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### New materials of *Argentoconodon fariatorum* (Mammaliaformes, Triconodontidae) from the Jurassic of Argentina and its bearing on triconodont phylogeny

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## NEW MATERIALS OF *ARGENTOCONODON FARIASORUM* (MAMMALIAFORMES, TRICONODONTIDAE) FROM THE JURASSIC OF ARGENTINA AND ITS BEARING ON TRICONODONT PHYLOGENY

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**ABSTRACT**—*Argentoconodon fariasorum* is the only triconodont from the Jurassic of South America. Originally described on the basis of an upper molariform, *A. fariasorum* is now known by several specimens, including one that preserves most of its dentition, upper and lower jaws, and several postcranial elements. Close anatomical similarity exists between *Argentoconodon fariasorum*, *Ichthyoconodon jaworowskorum*, from the Cretaceous of Morocco, and the likely Jurassic *Volaticotherium antiquus*, from China. The results of a phylogenetic analysis including most taxa relevant to addressing triconodont phylogenetic relationships show *Argentoconodon* and *Volaticotherium* as a clade, which in turn is more closely related to *Ichthyoconodon* than to any other taxon. Our most parsimonious hypotheses support a triconodontid ancestry for *Argentoconodon*, *Ichthyoconodon*, and *Volaticotherium* as members of the monophyletic traditional subfamily Alticonodontinae. The inclusion of *Argentoconodon* among alticonodontines extends the geographical and temporal distribution of this triconodont subfamily to the South American Early Jurassic, resulting in extensive ghost lineages for many triconodontid groups. Postcranial similarities between *Argentoconodon* and *Volaticotherium* make it possible that the Argentinean taxon might have had gliding capabilities; if this is the case, our cladistic analysis highlights the possible existence of a gliding clade of triconodonts of wide distribution from at least as early as the Early Jurassic.

### INTRODUCTION

Triconodonts are widely recognized as a paraphyletic assemblage of mammaliaforms (Rougier et al., 1996, 2001; Hu et al., 1997, 1998; Ji et al., 1999; Luo et al., 2001b, 2002, 2003; Kielan-Jaworowska et al., 2004). Despite the ambiguity generated by the lack of unifying synapomorphies, there is a consensus on what is understood as a triconodont, namely a mammaliaform with labiolingually narrow molariforms and at least three major cusps mesiodistally aligned. These morphological features (crown shape, cusp number, and arrangement) are putatively plesiomorphic for a variety of Mesozoic lineages and constitute a primitive pattern at the root of many other dental morphologies present in Mesozoic mammaliaforms (Gregory, 1934; Simpson, 1936; Butler, 1939; Patterson, 1956; Crompton, 1971). Subgroups of triconodonts, such as the specialized, probably faunivorous Triconodontidae (Simpson, 1933; Rougier et al., 2001), are consistently recovered as monophyletic, whereas the more generalized ‘amphilestids’ (traditionally included in the family Amphilestidae) can be variously grouped forming monophyletic clusters or paraphyletic stems of other, non-triconodont lineages (Rougier et al., 2007a; Montellano et al., 2008; Kusuhashi et al., 2009; Gao et al., 2010).

Discoveries of triconodont fossils date back to 1764 when Sir Christopher Sykes found remains later assigned to *Amphilestes broderipii* Owen, 1871, in the Stonesfield Slate, Great Britain. It was some decades after the original discovery that it was formally recognized as a Mesozoic mammal (Buckland, 1824). The report of mammals in the “Secondary Era” did not go

unnoticed and generated vitriolic arguments (see Simpson, 1928). The geological background of the specimen as being from the Jurassic Stonesfield Slate was well substantiated (Goodrich, 1894), as was the molariform nature of the teeth in the jaw of *Amphilestes* (Owen, 1838, 1842); the evidence eventually resulted in a paradigm change, leading to the recognition of coeval dinosaurs and mammals. The existence of Mesozoic mammals was accepted and has not been further questioned in scientific circles since mid-19th century.

Triconodonts are mostly represented by fragmentary specimens, and usually by isolated teeth (Simpson, 1925a, 1925b; Patterson, 1951; Fox, 1969; Sigogneau-Russell, 1995; Cifelli and Madsen, 1998; Engelmann and Callison, 1998; Heinrich, 1998; Prasad and Manhas, 2002; Martin and Averianov, 2007, 2010). Only recently more complete articulated specimens have come to light from the ever more impressive Jurassic and Cretaceous localities of China (Ji et al., 1999; Meng et al., 2006; Luo et al., 2007; Gao et al., 2010).

Despite the morphologically simple dental pattern characteristic of triconodonts (Marsh, 1887; Osborn, 1888a, 1888b), there are broad hypotheses of homology (Patterson, 1956; Simpson, 1961) that make it possible to include them in phylogenetic studies addressing relationships among this wide array of mammaliaforms (Ji et al., 1999; Luo et al., 2002, 2007; Kielan-Jaworowska et al., 2004; Rougier et al., 2007a, 2007b; Montellano et al., 2008; Kusuhashi et al., 2009; Gao et al., 2010). However, this plesiomorphic morphology represents an obstacle when comparing triconodonts with taxa bearing more specialized teeth. Because of the difficulty in the recognition of more than a few homologous structures, many dental characters widely used in cladistic analyses of non-triconodont taxa cannot be easily applied to triconodont teeth. Moreover, given the scarce non-dental remains of

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triconodont taxa, only a small number of them have been included in broader cladistic analyses (Luo et al., 2002, 2007; Meng et al., 2006; Rougier et al., 2007b).

