, 2000). The coronoid bone is not preserved, but the posterior margin of the dentary bears the notch that represents the anterior margin of the mandibular foramen, commonly shared with the surangular.

In *Sphenocondor* the adductor fossa is longer than high, eye-shaped, and centred ventral to the coronoid process (Figs 2, 3A); it differs from that of most sphenodontians, which is located posterior to the level of the coronoid tip. In *Sphenovipera* (Reynoso, 2005) the

adductor fossa is also located ventral to the coronoid process, but differs from that of *Sphenocondor* in being oblique rather than horizontal.

The posterior process of the dentary is broken and slightly out of place, but it is rather well preserved and the missing part left a clear mould indicating its size and shape. The process is very long, as much as the long coronoid base. No postdentary bones have been preserved.

### Teeth

There are around 20 preserved teeth in the holotype of *Sphenocondor*; all of them are acrodont and more or less conical in shape (Fig. 2). As in most sphenodontians, there are represented several dental generations arranged in an anterior-to-posterior sequence, comprising: (1) a successional dentition encompassing at least three teeth (probably four); (2) an alternating hatchling series composed of 15–16 teeth; (3) an additional generation composed of three large teeth uniform in size and shape (Fig. 2).

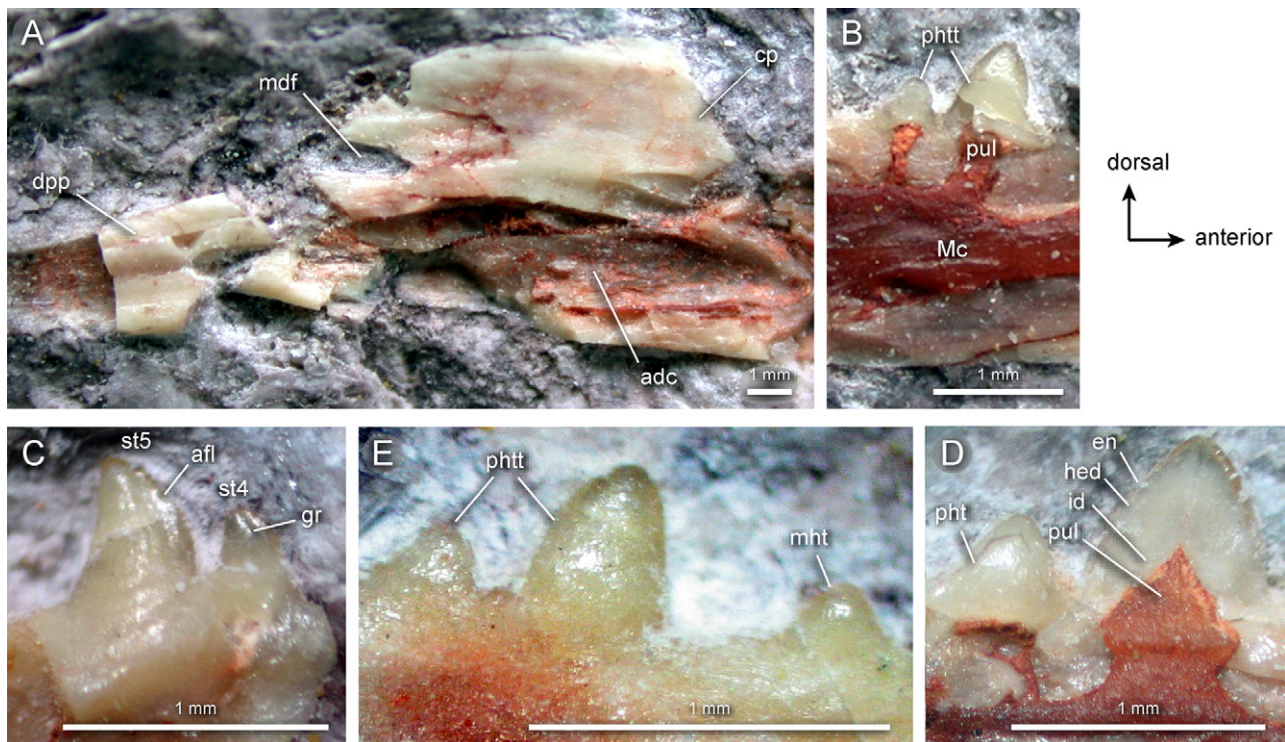
The anterior-most region is not well preserved. There is a large separated fragment of bone that could be considered as part of the anteromedial symphyseal spur (Figs 2, 4A), or part of a large successional tooth. However, the preservation does not allow certain identification. Behind it follow two strongly recurved and profusely striated successional teeth, the second much taller than the first. They are labiolingually compressed and bear on the labial side a groove or canal that delimits an anterior flange. This trait is also present in juvenile specimens of *Godavarisaurus* (Evans *et al.*, 2001; Fig. 4B), which also share the general shape and relative position of the pieces. More than one successional tooth in adults is also present in other sphenodontians (Table 2), such as *Theretairus* (Simpson, 1926) and *Sphenovipera* (Reynoso, 2005). However, they differ from *Sphenocondor* in having 'caniniforms' widely separated and rounded in cross-section. The presence in *Sphenocondor* of anterior flanges in the successional teeth probably represents a derived feature shared with *Godavarisaurus*.

Posterior to these successional teeth, after a short diastema, begins the hatchling series. The latter teeth are alternated in size, as characteristic for hatchling dentition (Robinson, 1976), and can be divided into three groups according to size (Fig. 2). The anterior group comprises four smooth, small teeth that are almost completely worn down and might have occluded with the maxillary successional. The second group is composed of five or six well-preserved, conical teeth that are intermediate in size, about twofold the anterior hatchling pieces, and bear sharp cusps relatively unworn. These hatchling teeth might have matched the anterior-most hatchling teeth on the maxilla, explaining the difference in wear with

