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First Amphilestid from South America: A Molariform from the Jurassic Cañadón Asfalto Formation, Patagonia, Argentina

Leandro C. Gaetano · Guillermo W. Rougier

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Abstract We report here the first amphilestid triconodont from the Jurassic of South America. The specimen, a single isolated molariform, was found at the Queso Rallado locality from where a growing mammalian fauna is known (including a triconodontid, two australosphenidans, and an as yet undescribed allotherian). The specimen, interpreted as a left lower tooth, presents five mesiodistally aligned, fairly symmetrical cusps, and is recognized as the type of a new taxon, *Condorodon spanios*. The phylogenetic analysis recovers *Condorodon* as a member of the clade Amphilestheria, closely related to *Tendagurodon janenschii*, an amphilestid triconodont from the Late Jurassic of Tanzania. *Condorodon spanios* is only distantly related to *Argentocodon fariatorum*, the other triconodont known from Queso Rallado quarry. The phylogenetic position of *Condorodon spanios* points to the origin and diversification of amphilestherians during the Early Jurassic in a paleogeographical setting that allowed wide dispersion of these forms and

argues, at least from the mammalian evidence, against a highly provincialized Pangaea. Some differences are however established between the filial western/eastern Gondwanan masses and their respective faunas.

Keywords Amphilestid · Triconodont · Jurassic · South America

Introduction

Amphilestids represent a paraphyletic group of mammaliaforms with triconodont-like cheek teeth characterized by the plesiomorphic presence of five cusps arranged in line, or forming a broadly triangular crown dominated by a taller cusp **A/a** flanked by cusps **B/b** and **C/c** of subequal size, and the presence of a distal cusp **D/d** and a mesial cusp **E/e**, which are in turn subequal among themselves (Owen 1871; Simpson 1928, 1929). Amphilestids have been recovered as successive stem taxa to cladotherians by several authors (Ji et al. 1999; Rougier et al. 2001, 2007a, b; Montellano et al. 2008; Kusuhashi et al. 2009; Gao et al. 2010; Gaetano and Rougier 2011; Meng et al. 2011; but see Luo et al. 2002, 2007; Kielan-Jaworowska et al. 2004; Hu et al. 2005 for alternative views), a suggestion argued early on by Mills (1971) under a non-cladistic paradigm that has now gained more acceptance.

The parphyly of amphilestids is not surprising when considering that Simpson (1928) originally diagnosed this grouping on the basis of traits he considered to be plesiomorphic (i.e., symmetrical and submolariform premolariforms and more than four molariforms with cusps **b** and **c** relatively small when compared to cusp **a**). The amphilestid tooth morphology is therefore a generalized mammalian

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morphology, which by slight modifications can be considered as a bauplan for a wide range of basal mammaliaform morphologies, including triconodontids, symmetrodonts, and ultimately cladotherians (Rougier et al. 2007a).

Originally represented by *Amphilestes* Owen, 1859, and *Amphitherium* de Blainville, 1838, the number of known amphilestids has grown since Simpson's days to also include *Tendagurodon* Heinrich, 1998, *Triconolestes* Engelmann and Callison, 1998, *Hakusanodon* Rougier et al., 2007a, *Acinacodus* Lopatin et al., 2010, and *Juchilestes* Gao et al., 2010, in addition to the classical representatives (*Amphilestes*, *Aploconodon* Simpson, 1925b, *Comodon* Kretzoi and Kretzoi, 2000, and *Phascolotherium* Owen, 1838) from the Jurassic of England and USA, but to the exclusion of *Amphitherium*.

Additionally, Sigogneau-Russell (2003) described a number of isolated teeth from the Early Cretaceous of Morocco and regarded them, not without doubts, as amphilestids. This author left most of the specimens in open nomenclature except for a few that were assigned to the new genus and species *Kryptotherium polysphenos*.

A form probably related to amphilestids, *Liaotherium* Zhou et al., 1991, was described on the basis of a dentary bearing a damaged last molariform (said to be of “amphilestid” morphology based on field observations). The fragmentary nature of the specimen makes comparison of *Liaotherium* with other taxa problematic; however, it has been suggested that it morphologically resembles “symmetrodontans” such as *Zhangheotherium* Hu et al., 1997 (Kielan-Jaworowska et al., 2004).

Paikasigudodon yadagirii Prasad and Manhas, 1997, from the Early-Middle Jurassic Kota Formation of India, was originally described as a tinodontid and then reinterpreted as a morganucodontid closely related to *Megazostrodon* Crompton and Jenkins, 1968 (Prasad and Manhas 2002). Lately, this taxon was again included among amphilestids somewhat arbitrarily (Kielan-Jaworowska et al. 2004: 240).

Affinities of *Jeholodens* Ji et al., 1999, *Gobiconodon* Trofimov, 1978, and *Repenomamus* Li et al., 2000, with other triconodonts are still a controversial issue among specialists, having been variously allied with triconodontids (Luo et al. 2007; Meng et al. 2011) or with amphilestids (Rougier et al. 2001, 2007a, b; Meng et al. 2006; Montellano et al. 2008; Kusuhashi et al. 2009; Gaetano and Rougier 2011). Hence, forms considered to be closely related to these taxa (*Ferganodon* Martin and Averianov, 2007, *Hangjinia* Godefroit and Guo, 1999, *Huastecodon* Montellano et al., 2008, *Klamelia* Chow and Rich, 1984, *Meemanodon* Meng et al., 2005, and *Yanoconodon* Luo et al., 2007) but not always included in phylogenetic analyses are also problematic (Chow and Rich 1984; Godefroit and Guo 1999; Meng et al. 2005; Luo et al. 2007; Martin and Averianov 2007; Montellano et al. 2008). To avoid possible confusion and for ease of reference,

the term amphilestid will here exclude these taxa unless made explicit.