Informally, triconodonts can be regarded as belonging to one of two major 'groups.' On one hand, there are forms representing derived non-mammalian cynodonts and most-basal mammaliaforms (*Sinoconodon*, *Adelobasileus*, *Morganucodon* and allies, *Dinnetherium*, and a variety of other taxa) (Rowe, 1988; Wible, 1991; Crompton and Luo, 1993; Wible and Hopson, 1993; Luo, 1994; Rougier et al., 1996; Ji et al., 1999; Luo et al., 2002), mainly from Late Triassic–Early Jurassic outcrops (Parrington, 1941; Kühne, 1949; Patterson and Olson, 1961; Rigney, 1963; Crompton, 1964; Crompton and Jenkins, 1968; Clemens, 1980; Jenkins et al., 1983; Sigogneau-Russell, 1983; Yadagiri, 1984; Lucas and Hunt, 1990; Hahn, 1993; Datta and Das, 1996). Only a reduced number of these forms have been included in phylogenetic analysis and no consensus has been reached (Rougier et al., 2001, 2007a, 2007b; Luo et al., 2002, 2007; Meng et al., 2006). Most of them have been found only on northern landmasses (Parrington, 1941; Kühne, 1949; Rigney, 1963; Clemens, 1980; Jenkins et al., 1983; Sigogneau-Russell, 1983; Hahn, 1993); however, a few taxa are exclusive of southern continents, i.e., *Erythrotherium* from the Clarence Formation, Stormberg Group in Lesotho (Crompton, 1964); *Megazostrodon* from the Stormberg Group and the Upper Elliot Formation in Lesotho and South Africa (Crompton and Jenkins, 1968); and three Indian taxa: *Gondwanodon* from the Tiki Formation (Datta and Das, 1996), and *Indotherium* and *Indozostrodon* from the Kota Formation (Yadagiri, 1984; Datta and Das, 1996).

On the other hand, there are forms considered to be more derived and grouped in an assemblage dubbed Eutriconodonta (Kermack et al., 1973). Eutriconodonta, in its original formulation, comprises several genera included in the families Amphilestidae, now thought to be paraphyletic, and Triconodontidae. More recently, some additional taxa (*Ferganodon*, *Gobiconodon*, *Juchilestes*, *Klamelia*, *Liaotherium*, *Meemanodon*, *Paikasigudodon*, *Repenomamus*, *Tendagurodon*, *Triconolestes*, *Victoriaconodon*, and *Yanoconodon*) were also regarded as eutriconodonts (Luo et al., 2007; Martin and Averianov, 2007, 2010; Montellano et al., 2008; Gao et al., 2010). In most, but not all, recent studies, amphilestids are more closely related to Theria than to triconodontids; hence, Eutriconodonta cannot be rendered monophyletic if the original taxonomic membership is preserved. However, a core of triconodonts can be regarded as members of a monophyletic Eutriconodonta if defined, for example, as the more inclusive group including those taxa more closely related to *Triconodon* than to Cladotheria (see Kielan-Jaworowska et al., 2004).

Eutriconodonta in its original (wide) sense includes taxa that cover a time span from the Early Jurassic to the Late Cretaceous (Owen, 1838, 1859; Marsh, 1887; Simpson, 1925a, 1925b, 1928; Patterson, 1951; Fox, 1969; Trofimov, 1978; Rasmussen and Callison, 1981; Chow and Rich, 1984; Jenkins and Schaff, 1988; Zhou et al., 1991; Sigogneau-Russell, 1995; Engelmann and Callison, 1998; Heinrich, 1998; Cifelli et al., 1999; Godefroit and Guo, 1999; Ji et al., 1999; Kretzoi and Kretzoi, 2000; Li et al., 2000; Rougier et al., 2001; Prasad and Manhas, 2002; Montellano et al., 2008). The Early Jurassic record is very poor. A few taxa showing a triconodont dentition were reported from Mexico by Montellano et al. (2008), but given their phylogenetic analysis (also supported by the phylogenetic results obtained in the present contribution) only one of them is an eutriconodont sensu stricto (i.e., *Victoriaconodon*). On southern landmasses, Early Jurassic eutriconodonts are only represented by a few isolated teeth belonging to two taxa from the Indian Kota Formation (Prasad and Manhas, 2002), *Dyskritodon indicus* and *Paikasigudodon*; and *Argentoconodon fariatorum*, from Argentina (Rougier et al., 2007c). The other *Dyskritodon* species (*D. amazighi*, known

by one isolated tooth) has been recovered only from Early Cretaceous outcrops in Morocco (Sigogneau-Russell, 1995). The existence of such a long-lived genus seems unlikely; however, the fragmentary nature of the specimens makes a more detailed taxonomic analysis of these forms unviable (Kielan-Jaworowska et al., 2004). Both *Dyskritodon* and *Paikasigudodon* have been regarded as eutriconodonts (Kielan-Jaworowska et al., 2004); nevertheless, neither triconodontid nor amphilestid affinities have been established for either one of them. *Argentoconodon fariatorum* has been tentatively allied with *Ichthyoconodon jaworowskorum* from the Early Cretaceous of Morocco and *Volaticotherium antiquus*, possibly from the Jurassic of China (Gaetano and Rougier, 2007, 2010), representing a specialized group of triconodontids (Gaetano and Rougier, 2007). If correctly dated, *Argentoconodon* might be the earliest representative of Triconodontidae. Further description of *Argentoconodon* specimens is the main purpose of our present contribution (see below).