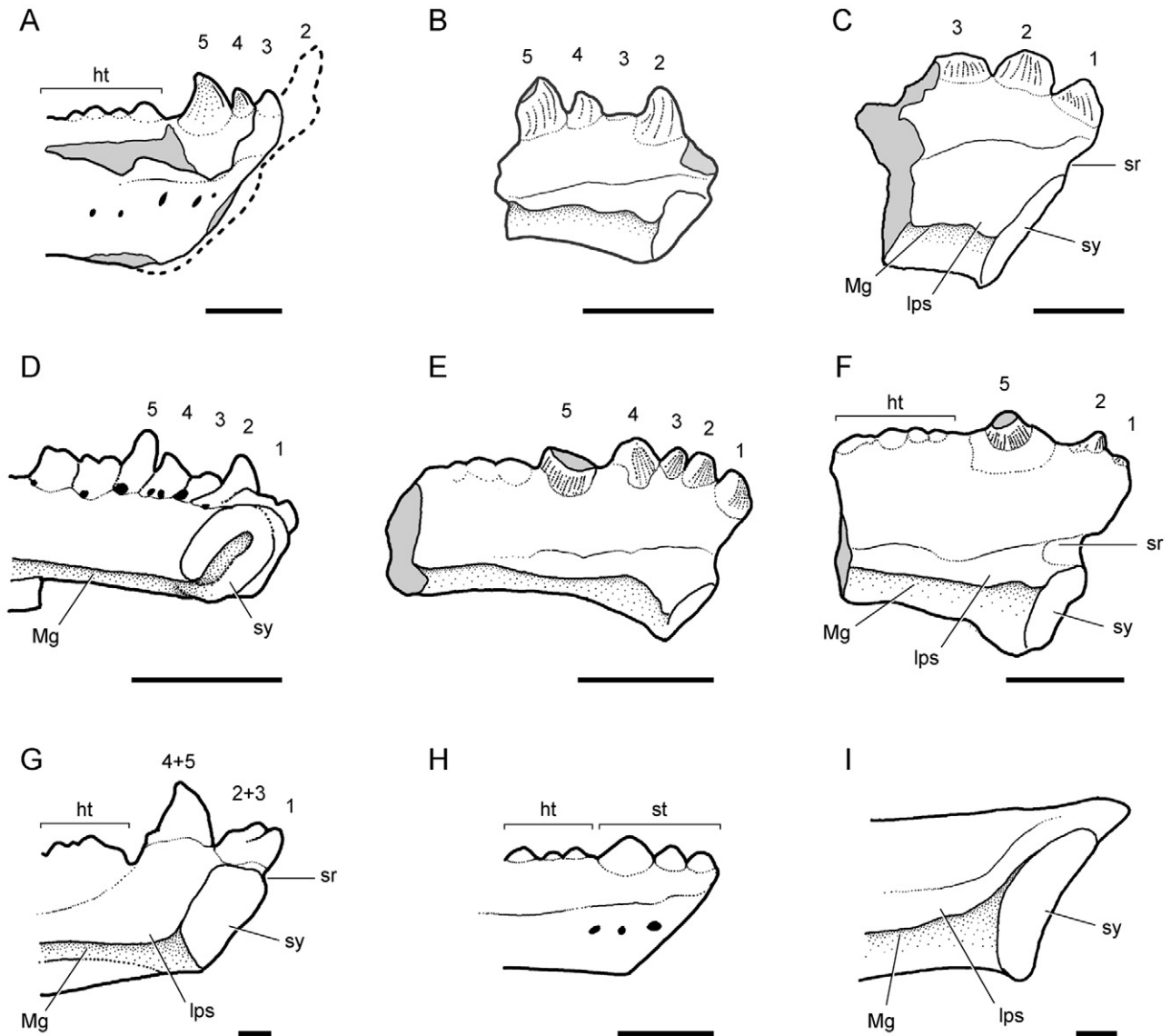
**Table 2.** Number of simultaneous successional teeth in rhyngocephalians

Taxon	Ontogenetic stage	Successionals	Notes
<i>Sphenocondor</i>	T2–T3	2 (posterior)	The last one larger, space enough for 3 anterior
<i>Diphydontosaurus</i>	Adult	5	2nd and 5th larger
<i>Rebbanasaurus</i>	Juvenile	5	Last 2 larger;
	Adult	2–3	The last 2 larger
<i>Godavarisaurus</i>	Juvenile and adult	At least 4, 5?	2nd? and last larger
Kirlington sphenodontid	Adult	2–3	The last larger, ‘caniniform’
<i>Cynosphenodon</i>	T3–T4	At least 4	The last larger
	Adult	1 ‘caniniform’	Secondary bone obscures anterior teeth
<i>Theretairus</i>	Adult	At least 2	Large, spaced ‘caniniforms’
<i>Sphenovipera</i>	Adult	At least 3	Two large, spaced ‘caniniforms’
<i>Clevosaurus hudsoni</i>	Immature (T3?),	3 replacing the	
	Adult	first 4–5 ht	
<i>Kaikaiiflusaurus avelasi</i>	Juveniles and adults	0	Secondary bone obscure anterior teeth Never developed

ht, hatchling teeth.



**Figure 3.** *Sphenocondor gracilis* gen. et sp. nov., holotype (MPEF-PV 2358), right dentary. A, close-up of coronoid region in lingual view. B, sagittal section of dentary bearing posterior hatchling teeth in lingual view. C, ‘caniniform’ successional teeth in lingual view. D, internal structure of most posterior hatchling teeth. E, last middle and first posterior hatchling teeth in labial view. Photographs in A, B, C, and D reversed. Abbreviations: adc, adductor fossa; afl, anterior flange; cp, coronoid process; dpp, dentary posterior process; en, enamel; gr, groove; hed, hyaline external dentine; id, internal dentine; Mc, Meckelian canal; mht, middle hatchling tooth; pht, posterior hatchling tooth; phtt, posterior hatchling teeth; pul, pulpar cavity; st4, fourth successional tooth; st5, fifth successional tooth.



**Figure 4.** Symphyseal region of the dentary and successional teeth of selected rhynchocephalians. A, *Spheenocondor gracilis* gen. et sp. nov., holotype (MPEF-PV 2358). B, *Godavarisaurus lateefi*, juvenile. C, *Godavarisaurus lateefi*, mature; D, *Diphydontosaurus avonis*. E, *Rebbanasaurus jaini*, juvenile. F, *Rebbanasaurus jaini*, immature. G, *Sphenodon punctatus*, mature. H, *Clevosaurus hudsoni*, immature. I, *Clevosaurus hudsoni*, adult. B, C, E, and F redrawn from Evans *et al.* (2001:figs 5B, D, 13A, C), C reversed; D redrawn from Whiteside (1986:fig. 28), but reversed; G redrawn from Throckmorton, Hopson & Parks (1981:fig. 1B), but reversed; H and I redrawn from Fraser (1988:figs 19b, 23b). Abbreviations: 1–5, successional tooth positions; ht, hatchling teeth; lps, postsymphyseal lamina; Mg, Meckelian groove; sr, symphyseal recess; sy, symphysis. Scale bars = 1 mm.

respect to the preceding hatchling teeth. The third and most posterior hatchling group comprises six high, conical teeth with rounded walls and devoid of striations. The latter are clearly larger and less worn than the other hatchling teeth, possibly indicating that these larger teeth belong to a younger hatchling generation that developed as the dentary bone grew during early ontogeny. The relative height of these posterior hatchling teeth is similar to those of Sphe-

nodontian B (Evans & Sigogneau-Russell, 1997), with respect to the dentary height below them. The aforementioned size variation in the alternating hatchling series with teeth becoming larger posteriorly is also present in other sphenodontian taxa, such as *Planoccephalosaurus* (Fraser, 1982).

As in other sphenodontians, which are typified by the addition of acrodont teeth at the rear of the jaw that are not replaced during ontogeny (Robinson, 1976), at

the posterior end of the tooth line of *Sphenocondor* there is an additional series made up of three badly preserved teeth exposed in labial view; this preservation prevents us from identifying flanges on the lingual surface of these teeth. These additional teeth are conical and sharp, with their bases being about twice as long as the bases of the posterior hatchling teeth. At least on the labial surface, *Sphenocondor* lacks well-developed flanges on the additional teeth, thus differing from additional teeth in many derived sphenodontians (e.g. *Tingitana*, *Clevosaurus*, *Homoeosaurus*, *Kallimodon*, *Sphenodon*). They resemble some of the teeth of *Planocephalosaurus*, and some of the additional teeth of *Godavarisaurus*.

The natural breakage in two slabs running diagonally along the jaw allowed us to study the lateral side of the anterior region, the medial side of the posterior region, and the sagittal inner structure of the mid region (Figs 2, 3). The posterior hatchling teeth allow the inspection of their respective pulpar cavities (Fig. 3B, D). As the more anterior tooth is not sagittally broken, only part of the pulpar cavity is visible, differing from the following, which sustained a sagittal break. The pulpar cavities are wide in both cases, expanded in the interior of every tooth and narrowing downwards, but remaining open. The pulpar cavities join each other before reaching the upper margin of the Meckelian canal, establishing an oblique ventral connection.