As presently known, amphilestids represent essentially a Northern Hemisphere radiation of basal forms of stem-cladotherians that flourished from the Middle Jurassic to the Late Cretaceous (Owen 1838, 1859, 1871; Simpson 1925b, 1928, 1929; Zhou et al. 1991; Engelmann and Callison 1998; Kretzoi and Kretzoi 2000; Rougier et al. 2007a; Gao et al. 2010; Lopatin et al. 2010; Hooker and Lawson 2011). So far, the only bona fide amphilestid from the Southern Hemisphere has been *Tendagurodon janenschii* from the Late Jurassic (Kimmeridgian-Tithonian) of Tanzania (Heinrich 1998). Here, we report on the first known representative of this informal group from South America and also one of the oldest amphilestids known to date.

Systematic Paleontology

Unnamed rank Mammaliaformes Rowe, 1988

Unnamed rank Amphilestheria Gaetano and Rougier, 2011

Condorodon, new genus

Type and Only Species—*Condorodon spanios*

Diagnosis—As for the species, by monotypy.

Condorodon spanios, new species

Etymology—*Condor*, after the village of Cerro Cónдор located close to the Queso Rallado quarry that yielded the specimen, *odon* from Greek (gen. odontos), meaning tooth; *spanios*, from Greek, scarce, rare.

Holotype—MPEF-PV 2365, isolated complete lower left molariform.

Institutional Abbreviations—MPEF, Museo Paleontológico Egidio Feruglio, Trelew, Chubut, Argentina.

Diagnosis—Amphilestid triconodont with a compressed lower molariform bearing five mesiodistally aligned cusps (a–e). Cusp **a** dominant, centered on the crown, and slightly recumbent. Cusp **b** smaller than **c**. Cusps **b** and **c** mesially and distally pointing, respectively. Cusps **d** and **e** relatively small. Cusp **e** not supported completely by the mesial root. Mesial interlocking structures absent. Enamel thicker lingually than labially. The following are the main differences with closely related forms: unlike *Tendagurodon*, *Condorodon* has larger cusp **b** and **c** relative to cusp **a**, higher cusp **c** when compared to **b**, better developed cusp **d**, broader and deeper notches between main cusps, more vertically oriented roots that are slender with respect to the crown length, and lacks cingula below cusps **b** and **e**; the absence of cusp **f** (a feature also common to *Juchilestes*, *Aploconodon*,

spalacotheriids, and zhangheotheriids) and the relative size of cusps **b** and **c** (shared with *Tendagurodon*) distinguishes *Condorodon* from other amphilestherians; *Condorodon* shares with *Argentoconodon* Rougier et al., 2007c, *Hakusanodon*, *Tendagurodon*, *Volaticotherium* Meng et al., 2006, spalacotheriids, and zhangheotheriids the lack of a mesial embayment indicative of an interlocking mechanism involving the fit of cusp **d** of the preceding tooth between mesial crests or cusps.

Locality and Horizon—Queso Rallado locality, 5.5 km northwest of the Cerro Cóndor village, Chubut Province, Argentina. The specimen was found by breaking assorted blocks of the fossiliferous level, corresponding to the lower member of the Cañadón Asfalto Formation (Rauhut et al. 2002; Rougier et al. 2007b, c; Gaetano and Rougier 2011). The age of the lowest part of the section has been reported to be late Early Jurassic (Cabaleri et al. 2010; Cuneo and Bowring 2010). The exact stratigraphic correlation of the outcrops at Queso Rallado with the dated strata of Cuneo and Bowring (2010) is not known precisely, but we believe that for all practical purposes the Toarcian age reported can be considered as the age of the fossiliferous level at Queso Rallado locality.

Description

The specimen (Fig. 1) is a complete isolated molariform almost symmetrical in lateral view and with five cusps (**a–e**) mesiodistally aligned. Determining the position of this tooth is not an easy task as there are not enough features to make the decision unambiguous. Wear facets suggest an upper right or lower left position for this element.

Upper molariforms of amphilestids are only known for *Juchilestes*, *Jeholodens*, and *Paikasigudodon*. In these genera, these teeth show slight triangulation of the main cusps with cusp **A** lingual to cusps **B** and **C** (Prasad and Manhas 1997, 2002; Ji et al. 1999; Gao et al. 2010). The same is true for the known upper molariforms of gobiconodontids and allies, which also present poorly compressed upper molariform crowns (Jenkins and Schaff 1988; Kielan-Jaworowska and Dashzeveg 1998; Rougier et al. 2001; Sigogneau-Russell 2003; Hu et al. 2005; Montellano et al. 2008). On the other hand, lower molariforms of amphilestids (with the exception of *Juchilestes* and *Kryptotherium*) and those of gobiconodontids, *Jeholodens*, and allies have the main cusps aligned mesiodistally with no or slight lingual displacement of cusps **b** and **c** with respect to cusp **a** (Owen 1838, 1859; Simpson 1925a, b; Chow and Rich 1984; Jenkins and Schaff 1988; Heinrich 1998; Kielan-Jaworowska and Dashzeveg 1998; Ji et al. 1999; Kretzoi and Kretzoi 2000; Rougier et al. 2001, 2007a; Hu et al. 2005; Meng et al. 2005; Martin and Averianov 2007, 2010; Luo et al. 2007; Lopatin et al. 2010). Hence, on the basis of

comparisons with known taxa, we choose to consider the type and only specimen of *Condorodon spanios* a lower left tooth given the mesiodistal alignment of the cusps and the labiolingual compression of the crown.

The tooth is cracked, but most of the fragments are not displaced. We regard the morphology as not deeply altered, with the main features of the crown and roots being still recognizable and retaining original associations. The crown is slightly longer than tall (length: 2.54 mm; height: 1.82 mm); the major cusps are rounded labially, while lingually they are slightly more flattened. There are no mesial structures, either a cusp **f** or a mesial groove, supporting the presence of a locking mechanism between molariforms. The main cusp (**a**) is centered on the crown between the roots and slightly distally oriented, with the distal margin shorter and steeper than the mesial one. A shallow notch is present on the distal cutting edge of cusp **a** at about 2/3 of its height. Cusp **a** is separated from the adjacent cusps **b** and **c** by wide valleys; the valley separating cusp **b** from cusp **a** is wider and extends more basally than the one between cusps **a** and **c**. Cusps **b** and **c** are smaller than cusp **a** and diverge from it, pointing mesially and distally, respectively. Cusp **b** is smaller than cusp **c**, reaching approximately 1/4 of cusp **a** height. This cusp (**b**) has a convex mesial margin and a shorter and straight distal margin. Cusp **c** is approximately half as high as cusp **a** and is almost symmetrical in lateral aspect, as both mesial and distal margins are slightly convex; the mesial one is shorter and steeper than the distal margin.