By the Middle Jurassic, amphilestid taxa were present at least on northern landmasses. Several specimens of *Amphilestes* and *Phascolotherium* have been reported from the Stonesfield Slate (Sharps Hill Formation) in Great Britain (Simpson, 1928). Although with some doubts concerning its triconodont nature, *Liaotherium* is a form from the Middle Jurassic of China that is also tentatively recognized as an amphilestid (Zhou et al., 1991). Two additional taxa, *Ferganodon narynensis* from Kyrgyzstan and *Klamelia zhaopengi* from China, were also reported from Middle Jurassic outcrops (Chow and Rich, 1984; Martin and Averianov, 2007, 2010) and proposed to be amphilestids closely allied with gobiconodontids. However, given their affinities, the inclusion of *Ferganodon* and *Klamelia* among amphilestids should be regarded as tentative due to the controversial relationships of gobiconodonts (Ji et al., 1999; Luo et al., 2001b, 2002; Rougier et al., 2001, 2007a; Meng et al., 2003a, 2006; Kielan-Jaworowska et al., 2004; Montellano et al., 2008; Kusuhashi et al., 2009; Gao et al., 2010).

Late Jurassic triconodonts are represented by both triconodontids and amphilestids (*Aploconodon*, *Comodon*, *Klamelia*, *Triconolestes*, *Priacodon*, and *Trioracodon*) and are mainly known from the Northern Hemisphere (China, Europe, and North America) (Owen, 1871; Marsh, 1879, 1880, 1881; Simpson, 1925a, 1925b, 1928; Rasmussen and Callison, 1981; Chow and Rich, 1984; Engelmann and Callison, 1998), the only exception being *Tendagurodon* (from the Late Jurassic of Tanzania) (Heinrich, 1998).

During the Cretaceous both eutriconodonts and amphilestids (including the much debated gobiconodontids) are diverse in Laurasia, but the latter do not reach the Late Cretaceous (Owen, 1859; Patterson, 1951; Trofimov, 1978; Jenkins and Schaff, 1988; Cifelli and Madsen, 1998; Cifelli et al., 1998, 1999; Godefroit and Guo, 1999; Ji et al., 1999; Li et al., 2000; Rougier et al., 2001; Hu et al., 2005; Meng et al., 2005, 2006; Martin and Averianov, 2007; Luo et al., 2007; Kusuhashi et al., 2009; Gao et al., 2010). *Ichthyoconodon jaworowskorum*, a taxon represented by two isolated teeth, is the only uncontested Gondwanan registry for triconodonts during the Cretaceous (Sigogneau-Russell, 1995).

Casamiquela (1964) first recognized the presence of Jurassic mammals in South America when he described the ichnogenus *Ameghinichnus patagonicus* from the Callovian–Oxfordian La Matilde Formation in Santa Cruz Province, Argentina. Casamiquela (1964) attributed these tracks to 'pantotheres'. Later, Kielan-Jaworowska and Gambaryan (1994) suggested they may represent multituberculates; more recently, de Valais (2009) regarded the ichnogenus as a Mammalia incertae sedis, a conclusion we share here.

Skeletal remains of South American Mesozoic mammals were not found until almost 40 years later in Jurassic outcrops of Chubut Province, Patagonia, Argentina (Rauhut et al., 2002; Rougier et al., 2007b, 2007c). A total of four different taxa are

present from a single locality. Rauhut et al. (2002) described *Asfaltomylos patagonicus*, considering it a basal australosphenidan (Luo et al., 2001a, 2002; Rauhut et al., 2002; Martin and Rauhut, 2005; Rougier et al., 2007a). Later, a closely related form, *Henosferus molus* Rougier et al., 2007, was described, and the same year the triconodont *Argentoconodon fariasorum* was published. Moreover, a probable allotherian, yet undescribed, was also found at this locality (Gaetano and Rougier, 2010).

The sparse record of Jurassic mammaliaforms from southern landmasses and their proved significance in understanding mammaliaform evolution renders new discoveries particularly significant. We report here on new specimens of *Argentoconodon fariasorum* that include postcranial, cranial, and dental materials, but at present we concentrate on the lower jaw and dental evidence and their bearing on triconodont phylogeny.

**Institutional Abbreviation**—MPEF, Museo Paleontológico “Egidio Feruglio,” Trelew, Chubut Province, Argentina.

### Terminology

**Taxa Terminology**—In the present contribution, we restrict Mammalia to the crown group following earlier authors (e.g., Rowe, 1988) and apply the more inclusive term Mammaliaformes Rowe, 1988, to group *Morganucodon*, Mammalia, their most recent common ancestor, and all its descendants.

Terms once thought to reflect natural units such as ‘triconodont’ and ‘amphilestid’ are now recognized as paraphyletic. However, they are still useful to ease expression and reference. Triconodont will be informally used for any mammaliaform with molariforms bearing three major cusps (A/a, B/b, C/c) roughly aligned mesiodistally. Amphilestids will informally refer to triconodonts with five major cusps mesiodistally aligned in the molariform crowns; in addition to the three main ones, the mesial cusp E/e and the distal cusp D/d. Defined as such, amphilestids exclude the nested symmetrodontans and ultimately Theria.

**Dental Terminology**—In this paper, the convention used by Crompton and Jenkins (1968) will be followed to name triconodont cusps. We accept Patterson’s (1956) hypotheses of homology between cusps of triconodonts and those taxa with more complex teeth such as ‘spalacotheriids’ and docodonts, as emended by other authors (such as Rougier et al., 2003).