The fifth posterior hatchling tooth is the best to study the inner structure of the teeth (Fig. 6B) because the pulpar cavity of this bulbous tooth is fully exposed by a perfect sagittal section and devoid of further damage. The outer layer of the tooth is formed by a uniform thick layer of enamel that covers the entire dental piece. Under the enamel there is a thick cover of dentine composed by two morphological types. The upper part of the dentine is represented by a hyaline dentine that is thicker in the top of the tooth crown. The lower part of the dentine is thick and whitish. A conspicuous odontoblastic line runs from the enamel base to the upper part of the pulp across the dentine layers. Additionally, numerous radiating lines, the odontoblast prolongations, run across the dentine layer. The pulp cavity is rhomboid in shape and increases its width downwards to reach a maximum at the dorsal margin of the dentary, where it narrows abruptly, separating the main pulp cavity from the dorsal margin of the Meckelian groove.

#### PHYLOGENETIC ANALYSIS

In order to assess the evolutionary relationships of *Sphenocondor gracilis* within Sphenodontia, a parsimony analysis was performed. In light of recent phylogenetic hypotheses of rhyngocephalians, *Youngina*,

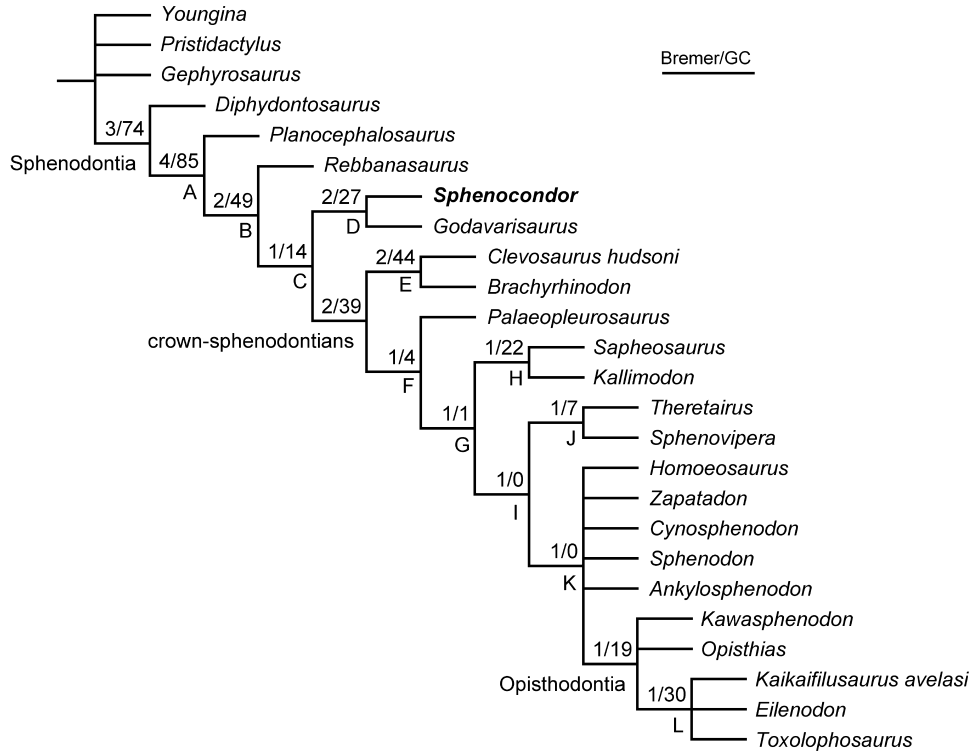
the squamatan *Pristidactylus*, and *Gephyrosaurus* were used as sphenodontian outgroups to root the recovered optimal topologies. The ingroup taxon sample includes, besides *Sphenocondor*, most of the taxa previously considered in phylogenetic analyses plus three additional Gondwanan taxa, whose relationships have never been rigorously tested. Most of the characters used in the analysis are based on those of Wu (1991, 1994), Sues, Shubin & Olsen (1994), Reynoso (1996, 1997, 2005), Reynoso & Clark (1998), Apesteguía & Novas (2003), and Apesteguía (2008). However, several characters and character states were modified to make more explicit the way they were coded herein. In some cases other states were added to include observed variation within the taxon sample. As many sphenodontians are only known from jaw remains and only a small proportion of characters deal with lower jaw morphology in most published analyses, seven characters of the dentary bone and dentition were added (see Appendix).

The resulting data matrix of 73 characters coded for 26 taxa (see Appendix) was analysed under equally weighted maximum parsimony in TNT v. 1.1 (Goloboff, Farris & Nixon, 2008a, b), treating multi-state characters as unordered. A heuristic search of 500 random-addition sequences followed by tree bisection and reconnection branch swapping (with retention of ten trees per replicate) was performed. Zero-length branches were collapsed following rule 1 of Coddington & Scharff (1994). The node support was estimated using Bremer-support indices and by 1000 rounds of symmetric resampling, expressed as frequency difference (GC) values (Goloboff *et al.*, 2003).

The analysis yielded 24 most parsimonious trees (MPTs) of 186 steps (consistency index = 0.538; retention index = 0.751), the reduced strict consensus of which is shown in Figure 5. Sphenodontia (*sensu* Benton, 1985) was consistently recovered as a monophyletic group, as were also several groupings obtained in previous analyses, including 'derived sphenodontians' (Sphenodontidae *sensu* Reynoso, 1996, 1997), clevososaurs (*Clevosaurus* + *Brachyrhinodon*; Reynoso, 1996; Arantes, Soares & Schultz, 2009), saphesosaurs (*Sapheosaurus* + *Kallimodon*), Opisthodontia (*sensu* Apesteguía & Novas, 2003), eilenodontines (Reynoso, 1996; Apesteguía & Novas, 2003), and a clade formed by *Sphenovipera* and *Theretairus* (Reynoso, 2005).

Sphenodontidae Cope, 1869 is an early name created to include *Sphenodon* alone and later incorporated most fossil allies. However, Sphenodontidae results, under current knowledge, in a vast group and the use of a familiar name to include *Clevosaurus* and *Sphenodon* might be misleading. Hence, it is preferred herein to use the informal term 'derived sphenodontians' for this clade.





**Figure 5.** Reduced strict consensus (after removing *Pamizinsaurus*) of sphenodontian interrelationships from 24 most parsimonious trees of 186 steps showing the phylogenetic position of *Sphenocoondor gracilis* gen. et sp. nov. Bremer support and frequency differences (GC), calculated by symmetric resampling, are indicated above the nodes.

In all MPTs *Sphenocoondor* is placed within Sphenodontia (Fig. 5), a position supported by the presence of additional teeth at the rear of the jaw in the new taxon. Additionally, *Sphenocoondor* lies within a clade of sphenodontians that excludes *Diphydontosaurus* and *Planocephalosaurus* because of the presence of a fully acrodont dentition, a large mandibular foramen, a well-developed coronoid process of the dentary, and unribbed hatchling dentition.

Within Sphenodontia, *Sphenocoondor* is consistently depicted as external to the derived sphenodontians (including clevososaurs, *Sphenodon*, and eilenodontines) because of the absence of derived states regarding wear facets in marginal teeth as well as characters of the successional and additional dentition of the dentary.