Two small accessory cusps, **d** and **e**, are present at the distal and mesial ends of the tooth, respectively. Cusp **d** develops in the interface between crown and root; it is more basal than the main cusps and points distally. Cusp **e** has been almost fully worn down and only the basalmost sector is preserved. It was not completely supported by the mesial root and seems to have been smaller and more basally located than cusp **d**.

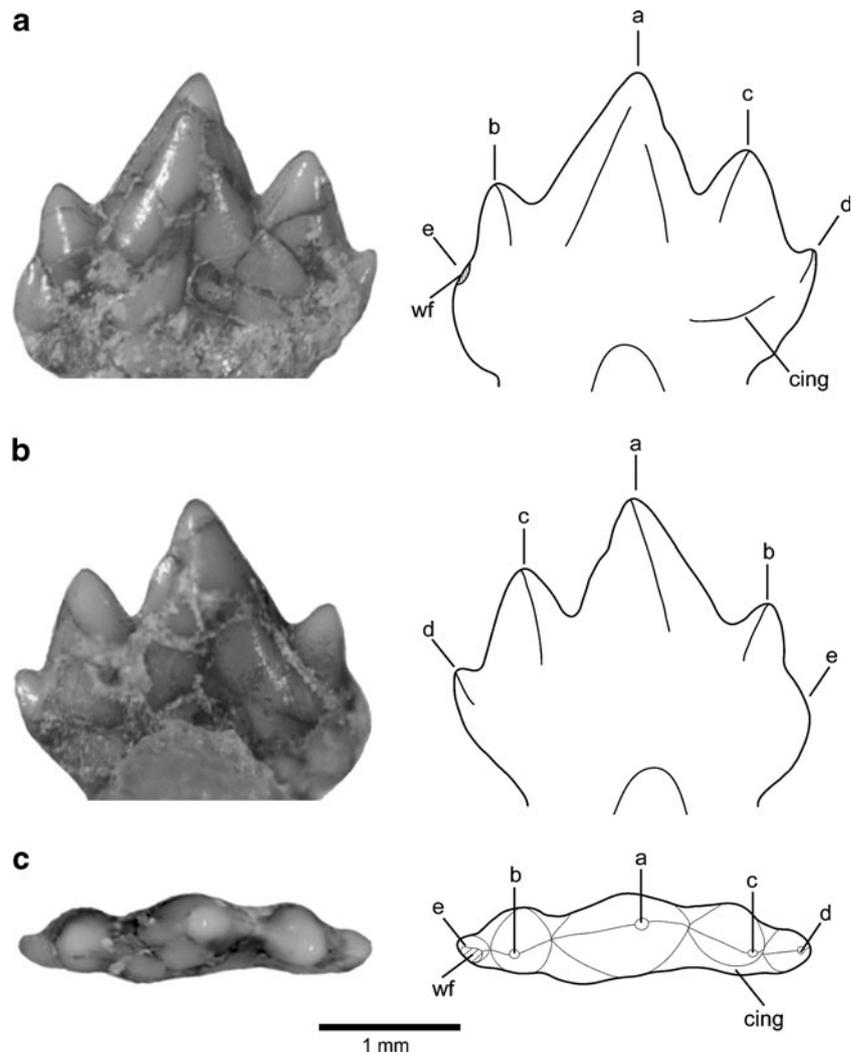
Wear is present on the mesial slopes of cusps **b** and **e** in labial view. Labially, a very weak cingulum is present below cusp **c**. However, a more detailed description as well as its distal extension is precluded due to the cracked surface and the presence of matrix remaining in this portion of the tooth. No lingual cingula are present. The enamel covering of the crown is thicker lingually than labially.

The roots are fully separated, subequal in diameter, and slightly divergent from each other. The roots seem to be as laterally compressed as the crown; however, this may, in part, be the result of postmortem deformation.

Phylogenetic Results

We employed the data matrix first compiled by Rougier et al. (2001, 2007a) to test the phylogenetic position of

Fig. 1 Photograph and outline drawing of the left lower molariform of *Condorodon spanios* (MPEF-PV 2365) in **a** labial, **b** lingual, and **c** occlusal views. **Abbreviations:** **a, b, c, d, e**, triconodont cusp nomenclature; **cing**, cingulum; **wf**, wear facet



Condorodon spanios including the ulterior modifications made by Gaetano and Rougier (2011) (see [Online Resources](#)), who in turn took into account other matrices published after 2007 that included triconodonts (Montellano et al. 2008; Kusuhashi et al. 2009; Lopatin et al. 2010; Gao et al. 2010). In most cases, single teeth are not included in phylogenetic analyses, but in our case it was unavoidable given the specimen available to us. Additionally, despite its fragmentary nature, we also included *Tendagurodon* in the analysis because of the morphological similarities with *Condorodon spanios* and its African provenance.

We conducted a heuristic search by means of the program TNT v1.1 (Goloboff et al. 2003, 2008) starting from 100 random addition sequences (RAS) and keeping up to 100 trees in memory followed by the application of the TBR algorithm. All characters were treated as unordered except for those that were originally considered additive by Rougier et al. (2007a). Our analysis yielded two equally parsimonious trees of 305 steps with an associated CI and RI of 0.367 and 0.687, respectively.