The separation between premolars and molars rests on the recognition of non-replacement of the latter (Owen, 1840; Ziegler, 1971; Williams et al., 1989; Nowak, 1991; Evans, 1995). Distinction between molars and premolars is not always straightforward when dealing with incomplete specimens for which information regarding dental replacement is lacking (Luo et al., 2004). Replacement of molariform teeth has been documented in a variety of Mesozoic lineages (Owen, 1871; Thomas, 1887; Osborn, 1888a, 1888b; Simpson, 1928; Jenkins and Schaff, 1988; Godefroit and Guo, 1999; Meng et al., 2003a, 2003b, 2005; Rougier et al., 2003; Tsubamoto et al., 2004; Hu et al., 2005; Luo and Ji, 2005). Hence, it is not possible to decide unequivocally the molar or premolar nature of a tooth (or whether it is a molarized deciduous tooth) based exclusively on morphological complexity. For this reason, as suggested by Jenkins and Schaff (1988), the terms molariform and premolariform will be used to refer to those teeth that morphologically resemble molars and premolars, respectively.

### GEOLOGIC SETTING AND AGE

So far, all the Jurassic mammaliaforms of the Cañadón Asfalto Formation have been found in the small locality of Queso Rallado, about 5.5 km northwest from Cerro Cóndor Village, Chubut Province, Argentina (Rauhut et al., 2002; Martin and Rauhut, 2005; Rougier et al., 2007b, 2007c; Gaetano and Rougier, 2010) (Fig. 1).

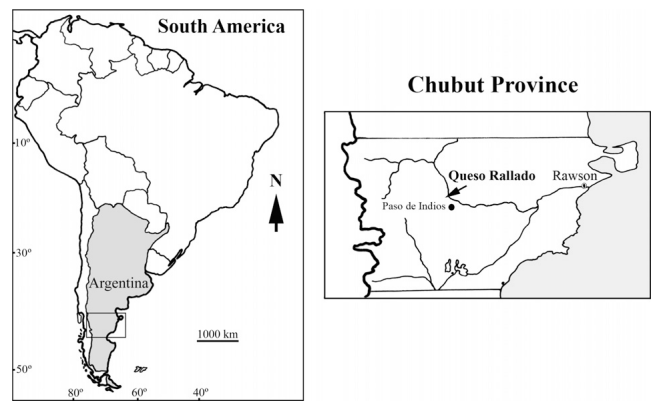


FIGURE 1. Map showing Queso Rallado locality, Chubut Province, Argentina. Modified from Rougier et al., 2007b.

The age of the Cañadón Asfalto Formation has been much discussed, as diverse sources of evidence led to different conclusions (Stipanovic et al., 1968; Stipanovic and Bonetti, 1969; Tasch and Volkheimer, 1970; Baldoni, 1986; Bonaparte, 1986; Masiuk, 1991; Viña and Seiler, 1992; Figari and Courtade, 1993; Musacchio, 1995; Silva Nieto et al., 2002; Cabaleri et al., 2010). A Callovian–Oxfordian age is accepted by most workers (Stipanovic et al., 1968; Tasch and Volkheimer, 1970; Musacchio et al., 1990; Silva Nieto et al., 2002; Martin and Rauhut, 2005; Rougier et al., 2007c; Escapa et al., 2008); however, new radiometric data (Cuneo and Bowring, 2010) suggest the deposition of the Cañadón Asfalto Formation began during the late Early Jurassic (Toarcian) but exact dates await publication.

The fossiliferous stratum at Queso Rallado is part of a highly deformed stratigraphic succession deposited in the Cañadón Asfalto basin (Rougier et al., 2007c). This layer is thought to be part of the lower member of the Cañadón Asfalto Formation (Martin and Rauhut, 2005; Rougier et al., 2007c). The lower member of the Cañadón Asfalto Formation (Volcanic Member sensu Nullo, 1983; Las Chacritas Member sensu Silva Nieto et al., 2003) is mainly composed of limestone, clastic, and gypsum levels (some of them bearing plant, ostracod, and conchostracan remains) intercalated with basaltic flows and pyroclastic deposits (Figari et al., 1996), and represents a lacustrine carbonate environment (Figari et al., 1996).

The Cañadón Asfalto Formation is underlain by the Lonco Trapial Formation, which is dominated by volcanoclastic alluvial fan deposits of weak transport efficiency, mainly represented by volcanic conglomerates, tuffs, and basalts (Figari et al., 1996).

The Lonco Trapial Formation and the Las Chacritas Member of the Cañadón Asfalto Formation are both part of the volcanosedimentary synrift sequence deposited during the initial stages in development of the Somuncurá–Cañadón Asfalto Basin (Figari and Courtade, 1993). Several authors (Figari and Courtade, 1993; Figari et al., 1996; Page et al., 1999) have regarded the contact between the Lonco Trapial and Cañadón Asfalto formations as transitional; however, other geologists (Cortiñas, 1996; Silva Nieto et al., 2002; Volkheimer et al., 2009) have claimed that an angular discordance is present. If a transitional contact exists between these units in Cerro Cóndor area, unequivocal formal assignment of the bone-bearing levels to a formational unit should await proper delimitation of such lithostratigraphic units. At present it is not clear if Queso Rallado is younger or older than the strata dated by Cuneo and Bowring (2010); samples of the layers immediately above Queso Rallado are being processed for radiometric dating and should settle the age of the fossils.