All MPTs cluster *Sphenocoondor* in a clade with the Indian *Godavarisaurus* from the Jurassic Kota Formation. The monophyly of this Gondwanan clade is supported by two synapomorphies regarding the morphology of the dentary teeth, namely, the absence of ridges in posterior additionals (character 59 : 0) and the presence of an anterolingual groove in the posterior successional (character 71 : 1) (see Discussion). In addition, *Sphenocoondor* shares with *Godavarisaurus* the presence of successional markedly ribbed,

the posterior-most of which is relatively large and recurved posteriorly (Evans *et al.*, 2001: figs 13C, D, 14A–D), but the retention in basal forms of a large number of successional and, conversely, the reduction of them in derived forms, suggest that several of these features are likely to be plesiomorphic. The purported phylogenetic position of the other Kota sphenodontian, *Rebbanasaurus* (Evans *et al.*, 2001), is confirmed; it is placed in a more derived position than *Diphydontosaurus* and *Planocephalosaurus* and basal to all other sphenodontians.

In the strict consensus of the present analysis, the inter-relationships within recovered groupings of derived sphenodontians are poorly resolved, as in other analyses with somewhat similar taxon sampling (e.g. Reynoso, 2000, 2005). However, this is mainly because of the unstable position of *Pamizinsaurus*, which might be a consequence of the immature condition of the sole known specimen and its peculiar combination of character states (Reynoso, 1997). Therefore, *Pamizinsaurus* was excluded from the strict consensus (but not from the analysis), rendering a more resolved topology in the reduced strict consensus (Fig. 5).

In this analysis two forms represent clevososaurs, diagnosed by at least six synapomorphies, emerging

in a basal position within derived sphenodontians. They are followed in the branching pattern by *Palaeopleurosaurus* and the clustering of *Sapheosaurus* and *Kallimodon*, informally named as sapheosaurs, as in other analyses of sphenodontians (e.g. Apesteguía & Novas, 2003). As stated above, a clade formed by *Sphenovipera* and *Theretairus* is recovered; the purported monophyletic condition of Sphenodontinae (Reynoso & Clark, 1998) is not corroborated, but the support for the alternative is very weak. The affinities of *Homeosaurus* to other sphenodontians are still poorly understood, despite the analysis developed by Wu (1994); its nested position within eupropalinal sphenodontians (sphenodontines, eilenodontines, and allies) is in conflict with previous hypotheses in that it takes a more basal position within derived sphenodontians (e.g. Reynoso, 1996; Apesteguía & Novas, 2003). New data on *Homeosaurus*, or new interpretations of the material, are needed in order to clarify its phylogenetic relationships. Within eupropalinal sphenodontians, the formerly proposed monophyly of both Opisthodontia and Eilenodontinae (Apesteguía & Novas, 2003; Apesteguía, 2008) is corroborated and well supported (Fig. 5). Additionally, the Late Cretaceous *Kawasphenodon* appears as an opisthodontian as has been suggested (Apesteguía, 2005). In the reduced strict consensus of this analysis, sphenodontines lack resolution; however, the involved nodes collapsed because of the alternant positions of *Cynospheodon* within eupropalinal sphenodontians, including the sister-group relation with *Sphenodon* obtained in previous published analyses (e.g. Reynoso, 1996; Apesteguía & Novas, 2003).

Whatever the different positions of poorly understood or conflicting taxa within sphenodontians are, this analysis recovered essentially the same topology as previous studies, with *Diphydontosaurus* and *Planocephalosaurus* basal to the remainder sphenodontians, clevosaurus relatively basal within derived sphenodontians, and eupropalinal forms in a derived position, including *Sphenodon* and eilenodontines (e.g. Reynoso, 1996, 1997; Reynoso & Clark, 1998; Apesteguía & Novas, 2003). It is noteworthy that the inclusion of several fragmentary or poorly known taxa, such as *Theretairus*, *Sphenovipera*, *Kawasphenodon*, *Rebbannasaurus*, *Godavarisaurus*, and *Sphenococondor*, with a high amount of missing entries, does not necessarily interfere with the resolution of the optimal topologies as was previously suggested (Reynoso, 2005). Instead, the amount of conflict regarding character distribution amongst derived sphenodontians and homoplasy levels appear to be pivotal in the degree of internal resolution within the clade, supporting the overall inclusion of incomplete taxa in broad phylogenetic analyses (Kearney, 2002; Wiens, 2003, 2005).

## DISCUSSION

Based on the results of the phylogenetic analysis (Fig. 5), *Sphenococondor* is included in Sphenodontia and shares with other members the presence of acrodont teeth, a deep and wide Meckelian groove (and the related lack of ossified splenial bone), a long posterior process and a well-developed coronoid process of the dentary, and dental regionalization including successional, alternate hatchling, and additional teeth. *Sphenococondor* represents a key taxon for understanding the evolution of rhynchocephalians in southern continents, breaking a vast gap in the South American record that extended from the Upper Triassic to the Lower Cretaceous.

### ONTOGENETIC STAGE AND DENTITION DEVELOPMENT

*Sphenodon* is the sole rhynchocephalian for which reliable developmental data are available (e.g. Howes & Swinnerton, 1901; Rieppel, 1992) and, hence, it is almost invariably used as a model in assessing the ontogenetic stage of fossil forms (e.g. Evans & Sigogneau-Russell, 1997; Reynoso, 2003). However, it has been noted that *Sphenodon* is not representative of rhynchocephalians regarding skull and tooth morphology (Jones, 2008, 2009); furthermore, during its ontogeny, the skull of *Sphenodon* undergoes important changes that partially reflect differences between basal and derived taxa (Jones, 2008). Therefore, ontogenetic assessments derived from comparisons to *Sphenodon* must be considered with caution. Concerning fossil forms, information on ontogenetic variation is sparse and, with some exceptions (Fraser, 1988; Reynoso, 2003), insufficiently documented. Data on this issue provided by *Sphenococondor* are discussed below.

The presence of at least two well-developed anterior successional teeth, the second larger, the marked alternation in size of the 16 middle teeth (four worn anterior ones, six middle ones of intermediate size, and the six posterior ones, larger and relatively unworn), and the presence of three large posterior additionals of uniform size in *Sphenococondor*, suggest that it might represent a juvenile individual comparable to the T2 and T3 stages of *Sphenodon* as defined by Harrison (1901) and Robinson (1976). This corresponds to an individual of a few months after hatchling. Alternatively, if the posterior six larger teeth of the alternating series are considered anterior additionals that retained a hatchling morphology (Apesteguía, 2008), then the total count of additional teeth rises to nine, and the dentition pattern more closely resembles that of a *Sphenodon* T4 stage or even a young adult. The size range of *Sphenococondor* is not known; however, the dentary of *Sphenococondor*

(c. 24 mm) matches well with that of *Sphenodon* T3–T4 juvenile stages (head length of 25–35 mm).

Despite the alleged immaturity of the *Sphenococondor* holotype, its dentary bears all the tooth types present in young adults of most sphenodontians including *Sphenodon* (Harrison, 1901; Robinson, 1976). The complete dentition pattern from front to back includes successional-, alternate hatchling-, and additional teeth. These constitute a valuable data set and allow meaningful comparisons to other sphenodontian taxa, adding value to the taxonomical entity of *Sphenococondor*. It is noteworthy that a T2 or T3 stage of *Sphenodon* does not differ markedly from a young adult individual in the sort and amount of information that they offer (Harrison, 1901; Reynoso, 2003).