The strict consensus (Fig. 2) reflects the similarities between *Condorodon* and *Tendagurodon* showing them as sister taxa, a grouping supported by three unambiguous synapomorphies (characters 21, 29, and 83). These taxa share the presence of labiolingually compressed molariforms with crowns longer than tall bearing five cusps mesio-distally aligned (a–e), cusp c located at a higher level and taller than b, the valley separating cusp b from cusp a wider than the one setting apart cusps a and c, cusp d larger than cusp e, cusp e not supported by the mesial root, and the distal margin of the main cusp shallowly notched and shorter than the mesial one. Moreover, *Condorodon* and *Tendagurodon* lack an embayment on the mesial face of molariforms (a trait shared with *Argentoconodon*, *Hakusanodon*, *Volaticotherium*, spalacotheriids, and zhangheotheriids), indicating that cheek teeth interlocking did not occur through interlocking cusps or a tongue-in-groove mechanism, as it happens in other triconodontids. *Condorodon* differs from *Tendagurodon* in bearing larger cusps b and c when compared to cusp a, relatively higher cusp c than b,

Rougier 2011; Meng et al. 2011). This topology is driven mostly by the triangular occlusal arrangement of the molars and the concomitant cusp pattern, which groups together the trechnotheres (McKenna 1975; Prothero 1981).

Taxa traditionally included in the family Amphilestidae (Simpson 1925b, 1928), such as *Amphilestes*, *Aploconodon*, and *Phascalotherium*, are more closely related to “symmetrodontans” (i.e., to the therian lineage) than to other members of Amphilestheria with amphilestid-like teeth (*Acinacodus*, *Comodon*, *Juchilestes*, *Hakusanodon*, *Condorodon*, and *Tendagurodon*). *Amphilestes*, *Aploconodon*, and *Phascalotherium* form a monophyletic unit that also includes *Jeholodens*.

The present analysis supports triconodontid affinities for *Gobiconodon* and *Repenomamus* based on the reduced number of lower incisors (character 1), the high ratio between crown height to jaw height under the tallest molariform (character 16), the increasing height of the lower jaw horizontal ramus between the canine and last molariform (character 42), and the non-elevated mandibular condyle with respect to the alveolar margin (character 73). However, constrained searches excluding gobiconodontids from Eutriconodonta (sensu Gaetano and Rougier 2011) result in topologies that are only three steps longer and render *Gobiconodon* and *Repenomamus* as amphilestherians. This alternative hypothesis is supported by the occlusion of cusp A of the upper molariform posterior to cusp c and/or in the anterior face of cusp b (character 11, state 1), the arrangement of the main cusps of the upper molariforms in a broad obtuse triangle (character 63, state 1), the divergent orientation of the main axis of cusps b and c with respect to cusp a (character 90, state 0), and the development of cusps b and c on any of the slopes of cusp a (character 91, state 0). In light of the poor support for the position of gobiconodontids with either triconodontids or amphilestherians, we believe it is better to consider this issue as unresolved at present.

The clade Amphilestheria is recovered as a natural unit representing the sister taxa of eutriconodonts (sensu Gaetano and Rougier 2011). Hence, our results support a monophyletic clade of derived triconodonts (Eutriconodonta), and a step-wise paraphyletic series of triconodonts and symmetrodonts leading to Theria. The grouping of amphilestids and triconodontids recovered in other studies (Kermack et al. 1973; Luo et al. 2002, 2007; Meng et al. 2006) is not supported here, but it takes only an extra step to recover that topology, which is supported by a single synapomorphy (character 84).

An ambiguous synapomorphy of the Amphilestheria clade is the bulging of the labial slope of cusp a in lower molariforms (character 19) present in various degrees among the taxa included, also recognized in docodonts, *Kuehneotherium* Kermack et al., 1968, and *Woutersia* Sigogneau-Russell, 1983. Although several amphilestherians share this feature together with the slight labial

displacement of cusp a with respect to cusps b and c, only the most derived taxa (*Amphitherium*, *Tinodon*, spalacotheriids, and zhangheotheriids) and *Amphidon* are characterized by real triangulation of lower molariform cusps.

Biogeographical Analyses

Methodology

With the purpose of testing the biogeographic implications of the phylogenetic hypothesis obtained here, a Tree Reconciliation Analysis (TRA) was performed (see Page 1988, 1993, 1994a, b; Van Veller et al. 1999, 2000, 2001, 2002; Ebach 2001, Hunn and Upchurch 2001; Upchurch et al. 2002 for discussion of the method).

We pruned our data matrix excluding the taxon *Megazostrodon* to obtain a single most parsimonious fully resolved cladogram (Fig. 3) that could be analyzed with Component 2.0 (Page 1993) to search for optimal area cladograms.