## SYSTEMATIC PALEONTOLOGY

Unnamed rank MAMMALIAFORMES Rowe, 1988  
Order EUTRICONODONTA Kermack, Mussett, and Rigney,  
1973

Family TRICONODONTIDAE Marsh, 1887  
Subfamily ALTICONODONTINAE Fox, 1976  
Tribe VOLATICOTHERINI Meng, Hu, Wang, Wang, and Li,  
2006 (as family Volaticotheridae Meng, Hu, Wang, Wang, and  
Li, 2006)

Genus *ARGENTOCONODON* Rougier, Garrido, Gaetano,  
Puerta, Corbitt, and Novacek, 2007

**Type and Only Species**—*Argentoconodon fariasorum*.

**Diagnosis**—As for the species, by monotypy.

*ARGENTOCONODON FARIASORUM* Rougier, Garrido,  
Gaetano, Puerta, Corbitt, and Novacek, 2007

**Holotype**—MPEF-PV1877, isolated complete upper left molariform.

**Hypodigm**—MPEF-PV2362, fragmentary left maxilla with the M3 still in place. MPEF-PV2363 (field number CC115/04), partial skeleton, including fragmentary maxillae, dentaries, many isolated teeth, and disarticulated and partially articulated postcranial elements (including a femur and rib fragments). MPEF-PV2364, isolated complete right upper last molariform (M4).

**Emended Diagnosis**—Triconodont with imbricated upper and lower molariforms, imbrication also present in posterior premolariforms. Simple unicuspat incisors. Canines taller than other teeth, lower ones uniradicated and conical, upper canines with a constricted root and more labiolingually compressed. Premolariforms without mesial accessory cusps and cingula, with one simple or constricted root or two roots. Molariforms extremely labiolingually compressed and lacking conspicuous cingula. Upper molariforms pentacuspitated with three main cusps (A, B and C) and two accessory cusps (D and E). Cusp A subequal or taller than cusp C, both distally recumbent. Cusp B almost erect and lower than cusps A and C. Accessory cusps (D and E) project from the base of the crown. Lower molariforms with four cusps. Main cusps (a, b, and c) strongly recumbent. Distal accessory cusp (d) overhanging distally as a flange-like projection. Comparison of *Argentoconodon* with its close allies reveals the following differences: premolariforms of *Argentoconodon* differ from those of amphilestids and other triconodonts for lacking a mesial accessory cusp; lower molariforms of *Argentoconodon* differ from those of *Volaticotherium* and other non-Volaticotherini alticonodontines for lacking well-developed cingula and having main cusps separated by wider valleys; further differences with non-Volaticotherini alticonodontines includes more labiolingually compressed lower molariforms bearing four cusps (a–d) that are not subequal and are set apart by relatively wide valleys; discrepancies with the lower molariforms of *Ichthyoconodon* also comprise cusp proportions and recumbence; upper molariforms of *Argentoconodon* are distinguished from those of *Volaticotherium* for the presence of well-developed cusps D and E and cusp B less recumbent than the other main cusps; and unlike *Corviconodon* and *Astroconodon*, in *Argentoconodon* cusps A–D are well separated, cusp E is present, cusp D is proportionally lower than the main cusps and overhangs distally, and cingula are absent; *Argentoconodon* differs from *Priacodon*, *Triaracodon*, and *Triconodon* in having more labiolingually compressed molariforms with more recumbent main cusps and lacking well-developed cingula, and by the presence of cusp E in upper molariforms.

## DESCRIPTION

We will focus our description on the previously undescribed remains of *A. fariasorum*, particularly MPEF-PV2363, consisting of several bones scattered over the surface of two slabs that

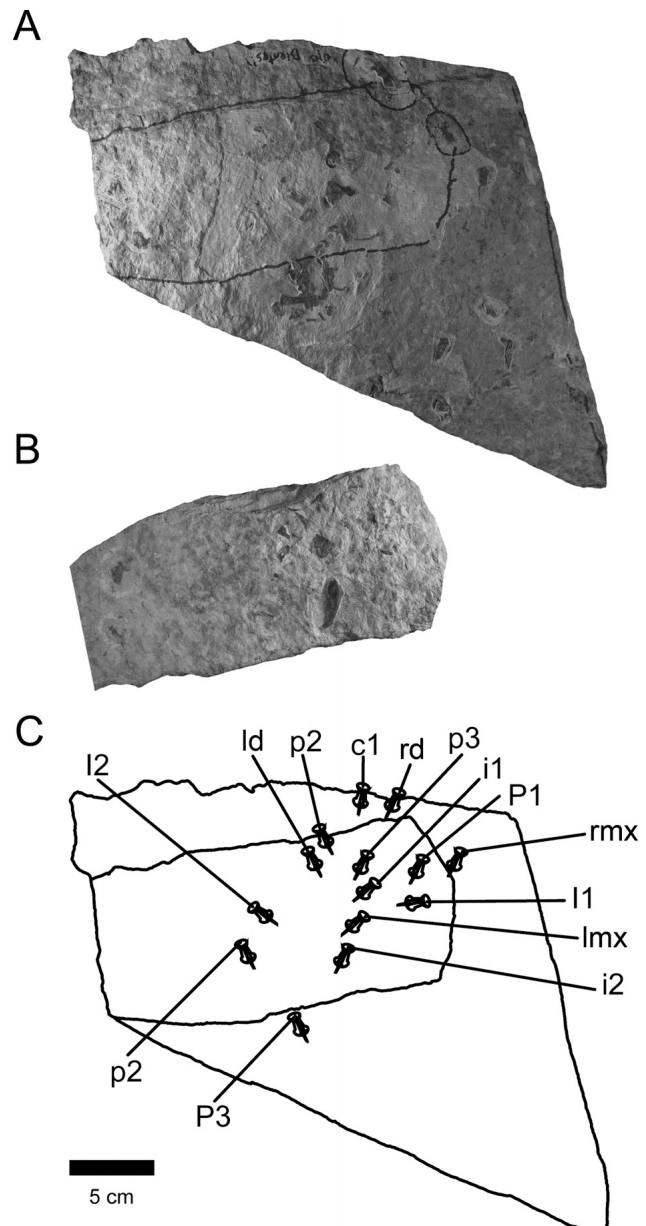


FIGURE 2. Slabs bearing the scattered specimen MPEF-PV2363 of *Argentoconodon fariasorum*. **A–B**, slab (**A**) and counter-slab (**B**) before the extraction of the bones; **C**, line drawing of superposed slab and counter-slab indicating the original position of remains corresponding to specimen MPEF-PV2363. **Abbreviations:** **c1**, first lower canine; **i1**, first lower incisor; **I1**, first upper incisor; **i2**, second lower incisor; **I2**, second upper incisor; **ld**, left dentary; **lmx**, left maxilla; **P1**, first upper premolariform; **p2**, second lower premolariform; **p3**, third lower premolariform; **P3**, third upper premolariform; **rd**, right dentary; **rmx**, right maxilla.