In most sphenodontian taxa, the additional teeth are the major components of the adult dentition, or even the only ones as in clevosaurus or eilenodontines (Fraser, 1988; Apesteguía & Novas, 2003), although basal taxa appear to preserve successional and hatchling teeth during adulthood together with a relatively lower number of morphologically simple additional teeth (Fraser, 1982, 1986; Whiteside, 1986; Evans *et al.*, 2001). *Sphenococondor* fits well the latter pattern of dentition and thus, its apparent immature condition in comparison to *Sphenodon* might be interpreted as a sign of primitiveness rather than youth; unfortunately, ontogenetic data on *Sphenococondor* to resolve this issue are lacking at present.

#### SUCCESSIONALS

The presence of ‘caniniform’ successional teeth in sphenodontians has been considered of great systematic value by some authors (Gauthier *et al.*, 1988; Reynoso, 1996, 2003, 2005). Fully grown adults of *Sphenodon* apparently retain a single successional tooth (‘caniniform’) in the dentary, but adults of basal sphenodontians, such as *Diphydontosaurus*, *Planocephalosaurus*, and *Godavarisaurus*, show at least four or five successional teeth in the anterior portion of the jaw (Fraser, 1986; Whiteside, 1986; Evans *et al.*, 2001). It is noteworthy that immature individuals of several fossil sphenodontians appear to have a higher count of successional teeth than fully grown adults; for instance, juveniles of *Rebbanasaurus* bear up to five successional teeth, whereas adult specimens have only two or three (Evans *et al.*, 2001). These ontogenetic changes are more striking in *Clevosaurus*, in which immature individuals show at least three uniform-sized successional teeth that in the adult are either absent or completely obscured by secondary bone (Fraser, 1988). In addition, the successional series usually exhibits some degree of heterodonty, in which one or two posterior successional teeth are

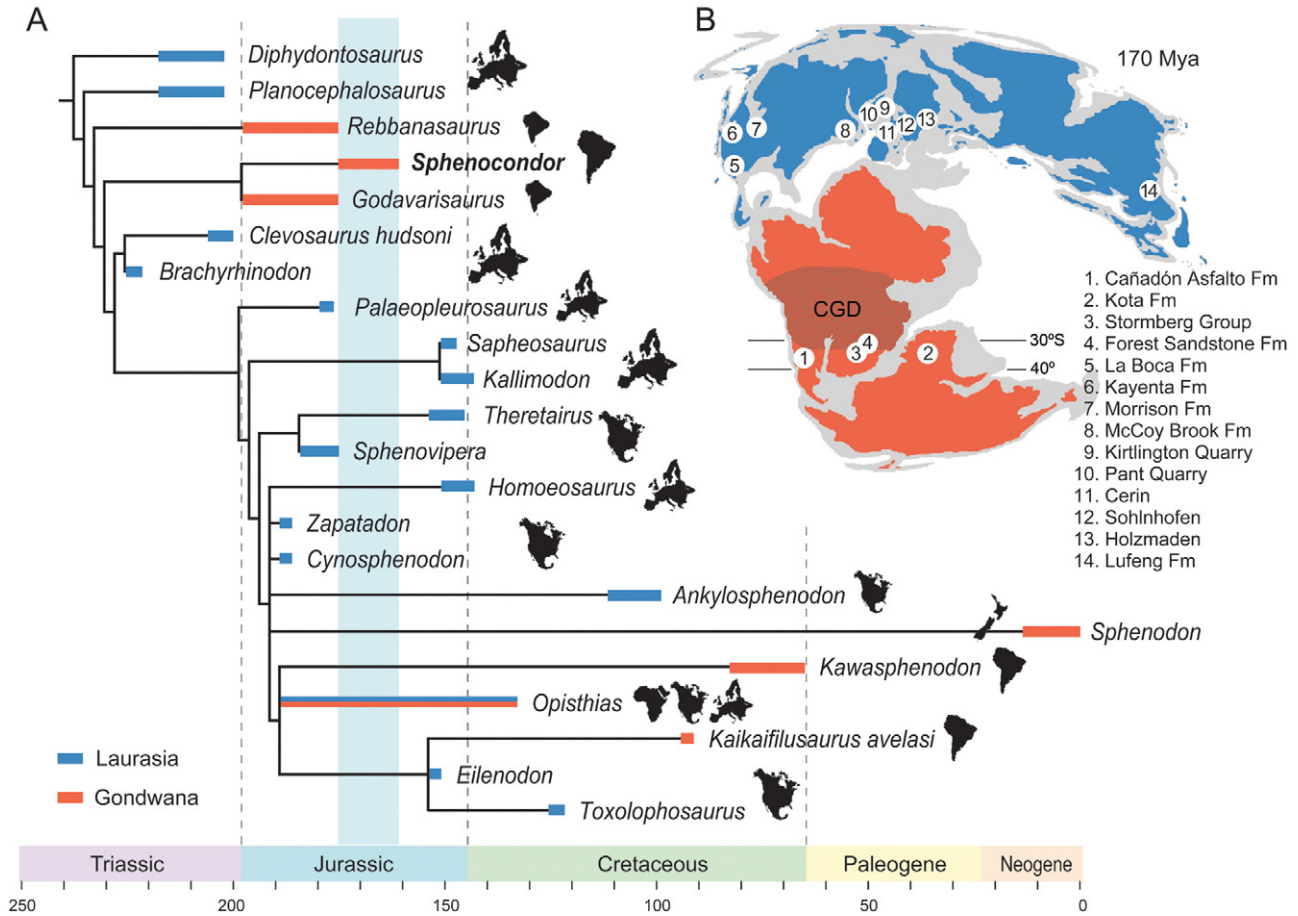
frequently larger than the other teeth (Evans, 1992; Evans *et al.*, 2001; Reynoso, 2003, 2005). The two posterior successional teeth of *Sphenococondor* closely match those of immature *Godavarisaurus* in their peculiar morphology as well as in relative size (Evans *et al.*, 2001); in view of the purported phylogenetic sister-group relation between *Sphenococondor* and *Godavarisaurus*, it is possible that *Sphenococondor* might have had up to three other successional teeth further anteriorly.

In some taxa successional teeth hypertrophy and develop into ‘caniniforms’ as in *Sphenodon* (e.g. Robinson, 1976; Reynoso, 2005). The presence of successional teeth in adult sphenodontians appears to be a plesiomorphic condition within the group and is not necessarily linked to the development of ‘caniniforms’ (Whiteside, 1986; Evans *et al.*, 2001). Besides, it has been acknowledged that tooth hypertrophy is variable within species and is scattered amongst lizard groups (Borsuk-Bialynicka, 1996). In consideration of the foregoing it is evident that new data and further analyses are needed to clarify some aspects of the evolution of successional dentition in sphenodontians; chief amongst them is the homology of sphenodontian ‘caniniforms’ and its systematic value.

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The oldest rhynchocephalians are Late Triassic, including Euramerican basal forms such as *Diphydontosaurus* (Whiteside, 1986), *Planocephalosaurus* (Fraser, 1982), *Paleollanosaurus* (Heckert, 2004), and *Whitakersaurus* (Heckert *et al.*, 2008), as well as clevosaurus and related forms (e.g. *Brachyrhinodon*, *Polysphenodon*) also from Europe (e.g. Fraser, 1988; Fraser & Benton, 1989; Evans & Kermack, 1994) and North America (Fraser, 1993; Heckert, 2004). Accordingly, Triassic Gondwanan rhynchocephalians only include clevosaurus, with records from Brazil (e.g. Ferigolo, 1999; Bonaparte & Sues, 2006) and India (Evans & Jones, 2010). Except for the remains of the controversial *Sigmala* and *Pelecymala* (Fraser, 1986), the record shows only two types of rhynchocephalians: basal taxa and clevosaurus or closely related forms, indicating an early split of the main sphenodontian lineages.