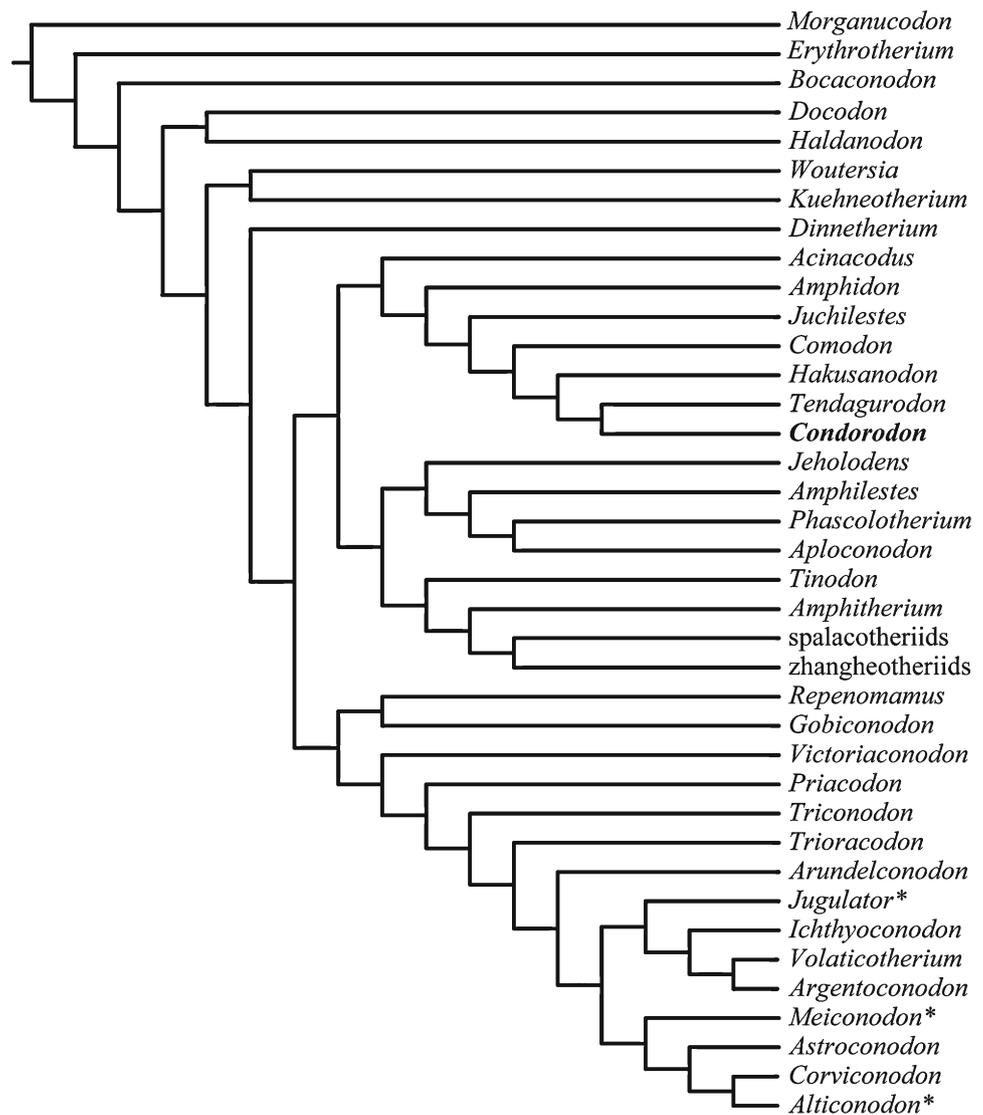
Those taxa of Late Triassic to Early Cretaceous age were included in the TRA (see Upchurch et al. 2002 for a description of the time slicing protocol; and Table 1 for the taxa considered). During this time frame, former blocks of Pangaea remained relatively close to each other suggesting that intercontinental dispersion was at least a possibility for terrestrial faunas. This seems unlikely after the Early Cretaceous, when wider ocean basins were already developed (Ziegler 1988; Royer and Sandwell 1989; Doré 1991; Kent 1991; Nürnberger and Müller 1991; Lawver et al. 1992; Lawver and Gahagan 1993; Golonka et al. 1994; Ricou 1996; Golonka and Bocharova 2000; Scotese 2008). Thus, Late Cretaceous taxa were excluded from the TRA.

Taxa were assigned to six broad geographical areas. These areas were in turn subdivided. Applying a time slicing protocol, we recognized Triassic to Middle Jurassic taxa from Late Jurassic to Early Cretaceous taxa (see Table 1). Only the earliest record of each taxon was taken into account for the purpose of the analysis.

Reconstruction of biogeographical events and randomization tests to check the statistical significance of the hypotheses recovered were achieved using the program TreeMap 1.0 (Page 1995).

TRA methodology has some drawbacks. One of the main problems is that there is no objective reason to expect taxa to be transmitted vertically in an area cladogram (Hovenkamp 1997, 2001; Arias et al. 2011). That is: taxa can theoretically radiate freely in any direction and only ecological or geographical barriers can prevent colonization of certain areas; hence, only when exact correspondence between the inhabited area and the dispersal barriers exists, the geographical distribution of a taxon will be coincident with

Fig. 3 Pruned cladogram used for biogeographical analyses. Taxa marked with an asterisk were excluded from the TRA



the area cladogram and reflect ancestral distributions (Arias et al. 2011). Another criticism by Arias et al. (2011) is the use by most workers of large areas with arbitrary limits that do not consider overlap or internally heterogeneous areas.

To solve these problems, Arias et al. (2011) proposed a method dubbed Spatial Analysis of Vicariance (SAV) implemented in VIP (Vicariance Inference Program), a freely available computer program (<http://www.zmuc.dk/public/phylogeny/vip>; Arias 2010). This procedure does not require predefined area information or hypothesized area cladograms; instead, the results of a SAV are based on the phylogenetic relationships of the taxa included and their observed distribution. The SAV focuses on the analysis of disjunct distributions to recognize possible dispersal barriers (Arias et al. 2011).

In order to explore the benefits of this new methodology, we also performed a Spatial Analysis of Vicariance (SAV) as a complement to the Tree Reconciliation Analysis (TRA).

Although VIP is capable of analyzing phylogenies that are not fully resolved, we preferred to exclude the same taxon that was pruned for the TRA as to make the methods comparable, but we included the Late Cretaceous taxa in the SAV (Fig. 3) given the arguments by Arias et al. (2011) (see below).

Arias et al. (2011) argue against reuniting different geographical localities into a single composite area. However, in the case of paleobiogeographical analysis like ours that include far from complete datasets, we think it is better to consider very close paleogeographical localities as a unit to avoid generating conflict during the analysis and proposing hypothetical dispersal barriers that have no correlate in the geological record, and thus seem unlikely (see Table 2 for a detail of taxa distribution considered for the SAV).

Despite the fact that VIP allows considering temporal disparities among taxa when reconstructing vicariance

Table 1 TRA input data

Area code	Areas included	Time frame	Taxa
AFR Tr-mJ	Africa	Triassic to Middle Jurassic	<i>Erythrotherium</i>
AFR IJ-eK	Africa	Late Jurassic to Early Cretaceous	<i>Ichthyoconodon, Tendagurodon</i>
ARG Tr-mJ	Argentina	Triassic to Middle Jurassic	<i>Argentoconodon, Condorodon</i>
ASIA IJ-eK	Asia (except China and Japan)	Late Jurassic to Early Cretaceous	<i>Acinacodus, Gobiconodon</i>
CH Tr-mJ	China and Japan	Triassic to Middle Jurassic	<i>Volaticotherium</i>
CH IJ-eK	China and Japan	Late Jurassic to Early Cretaceous	<i>Gobiconodon, Hakusanodon, Jeholodens, Juchilestes, Repenomamus, spalacotheriids, zhangheotheriids</i>
EUR Tr-mJ	Europe	Triassic to Middle Jurassic	<i>Amphilestes, Amphitherium, Kuehneotherium, Morganucodon, Phascolotherium, Woutersia</i>
EUR IJ-eK	Europe	Late Jurassic to Early Cretaceous	<i>Gobiconodon, Haldanodon, spalacotheriids, Triconodon</i>
NA Tr-mJ	North America	Triassic to Middle Jurassic	<i>Bocaconodon, Dinnetherium, Victoriaconodon</i>
NA IJ-eK	North America	Late Jurassic to Early Cretaceous	<i>Amphidon, Aploconodon, Arundelconodon, Astroconodon, Comodon, Corviconodon, Docodon, Gobiconodon, Priacodon, Tinodon, Trioracodon</i>

events, we chose to avoid weighting against time differences or to apply a time-slicing protocol in this analysis, as Arias et al. (2011) postulates that the important thing for the SAV is the hypothesized existence of a certain branch, not its length.