have partial superposition (Fig. 2). A few, much more fragmentary specimens, offer some additional information and are also included.

## Dentary

Both dentaries have been recovered; the left one is almost complete and bears two molars in their original position (Fig. 3). The right dentary is more damaged but it has one molariform and

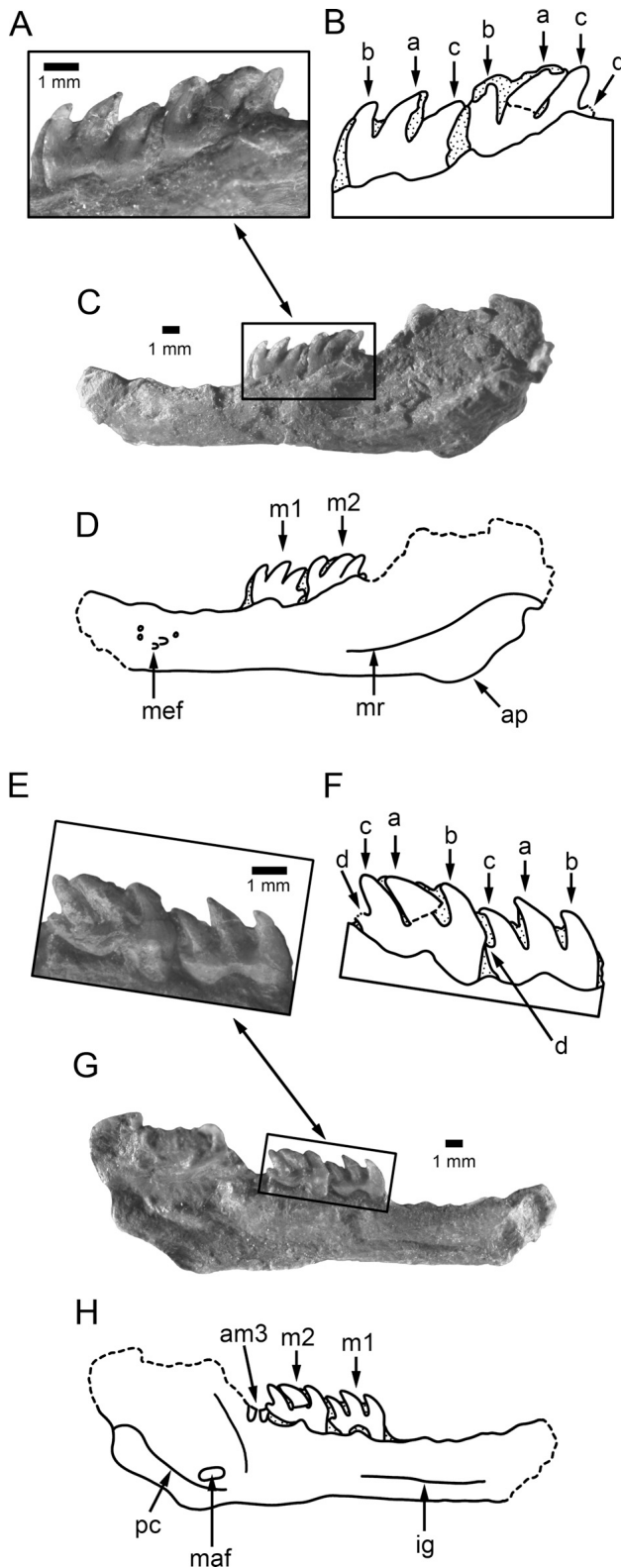


FIGURE 3. Left lower jaw of *Argentoconodon fariasorum* (MPEF-PV2363). Photograph and outline drawing of C–D, left dentary in lateral view; A–B, detail of the left m1 and m2 in labial view; G–H, left dentary in medial view; E–F, detail of the left m1 and m2 in lingual view. **Abbreviations:** a, b, c, d, triconodont cusp nomenclature; am3, third lower molariform alveoli; ap, angular process; ig, internal groove; m1, first lower molariform; m2, second lower molariform; maf, mandibular foramen; mef, mental foramina; mr, masseteric ridge; pc, pterygoid crest. Dotted areas indicate rock remains; dashed lines in B and F indicate fractures and in D and H indicate incomplete bone margins.

the probable last premolariform still in situ. The dentary is slender with a straight ventral margin. The horizontal ramus is deeper below the last molariform than under the first premolariform, as the alveolar margin rises posteriorly. Mesially, the alveolar margin rises abruptly at the level of the canine alveolus. A large lower canine alveolus is oriented approximately 50° to the horizontal axis of the jaw, accompanied by a vertical symphysis. There is no postcanine diastema. Behind the canine alveolus, there are six alveoli anterior to the first molar. We propose here that these alveoli were occupied by single-rooted p1 and p2 and double-rooted p3 and p4 (see below). Posterior to the second molariform locus, two relatively small alveoli for the m3 are present in both dentaries (see below). No remnant of a dental lamina groove can be identified.