The Jurassic rhynchocephalian record shows, in addition to clevosaurus and basal forms, a wealth of diversified and specialized sphenodontians, the vast majority of findings being from Laurasian landmasses, with only a few records from Gondwana. Actually, our understanding of the evolution of the Jurassic Rhynchocephalia is based almost exclusively on their northern record. Early Jurassic findings from Laurasia include basal forms from the UK (e.g. *Gephyrosaurus*; Evans, 1980) and clevosaurus from the UK (e.g. Evans & Kermack, 1994; Säilä, 2005), North



**Figure 6.** A, time-tree of rhynchocephalians with the latest possible branching points for lineages, based on the reduced strict consensus of Figure 5. The Middle Jurassic is depicted by a shaded bar. B, palaeobiogeographical distribution of Jurassic rhynchocephalians. Palaeogeographical reconstruction modified from Blakey (2008), using the timescale of Gradstein *et al.* (2004). Abbreviation: CGD, Central Gondwanan Desert.

America (e.g. Reynoso, 1993; Sues *et al.*, 1994), and China (Wu, 1994; Jones, 2006). Additionally, the diverse sphenodontians from the lower member of the La Boca Formation of Mexico (now considered to be Early Jurassic; Clark *et al.*, 1994; Reynoso, 1996, 2005; Rubio-Cisneros & Lawton, 2011) and the highly derived marine *Palaeopleurosaurus* from Germany (Carroll, 1985) show that rhynchocephalians were well diversified by then. Conversely, the Early Jurassic records from southern landmasses are restricted to the basal sphenodontians from India (*Rebbanasaurus* and *Godavarisaurus*; Evans *et al.*, 2001) and putative clevososaurs from South Africa (Sues & Reisz, 1995) and Zimbabwe (Gow & Raath, 1977).

The Middle Jurassic record is extremely scarce worldwide so far, consisting of a few fragmentary fossils of uncertain taxonomic affinities from the UK (e.g. Evans, 1992). The discovery of *Sphenocondor*, the first Gondwanan Middle Jurassic rhynchocephalian, and the resulting phylogenetic analysis suggests an

early, or basal, Triassic diversification including plesiomorphic forms and clevososaurs, whose descendants would later reach a Pangaeian distribution. After this initial diversification, our results highlight the occurrence of a second sphenodontian radiation during the Early Jurassic, in which two distinct, geographically separated lineages (i.e. Euramerica and South Gondwana) diversified and replaced most of the early forms (e.g. clevososaurs) by the Middle Jurassic (Fig. 6). It is noteworthy that the Jurassic Euramerican and South Gondwanan forms are mostly restricted to Dry Subtropical (winter wet) belts (i.e. the Central North American–Northern Tethys, in Laurasia, and the 30° to 40° South Gondwanan strip; Fig. 6B), suggesting palaeoclimatic constraints in the geographical distribution of Early–Middle Jurassic sphenodontians. Under this scenario, the Central Gondwanan Desert arose as an extensive barrier that isolated southern Gondwana from the equatorial region and Laurasia in the Jurassic (Fig. 6B).

The recognition of a probably endemic Southern Gondwanan clade (i.e. *Sphenocondor* + *Godavarisaurus*) that originated during the Early Jurassic and evolved isolated during the Middle Jurassic from the main radiation of Sphenodontia mirrors the pattern recovered for other tetrapod groups such as Eusauropoda (e.g. Remes *et al.*, 2009). Eusauropod dinosaurs from the Cañadón Asfalto (Patagonia), Kota (India), Elliot and Clarens (Zimbabwe), Tendaguru (Tanzania), and Hanson (Antarctica) formations depict a panorama similar to that of rhychocephalians, in which Early Jurassic Pangaeian distributions were replaced by Middle Jurassic partially endemic forms. The hypothesis of increased endemism in response to the initial breakup of Pangaea, formerly furnished by data provided by Jurassic archosaurs (e.g. Bonaparte, 1986), gains support from the new evidence offered herein. However, as pointed out previously (Rauhut & López-Arbarello, 2008), this scenario is hard to test when it is largely based on findings from the Northern Hemisphere. The information provided herein by rhychocephalians helps us to have a glimpse at the evolutionary path that this peculiar group of lepidosaurs underwent.

## CONCLUSIONS

*Sphenocondor* represents the first rhychocephalian for the Jurassic of South America and one of the few Middle Jurassic records of the group worldwide. The new taxon exhibits some uncommon features in the dentary, including an adductor fossa that is centred under the coronoid process. Additionally, the dentition shows some peculiar traits such as a basally constricted hatchling dentition organized in three different groups according to size, as well as the presence of two strongly recurved and profusely striated successional teeth bearing a grooved anterior flange. These successional teeth clearly differ from those of *Theretairus* and *Sphenovipera* in the lack of interdental space, amongst other features.

The morphological evidence provided by *Sphenocondor* allows us to discuss some aspects of the evolution of successional dentition in rhychocephalians. The main results indicate that within the successional series typically there exists a size and shape heterodonty from the anterior to posterior teeth. Additionally, the persistence of several successional teeth in adult sphenodontians emerges as a plesiomorphic feature within the group, which might not be connected to the development of 'caniniforms'.

The phylogenetic analysis places *Sphenocondor* as a relatively basal form within Sphenodontia, clustered with the Indian *Godavarisaurus* from the Jurassic Kota Formation. This probably endemic Southern Gondwanan clade, as also expressed by other tetrapod

groups (e.g. Eusauropoda), gives support to the hypothesis of increased endemism in response to the initial breakup of Pangaea.

A further explanation for this observed pattern arises from the restriction of the Jurassic Euramerican and South Gondwanan forms to the Dry Subtropical (winter wet) climatic belts, both separated by the extensive Central Gondwanan Desert. The latter might have constituted an effective barrier for the dispersal of some groups of terrestrial organisms.

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## APPENDIX

## CHARACTER LIST

Description of 73 characters used in the phylogenetic analyses. Characters were mainly taken from the literature (source indicated in parentheses after each character; see below), although some of them were modified (denoted with an asterisk). In addition, seven new characters regarding dentary and tooth morphology were added. Multistate characters were treated as unordered. Abbreviations: AN03, Apesteguiá & Novas (2003); B85, Benton (1985); E88, Evans (1988); FB89, Fraser & Benton (1989); G88, Gauthier *et al.* (1988); R96, Reynoso (1996); R97, Reynoso (1997); RC98, Reynoso & Clark (1998); S94, Sues *et al.* (1994); W94, Wu (1994).