It is worth mentioning that both TRA and SAV are deeply affected by sampling problems such as poor representation of geographical areas and underrepresented time spans. In this sense, the scarcity of southern landmasses representatives of the mammaliaform groups analyzed makes the

presence of barriers to southern-northern dispersion difficult to evaluate.

A detailed account of the protocol for the TRA and SAV is provided in the Online Resources.

TRA Results

A single statistically significant optimal area cladogram was obtained for the Triassic to Early Cretaceous time slice

Table 2 SAV input data

Geographical area	Taxa
Canada	<i>Alticonodon</i>
East of USA (Maryland)	<i>Arundelconodon</i>
West of USA and Mexico	<i>Amphidon, Aploconodon, Astroconodon, Bocaconodon, Comodon, Corviconodon, Dinnetherium, Docodon, Gobiconodon, Jugulator, Morganucodon, Priacodon, spalacotheriids, Tinodon, Trioracodon, Victoriaconodon</i>
United Kingdom	<i>Morganucodon, Docodon, Kuehneotherium, Amphilestes, Phascolotherium, Tinodon, Amphitherium, spalacotheriids, Triconodon, Trioracodon</i>
Portugal and Spain	<i>Gobiconodon, Haldanodon, Priacodon, spalacotheriids, Tinodon</i>
Central Europe	<i>Kuehneotherium, Morganucodon, Woutersia</i>
Siberia	<i>Acinacodus, Gobiconodon</i>
Central Asia	<i>Gobiconodon, spalacotheriids</i>
North China	<i>Volaticotherium</i>
South of China and Japan	<i>Gobiconodon, Hakusanodon, Jeholodens, Juchilestes, Meiconodon, Morganucodon, Repenomamus, spalacotheriids, zhangheotheriids</i>
North of Africa (Morocco)	<i>Ichthyoconodon</i>
Central Africa (Tanzania)	<i>Tendagurodon</i>
South Africa	<i>Erythrotherium</i>
Argentina	<i>Argentoconodon, Condorodon</i>

(Fig. 4; Online Resources: Fig. 1). The biogeographical reconstruction shows that 36% of the events can be explained by sympatric splits (that means true sympatry or within area vicariance given the coarse geographical divisions considered here) and 64% of the biogeographical events can be explained by vicariance.

Our results do not show northern areas clustering together as the sister group of a southern areas clade, not even if only the Late Jurassic to Early Cretaceous time span is considered, suggesting that southern-northern dispersal of mammaliaforms during this temporal interval was not precluded.

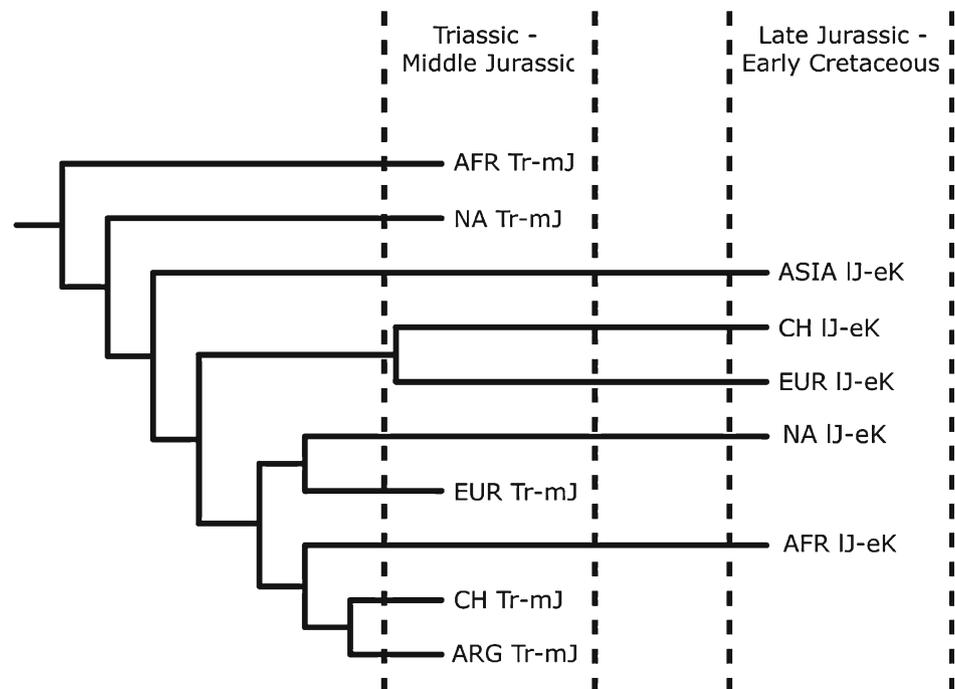
Late Triassic—Middle Jurassic Argentinean and Chinese localities are depicted as the sister group of Late Jurassic—Early Cretaceous African localities forming a monophyletic cluster that is in turn closely allied with a clade integrated by Late Triassic—Middle Jurassic European and Late Jurassic—Early Cretaceous North American geographical areas. This scheme of relationships envisages migration of the mammaliaforms analyzed through China and Argentina after the establishment of an impediment to dispersal between these geographical areas and Africa. Similarly, our analysis suggests that North America and Europe would have been isolated from Africa, Argentina, and China while dispersal among the latter three areas was still possible. These results are surprising considering past and current paleogeographical reconstructions (DuToit 1937; Ziegler 1988; Royer and Sandwell 1989; Doré 1991; Kent 1991; Nürnberger and Müller 1991; Hawkesworth et al. 1992; Lawver et al. 1992; Wilson 1992; Lawver and Gahagan 1993; Golonka et al. 1994; Ricou 1996; Golonka and Bocharova 2000; Scotese 2008) that show South America and

Africa in close contact and a distantly positioned Chinese block. These biogeographic hypotheses rest mostly on the recovered relationships of *Ichthyoconodon* Sigogneau-Russell, 1995, *Argentoconodon*, and *Volaticotherium*, which are relatively well supported in our analysis.