The mandibular condyle is missing in the right dentary and not fully free of matrix in the left lower jaw. However, the mandibular condyle seems to have been supported by the posteriorly expanded dentary reaching approximately the level of the alveolar margin.

The posteroventral sector of the lower jaw is only preserved in the left dentary; although it is partially covered with matrix, it can be ascertained that an obtuse angular process was present.

The coronoid process is not completely preserved in any dentary. Nevertheless, enough of it is present to infer that the coronoid process was relatively broad, with an almost vertical posterior margin. The coronoid process covers labially part of m2 and probably almost the entire last molariform.

The medial aspect of right and left jaws is not well preserved. The posterior extension of the symphysis cannot be ascertained, because the medial wall of the canine alveolus is lacking and no trace of the symphysis is recognized below the p1 alveolus.

Despite the poor preservation of the medial surface of both lower jaws, an internal groove can be recognized. It is straight and parallel to the ventral margin of the jaw, running approximately 1/3 of the dentary height from the ventral margin of the jaw. Posteriorly, an anteroposteriorly elongated mandibular foramen is present at about the middle height of the dentary just posterior to the well-defined pterygoid fossa anterior margin. There is no medial flange or groove that would indicate the presence of postdentary bones. A strong pterygoid crest is present, curving around the ventral margin of the dentary. Although the pterygoid crest continues along the condylar process, this crest seems to end before reaching the distal-most portion of the condylar process.

In labial aspect, five mental foramina are recognized approximately at the mid-height of the dentary anterior to the position of p3. Two of them are circular, similar in size, and aligned below the alveolus for p1. Another circular mental foramen is present below the position of p3, whereas two poorly preserved larger foramina are placed below the alveolus for the second premolariform.

The masseteric fossa is shallow. There is not a pronounced mesial margin but a round elevation. It continues anteriorly toward the mesial sector of m2. Ventrally, the masseteric ridge flares out markedly behind the m3 and is directed toward the mandibular condyle.

### Dentition

Based on the available material, we reconstruct the dental formula of *Argentoconodon* as: I2?.C1.P4.M4/i2.c1.p4.m3 (Fig. 4).

**Incisors**—Four isolated incisors were recovered. All known incisors of *Argentoconodon* are well-preserved complete teeth but the crown of one was lost after casting and photographing.

**Upper Incisors:** One of them (Fig. 5A–B) is probably a right upper tooth, because it was found near the right maxilla (Fig. 2). The presence of an enlarged upper mesial incisor has been unambiguously recorded in other taxa (e.g., *Volaticotherium*, *Repenomamus*) (Hu et al., 2005; Meng et al., 2006), so we consider this tooth an I1. It is a large (Table 1) labiolingually compressed tooth with steeper lingual than labial face. No cingula or wear can be

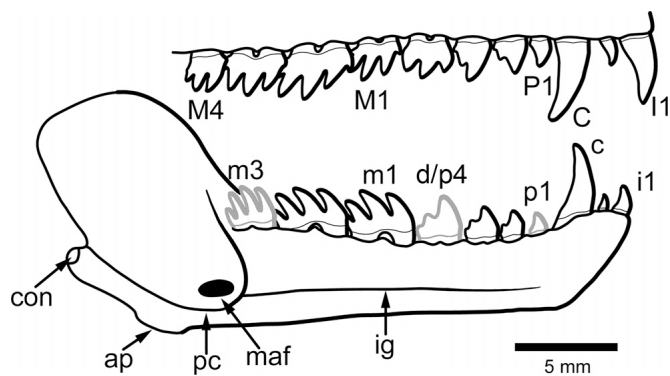


FIGURE 4. Reconstruction of *Argentoconodon fariatorum* lower jaw and dentition in medial view. Teeth in gray are not presently known. **Abbreviations:** ap, angular process; c, lower canine; C, upper canine; con, mandibular condyle; d/p4, fourth deciduous premolariform or fourth premolariform; i1, first lower incisor; I1, first upper incisor; ig, internal groove; m1, first lower molariform; M1, first upper molariform; m3, third lower molariform; M4, fourth upper molariform; maf, mandibular foramen; mef, mental foramina; ms, masseteric shelf; p1, first lower premolariform; P1, first upper premolariform; pc, pterygoid crest.

recognized. The single cusp is distally recumbent and slightly lingually inclined. The root is constricted, unlike the roots of other incisors.

A second incisor (Fig. 5C–D) was found equally distant from the left dentary and the left maxilla and relatively far from other tooth-bearing elements (Fig. 2). Its labiolingual asymmetry suggests this tooth is a right lower or a left upper incisor. Thus, given its proximity to the left upper jaw, we think it is best to consider this tooth a left upper incisor. Given the presence of a purported enlarged I1 and lacking any evidence on the total number of upper incisors, we adopt a conservative posture and regard this tooth provisionally as a left I2. The crown of this tooth is now lost but it has been well documented. The purported I2 is not compressed and has a sigmoidal aspect in lateral view. The only cusp is recumbent and somewhat inclined lingually, with the lingual face of the crown steeper than the labial one. There is no

trace of cingula or wear. The root is ovoidal in cross-section and isodiametric along its length.

**Lower Incisors:** The other two incisors recognized are regarded as lower teeth. Both of them bear a single, recumbent, lingually inclined cusp. They lack cingula and wear facets, and no evidence of interdental contact among successive teeth can be recognized. However, similar in these general traits, they differ from each other in their size (Table 1) and root characteristics.