1. Antorbital region, length relative to skull length: one third or more (0); between one quarter and one third (1); one quarter or less (2). (S94, W94, R96, AN03)
2. Orbit, length relative to skull length: one third or greater (0); less than one third (1). (RC98, AN03)
3. Supratemporal fenestra, length relative to orbit length: less than 75% (0); 75% or greater (1). (S94, AN03)
4. Supratemporal fenestra, length relative to skull length: one quarter or less (0); more than one quarter (1). (W94, R96, AN03)
5. Lower temporal fenestra, length relative to skull length: one quarter or less (0); more than one quarter (1). (W94, R96, AN03)
6. Maxilla, premaxillary process: elongate (0); reduced (1). (S94, W94, R96, AN03)
7. Maxilla, participation in margin of external naris: entering into margin (0); excluded from margin by posterodorsal process of premaxilla (1). (S94, R97, AN03)
8. Maxilla, shape of posterior end: tapering posteriorly or very narrow (0); dorsoventrally broad (1). (W94, R96, AN03)
9. Lacrimal: present (0); absent (1). (S94, W94, R96, AN03)
10. Jugal, shape of dorsal process: broad and short (0); narrow and elongate (1). (W94, R96, AN03)
11. Prefrontal and postfrontal, profuse sculpture on bone surface: absent (0); present (1). (AN03)
12. Prefrontal-jugal contact: absent (0); present (1). (S94, R97, AN03)
13. Postorbital, marked dorsal ridge and deep ventrolateral concavity: absent (0); present (1). (AN03)
14. Frontals, relation: separated (0); fused (1). (S94, W94, R96, AN03)
15. Parietals, relation: separated (0); fused (1). (S94, W94, R96, AN03)
16. Parietal, width between supratemporal passages relative to interorbital width: broader (0); narrower (1). (S94, W94, R96, AN03)
17. Parietal crest: absent (0); present (1). (S94, W94, R96, AN03)
18. Parietal, shape of posterior edge: greatly incurved inward (0); slightly incurved inward (1); convex (2). (W94, R96, AN03)
19. Parietal foramen, position relative to anterior border of supratemporal fenestra: posterior (0); at the same level or anterior (1). (S94, W94, R96, AN03)
20. Lower temporal bar, position: aligned with the maxillary tooth row (0); bowed away beyond the limit of the abductor chamber (1). (S94, W94, R96, AN03)
21. Lower temporal bar, posteroventral process of jugal\*: absent (0); poorly to moderately developed, less than half the length of the lower temporal fenestra (1); well developed, half the length of the lower temporal fenestra or more (2). (S94, W94, R96, AN03)
22. Palatine, shape of posterior end: tapers posteriorly (0); widens posteriorly (1). (S94, W94, R96, AN03)
23. Pterygoids, anterior contact between bones: small or absent (0); broad (1). (R97, AN03)
24. Pterygoids, posterior opening of the interpterygoid vacuity between posteromedial processes: widely open (0); moderately open, as wide as the vacuity (1); almost closed by the posteromedial processes (2). (R97, AN03)
25. Pterygoid, central region between three rami: short (0); elongate (1). (S94, W94, R96, AN03)
26. Pterygoid, participation in margin of suborbital fenestra: form part of the margin (0); excluded from margin (1). (S94, W94, R96, AN03)
27. Suborbital fenestra, enclosing: by more than two bones (0); only by ectopterygoid and palatine (1). (S94, R97, AN03)
28. Quadrate-quadratojugal foramen, relative size: small (0); large (1). (RC98, AN03)
29. Quadrate-quadratojugal foramen, location: between the quadrate and the quadratojugal (0); entirely within the quadrate (1). (RC98, AN03)
30. Quadrate-quadratojugal emargination, shape: pronounced (0); reduced (1). (E88, S94, W94, RC98, AN03)
31. Supratemporal, as a discrete bone: present (0); absent (1). (S94, R97, AN03)
32. Inferred jaw motion: orthal (0); propalinal (1). (S94, W94, R96, AN03)
33. Degree of propalinality, measured either as palatal tooth row extension or length over which palatines keep parallel to the maxillae: small palatal row, parallel line restricted to the anterior region (0); enlarged, palatines accompanying maxilla for half its own length (1); palatines accompanying maxilla for its complete length, 'eupropalinality' (2). (S94, W94, R96, AN03)
34. Mandibular symphysis, mentonian process\*: reduced or absent (0); well developed and pointed (1); well developed and rounded (2). (AN03)
35. Mandibular symphysis, shape\*: almost circular, height/length relation near one (0); oval, height/length clearly greater than one (1). (B85, R96, AN03)
36. Mandibular symphysis, angle between anterior margin and longitudinal axis of the mandible in lateral view\*: < 120°, symphysis nearly vertical, typically devoid of ventral projections (0); ≥ 120°, symphysis anterodorsally projected (1). (AN03)
37. Mandibular symphysis, symphyseal spur\*: reduced or absent (0); well developed, anterodorsally projected (1); moderately developed (2). (AN03)

38. Mandibular foramen, relative size: small (0); large (1). (B85, R96, AN03)
39. Glenoid cavity, shape: smooth surface, lacking an anteroposterior central ridge (0); elongate and asymmetrical surface, with a strong anteroposterior central ridge (1); symmetrical facet with a strong anteroposterior central ridge (2). (AN03)
40. Coronoid process, height relative to that of the jaw at the level of the anterior end of the coronoid process: low, weak, less than half the jaw (0); moderately high, around half jaw height (1); very high, nearly as high as the jaw (2). (S94, W94, R96, AN03)
41. Retroarticular process, shape: pronounced (0); reduced, caudally projected (1); reduced, dorsally curved (2). (S94, W94, R96, AN03)
42. Dentary, posterior process, relative length: short, not reaching glenoid level (0); elongate, reaching glenoid level (1); elongate, reaching the end of glenoid level (2). (S94, R97, AN03)
43. Marginal dental implantation, type: pleurodont (0); degree of posterior acrodonty (1); fully acrodont (2). (S94, W94, R96, AN03)
44. Tooth replacement, type: alternate (0); addition at back of jaw (1). (B85, R96, AN03)
45. Dentary regionalization with small juvenile teeth (hatchling) in the anterior region of maxilla and dentary: absent, only pleurodont teeth (0); present, with hatchling pleurodont teeth (1); present, with hatchling, successional and additional acrodont teeth (2); absent both in juveniles and adults, only additional acrodont teeth (3). (B85, R96, AN03)
46. Dentary, posterior successional, number in mature individuals\*: zero (0); one (1); two or more (2). (G88, R96, AN03)
47. Marginal teeth, lateral wear facets on dentary and/or medial wear facets on maxilla: absent or smooth (0); present, conspicuous (1). (S94, W94, R96, AN03)
48. Marginal teeth, shape of cross-section of posterior teeth: nearly circular (0); squared (1); rectangular, wider than long (2). (FB89, R96, AN03)
49. Premaxillary teeth, number in mature individuals: more than seven (0); seven to four (1); three or fewer (2). (S94, W94, R96, AN03)
50. Premaxillary teeth, general organization in adults: present as discrete teeth (0); merged into a chisel-like structure (1). (S94, W94, R96, AN03)
51. Maxillary teeth, posteromedial flanges on posterior teeth\*: absent or inconspicuous (0); present as small flanges on at least one tooth (1); present as extensive flanges on most teeth (2). (S94, W94, R96, AN03)
52. Maxillary teeth, anterolateral flange on posterior teeth: absent (0); present (1). (AN03)
53. Palatine teeth, number of tooth rows: two or more (0); a single row plus one isolated tooth (1); a single lateral row (2). (S94, W94, R96, AN03)
54. Palatine teeth, flanges: completely absent (0); present at least on a few teeth (1). (FB89, R96, AN03)
55. Palatine teeth, hypertrophied tooth on anterior region of the palatine bone (stabbing palatine): absent (0); present (1). (AN03)
56. Pterygoid teeth, number of tooth rows: three or more (0); two (1); one or none (2). (S94, W94, R96, AN03)
57. Mandibular teeth, anterolateral flanges: absent (0); present, at least in one tooth (1). (S94, W94, R96, AN03)
58. Mandibular teeth, anteromedial flanges: absent (0); present (1). (AN03)
59. Mandibular teeth, additional, dental ridges in adults: absent (0); present (1). (AN03)
60. Second sacral vertebra, posterior process: present, small (0); present, prominent (1); absent (2). (G88, R96, AN03)
61. Ischium, process on posterior border\*: absent (0); present as small tubercle (1); present as prominent process (2). (E88, FB89, R96, AN03)
62. Humerus, length relative to length of presacral column:  $\leq 0.2$  (0);  $> 0.2$  (1). (FB89, R96, AN03)
63. Tibia, length relative to length of presacral column:  $\leq 0.25$  (0);  $> 0.25$  (1). (FB89, R96, AN03)
64. Femur, length relative to length of presacral column:  $< 0.3$  (0);  $\geq 0.3$  (1). (FB89, R96, AN03)
65. Radius, length relative to length of presacral column:  $< 0.15$  (0);  $\geq 0.15$  (1). (FB89, R96, AN03)
66. Skull, length (as an estimation of the body size): small,  $< 3$  cm (0); medium size, between 3–10 cm (1); large,  $> 10$  cm (2). (AN03)
67. Dentary, proportions (length/height ratio, L/H): gracile, long and low,  $L/H < 0.18$  (0); average,  $L/H$  between 0.18–0.28, robust, short and high,  $L/H > 0.28$  (2).
68. Dentary, successional teeth, maximum concurrent number during ontogeny: six or more (0); three to five (1); two or fewer (2).
69. Dentary, anterior successional teeth (not ‘caniniform’), number in the adult: two or more clearly discrete teeth (0); one or two poorly distinct (1); none or indistinct (2).
70. Dentary, successional teeth, striation: present (0); absent (1).
71. Dentary, posterior successional teeth, lingual groove: absent (0); present (1).
72. Dentary, hatchling teeth, striation: absent (0); present (1).
73. Dentary, successional ‘caniniform’ teeth, shape of basal cross section: nearly circular (0); clearly oval, labiolingually compressed teeth (1).