The sister-group relationship of Chinese, Japanese, and European areas during the Late Jurassic—Early Cretaceous indicates that dispersion among these areas was possible for the mammaliaforms considered here. This result contrasts with previous studies based on archosaur faunas suggesting that eastern Asia (China and Japan of our analysis) was geographically isolated from the rest of Laurasia during the Middle Jurassic to the Early Cretaceous (Milner and Norman 1984; Dong 1992; Russell 1993, 1995; Russell and Zheng 1993; Upchurch 1995; Barrett et al. 2002; Wilson and Upchurch 2010; see Barrett et al. 2002 and Wilson and Upchurch 2010 for a discussion of an alternative hypothesis). In the case of mammaliaforms, it is only during the Late Cretaceous that eastern Asiatic forms are recognized to represent an endemic fauna (Rougier et al. 1997). The possibility exists that the incongruence between hypotheses regarding the interval when eastern Asia was isolated from the rest of Laurasia is due to dispersal impediments influencing archosaurs and mammaliaforms differently. However, it cannot be ruled out that the incompleteness of the fossil record has led researchers to dissimilar conclusions.

The ghost lineages for African taxa (*Tendagurodon* and *Ichthyoconodon*) are clearly recognized as well as those of the representatives of the genera registered in Late Jurassic to Early Cretaceous strata of the Asiatic area (*Acinacodus* and *Gobiconodon*). Extensive ghost lineages are also identified

Fig. 4 TRA optimal area cladogram obtained



true for the forms found in the Late Jurassic to Early Cretaceous strata of the Asiatic, European, and North American areas: *Amphidon*, *Aploconodon*, *Arundelconodon* Cifelli et al., 1999, *Astroconodon* Patterson, 1951, *Comodon*, *Corviconodon* Cifelli et al., 1998, *Gobiconodon*, *Hakusanodon*, *Jeholodens*, *Juchilestes*, *Priacodon* Marsh, 1887, *Repenomamus*, *Tinodon*, *Triconodon* Owen, 1859, *Trioracodon* Simpson, 1928, spalacotheriids, and zhangheotheriids.

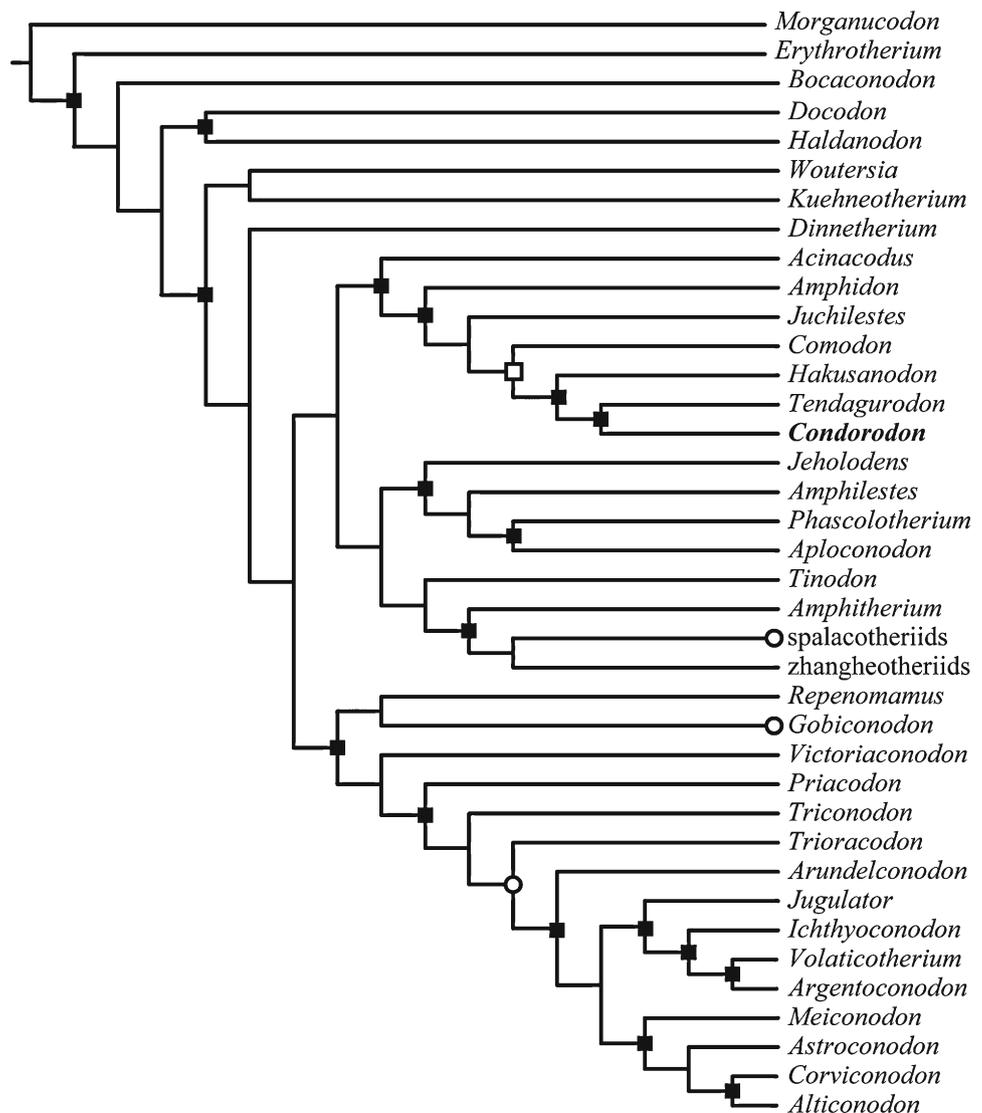
SAV Results

The SAV found two equally parsimonious reconstructions with a cost of 20.5. The consensus shows 19 vicariant nodes, a vicariant node whose distribution was removed, and two taxa and a node with their distribution removed (Fig. 5).

At the base of our phylogenetic hypothesis, a vicariant event is recognized at the node uniting *Erythrotherium* Crompton, 1964, and those taxa more closely related to derived triconodonts than to *Morganucodon* Kühne, 1949. The hypothetical barrier precluded southern-northern dispersal, isolating the African taxon *Erythrotherium* from more derived taxa. Our TRA results also suggest an impediment to dispersal between Late Triassic—Middle Jurassic African localities and all other geographical areas considered (including the Late Jurassic—Early Cretaceous African localities); however, TRA does not allow detecting the node on the taxon cladogram in which the dispersal barrier was effective.

Among amphilestherians and eutriconodonts, disjunct distributions are recognized in the majority of the nodes recovered (16 out of 25 were reconstructed as vicariant nodes; see Online Resources: Fig. 2), suggesting the presence of endemic genera reunited in a widely distributed clade. In these groups

Fig. 5 Consensus cladogram depicting SAV biogeographical reconstruction. Black squares represent nodes with allopatric distribution, white squares represent nodes with allopatric distribution and removed, and white circles represent node or taxa with removed distribution



most of the barriers to dispersal reconstructed had acted separating eastern-western areas.

Biogeographical reconstructions for the amphilestherian clade reuniting *Comodon*, *Hakusanodon*, *Tendagurodon*, and *Condorodon* support the absence of dispersal barriers between eastern Asia, Africa, and South America, in contrast to an isolated North American landmass. The same is true for the alticonodontine group comprising *Jugulator* Cifelli and Madsen, 1998, *Ichthyoconodon*, *Volaticotherium*, and *Argentoconodon*. Continental connections between Gondwana and North America during the Triassic and Jurassic (Ziegler 1988; Ricou 1996; Golonka and Bocharova 2000) point to dispersal of ancestral forms as a possible explanation for close relationship between Gondwanan (*Argentoconodon*, *Condorodon*, *Ichthyoconodon*, and *Tendagurodon*) and North American taxa (*Amphidon*, *Comodon*, and *Jugulator*).

Given the paleogeographic setting proposed for Jurassic and Early Cretaceous times (Ziegler 1988; Royer and Sandwell 1989; Doré 1991; Kent 1991; Nürnberger and Müller 1991; Lawver et al. 1992; Lawver and Gahagan 1993; Golonka et al. 1994; Ricou 1996; Golonka and Bocharova 2000), the results suggesting the absence of dispersal barriers between eastern Asia and Gondwanan landmasses (coincident with those of the TRA) are difficult to explain based on the evidence at hand, requiring ad hoc hypotheses such as extensive ghost lineages and wide distribution of ancestral forms. These alternatives are reasonable given the paucity of our knowledge of Gondwanan Jurassic mammals.

The TRA reconstruction of paleobiogeographical events indicates that the dispersal of forms through South America and the Chinese block was still possible after the isolation of these areas from Africa, while the SAV allows the possibility of barriers acting distinctly for different taxa. In this sense, among amphilestherians, a barrier to dispersion was first established between eastern Asia and Gondwanan landmasses (as evidenced by the disjunct distribution of *Hakusanodon* and the *Condorodon-Tendagurodon* clade) and then between South America and Africa. On the other hand and coincident with the TRA, a scenario where dispersal of African forms through Asiatic and South American areas was prevented before the establishment of a barrier between Asia and South America is suggested for derived eutriconodonts.

Finally, our results suggest that South America and Africa would not have been a homogeneous ecological unit as *Condorodon* and *Tendagurodon* on one side and *Argentoconodon* and *Ichthyoconodon* on the other show disjunct distributions.

Conclusions

Condorodon spanios is one of the earliest representatives of Amphilestheria and the oldest amphilestid known to date in the Southern Hemisphere (see Kielan-Jaworowska et al.

2004 for a review on most Mesozoic mammaliaforms and their distribution; Engelmann and Callison 1998; Heinrich 1998; Rougier et al. 2007a; Gao et al. 2010; Lopatin et al. 2010). *Paikasigudodon*, from the early Middle Jurassic Indian Kota Formation, is the only other Gondwanan taxon of similar age that was allied with amphilestids. However, more specimens of *Paikasigudodon* need to be recovered to sustain this assignation, which lacks, at present, enough support (Kielan-Jaworowska et al. 2004: 240).

The fragmentary nature of the only known specimen of *Condorodon* restricts comparisons with other taxa to molariform morphology only. Nevertheless, the results of our cladistic analysis show that *Condorodon spanios* is unambiguously allied with *Tendagurodon janenschi*, from the Late Jurassic of Tanzania, and with Late Jurassic and Early Cretaceous amphilestherians from northern landmasses.

Condorodon is only distantly related to *Argentoconodon fariatorum*, the other triconodont known from the Cañadón Asfalto Formation. Although similar in size, they differ greatly in molariform morphology, which suggests that these forms might have had different trophic habits and probably did not occupy the same ecological niche.

The biogeographical analyses performed based on the phylogenetic relationships of *Condorodon* suggest radiation of Amphilestheria in a continental configuration that allowed global dispersion by Early Jurassic times, with only limited provincialism indicated by the putative affinities of *Condorodon* and *Tendagurodon*. The same holds true for derived eutriconodonts, as indicated by *Argentoconodon*.

Both the Tree Reconciliation Analysis (TRA) and the Spatial Analysis of Vicariance (SAV) proved to be useful in the reconstruction of hypothetical biogeographical events. Although based on different methodological concepts, they seem to be complementary rather than mutually exclusive.

The discovery of *Condorodon* adds to the peculiar character of the mammalian fauna from Queso Rallado quarry. The presence of an allotherian, a basal amphilestherian, australosphenidans, and an alticonodontine triconodontid makes Queso Rallado one of our best sources to try to understand the taxonomical diversity of Early/Middle Jurassic mammaliaforms.

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