## DATA MATRIX

Data matrix of 73 characters scored for 26 taxa used in the phylogenetic analysis. Symbols: ?, missing data or not applicable; A = 0/1; B = 0/2; C = 1/2; D = 1/3

	5	1 0	1 5	2 0	2 5	3 0	3 5	4 0
<i>Ankylosphenodon</i>	??1?	????1	?????	?????	?????	?????	?1?31	1?1?1
<i>Brachyrhinodon</i>	21111	10111	00?00	00001	20120	?????	?0?31	101?1
<i>Clevosaurus hudsoni</i>	21111	11111	01000	10001	20210	11000	00131	00111
<i>Cynosphenodon</i>	?????	?????	?????	?????	?????	?????	?1?11	12??1
<i>Diphydontosaurus</i>	10000	00010	00010	00001	20100	00000	10100	00100
<i>Eilenodon</i>	?????	?????	1????	?????	?????	?????	?1?21	1?120
<i>Gephyrosaurus</i>	00000	00000	00011	00001	20000	00000	10100	?0000
<i>Godavarisaurus</i>	?????	?1???	?????	?????	?????	?????	??31	0B???
<i>Homoeosaurus</i>	0A000	00110	00?00	00A11	?1200	10???	?1?11	101?1
<i>Kaikaiifilusaurus</i>	01100	11111	11100	11111	01220	10000	11221	11120
<i>Kallimodon</i>	01110	?011?	00?00	11111	11200	10???	10111	021?1
<i>Kawasphenodon</i>	?????	?????	?????	?????	?????	?????	?1???	?????
<i>Opisthias</i>	?1???	11111	?1100	11?11	?1220	?????	?1221	111?0
<i>Palaeopleurosaurus</i>	01110	00010	00101	11200	00211	00110	10011	1?1?1
<i>Pamizinsaurus</i>	?????	?1???	0???	?????	??21	1???	001D1	1?1?1
<i>Planocephalosaurus</i>	00000	00010	00011	00001	20200	00010	10131	00001
<i>Pristidactylus</i>	11111	00001	10011	0001?	00010	000?0	00?00	?0000
<i>Rebbanasaurus</i>	?????	??01?	?0???	?????	?????	?????	?0?21	02???
<i>Sapheosaurus</i>	11?10	0?1?0	???00	11111	01100	1????	???01	021?1
<i>Sphenocondor</i>	?????	?????	?????	?????	?????	?????	?????	1C1?1
<i>Sphenodon</i>	11111	00111	00100	11111	11221	10101	11231	12111
<i>Sphenovipera</i>	?????	?????	?????	?????	?????	?????	?1?11	0?1??
<i>Theretairus</i>	?????	?????	?????	?????	?????	?????	?1?11	0????
<i>Toxolophosaurus</i>	?????	?????	?????	?????	?????	?????	?1?21	111?0
<i>Youngina</i>	00000	00000	00000	00000	20000	00000	?0000	?0?00
<i>Zapatadon</i>	10?01	??01?	?1??1	?1?1?	10221	0?101	01?31	12??1

	4 5	5 0	5 5	6 0	6 5	7 0	7 3
<i>Ankylosphenodon</i>	1121?	012??	?????	?0??1	2?000	?121?	???
<i>Brachyrhinodon</i>	01212	01121	101??	1????	?0000	01???	???
<i>Clevosaurus hudsoni</i>	01212	01121	20110	11011	10000	1112?	?0?
<i>Cynosphenodon</i>	??212	11121	?0???	?100?	?????	?1121	001
<i>Diphydontosaurus</i>	01111	20010	00000	000?1	10000	00000	01?
<i>Eilenodon</i>	22213	0122?	21210	?111?	?????	?222?	?0?
<i>Gephyrosaurus</i>	01000	20000	0?000	000?0	?????	00001	0??
<i>Godavarisaurus</i>	??212	200C0	1?21?	?100?	?????	0A100	101
<i>Homoeosaurus</i>	11212	01A21	200??	21??1	21111	01???	???
<i>Kaikaiifilusaurus</i>	22213	01221	21210	31111	?????	1222?	?0?
<i>Kallimodon</i>	01212	01121	202??	21011	20000	1122?	???
<i>Kawasphenodon</i>	??212	?10??	?????	?110?	?????	?2???	???
<i>Opisthias</i>	11213	0102?	2?210	21111	?????	?122?	???
<i>Palaeopleurosaurus</i>	01212	01121	1?200	21??1	10000	0022?	???
<i>Pamizinsaurus</i>	1?212	0?A2?	1?2??	?1?1?	?????	012??	?1?
<i>Planocephalosaurus</i>	01212	?0A20	1?000	11011	10000	01C00	?1?
<i>Pristidactylus</i>	00000	20000	00???	200??	?????	?0001	0??
<i>Rebbanasaurus</i>	??212	20020	1?01?	?101?	?????	0A110	001
<i>Sapheosaurus</i>	0?2??	0??21	?0???	?????	20???	1122?	???
<i>Sphenocondor</i>	?1212	200??	?????	??0?	?????	00C?0	101
<i>Sphenodon</i>	11212	11A21	10211	21002	10000	0C221	000
<i>Sphenovipera</i>	?1212	211??	?????	?1???	?????	01C21	1??
<i>Theretairus</i>	??212	210??	?????	?1???	?????	?1221	0??
<i>Toxolophosaurus</i>	??213	012??	?????	?11??	?????	?222?	?0?
<i>Youngina</i>	00000	20000	0?000	000?0	00000	?0001	0??
<i>Zapatadon</i>	??212	0?A??	1?2??	2???	?????	?12??	???