One of them (Fig. 5E–F) was discovered lying very close to the left dentary (Fig. 2) supporting a left lower position for this tooth. This element has an ovoidal root in cross-section whose diameter is relatively constant.

The other purported lower incisor (Fig. 5G–H) is considerably smaller than the latter (Table 1) and its root is almost circular in cross-section, with its diameter increasing away from the crown. It was found closer to the left maxilla than to any other tooth-bearing bone (Fig. 2); however, the labiolingual asymmetry of its crown suggests an upper right or a lower left position for this element. Thus, because it was closer to the left dentary than to the right maxilla, we interpret it as a left lower tooth.

The anterior portion of the dentary does not allow inferences concerning incisor number or characteristics, because the respective alveoli are not preserved. However, the presence of a larger i1 than i2 occurs in many taxa (such as *Gobiconodon*, *Jeholodens*, *Repenomamus*, and *Volaticotherium*; Jenkins and Schaff, 1988; Ji et al., 1999; Hu et al., 2005; Meng et al., 2006). We suggest the same positional relationship for the known lower incisors of *Argentoconodon*.

**Canines**—Both right and left upper canines have been recovered, the left one in place and the right one very close to the right maxilla. A caniniform tooth closely associated with the right dentary is thought to be the lower right canine (Fig. 2). Both upper and lower canines of *Argentoconodon* are large teeth (Table 1), bearing a single recumbent cusp and lacking distinct cingula.

**Upper Canines:** Upper canines (Fig. 6C–F, I–L) have equally convex labial and lingual faces. The labial face is well rounded. On the other hand, the mesial and distal margins of the lingual surface of the crown are depressed with respect to its central sector. Upper canines bear a single root. The root is well rounded labially whereas a constriction is present in lingual view.

**Lower Canines:** A single lower canine (Fig. 5I–J) interpreted as a right tooth was recovered. This canine is more slender than

TABLE 1. Crown measurements (in mm) for upper and lower teeth of *Argentoconodon fariatorum*.

Tooth	MPEF-PV2363		MPEF-PV1877		MPEF-PV2362		MPEF-PV2364	
	Length	Height	Length	Height	Length	Height	Length	Height
Right I1	1.68	3.55	—	—	—	—	—	—
Left I2	0.65	1.16	—	—	—	—	—	—
Left i1	0.8	1.14	—	—	—	—	—	—
Left i2	0.4	0.58	—	—	—	—	—	—
Left C	1.68	4	—	—	—	—	—	—
Right c	1.69	4.4	—	—	—	—	—	—
Right P1	1	1.3	—	—	—	—	—	—
Left P2	1.75	1.75	—	—	—	—	—	—
Right P3	2.14	—	—	—	—	—	—	—
Left dP4/P4	2.48	1.61	—	—	—	—	—	—
— p1	—	—	—	—	—	—	—	—
Right p2	1.26	1.28	—	—	—	—	—	—
Left p3	1.59	1.5	—	—	—	—	—	—
— dp4/p4	—	—	—	—	—	—	—	—
Right M1	—	1.63	—	—	—	—	—	—
Left M2	3.39	2.22	2.85	1.96	—	—	—	—
Right M3	3.18	2.01	—	—	3.47	1.97	—	—
Right M4	—	—	—	—	—	—	1.98	1.87
Left m1	3.26	2.25	—	—	—	—	—	—
Left m2	3.83	—	—	—	—	—	—	—
— m3	—	—	—	—	—	—	—	—



the upper ones. The lower canine cusp is steeper lingually than labially. Distally, a wear facet is present on the lower canine recovered, extending from almost the tip of the crown to a small labial bulging near the base of the crown. Unexpectedly, no wear facet is recognized on the mesial margin of the upper canines. A single unconstricted root, more convex lingually than labially, is present in the lower canine.

**Premolariforms**—Six isolated premolariforms representing five morphotypes have been recognized. They are labiolingually compressed teeth lacking the three relatively large cusps dominating the crown characteristic of molariforms. They bear no conspicuous cingula. All recovered premolariforms have a main distally recumbent cusp (A/a) and at least an accessory distal cusp (C/c).

**Upper Premolariforms:** Three isolated upper premolariforms have been recovered. A relatively simple premolariform (Fig. 5K–L) has been found very close to the right maxilla (Fig. 2), thus we propose a right upper position for this tooth. We consider this tooth as the right P1. The main cusp (A) occupies the entire crown length. This cusp has a convex mesial margin and a concave distal margin in lateral view, being strongly recumbent. An accessory distal cusp (C) is developed as a tiny bulge on the basal portion of the crown displaced labially. Both cusp apices are connected by a small ridge. The crown is not very compressed labiolingually. The single root is ovoidal in transverse section and it tapers faintly away from the crown. There is no constriction between crown and root. The root is narrower than the crown.

An isolated premolariform (Fig. 6A–D, G–J) found in contact with the left maxilla is considered an upper left tooth. This tooth shows a relatively complex morphology and here we hesitantly propose it as a P2. It has three conspicuous almost conical cusps aligned mesiodistally on the crown: A, C, and D (from mesial to distal). Distally, cusp sizes decrease and they arise progressively more basally on the crown. Cusp A is robust, dominant, and located in the mesial half of the tooth. It is slightly recumbent, because its mesial margin is faintly convex whereas the distal one is almost straight in lateral view. It is somewhat curved lingually and its labial face is more convex than the opposite one. Cusp A is separated from cusp C by a shallow and wide valley. Cusps C and D are distally pointing. Cusp C reaches approximately 1/4 of the principal cusp height. Cusp D is very small; it arises from the crown base without defining a conspicuous cingulum and hangs distally from the distal edge of the root. Two fully independent roots, cylindrical in cross-section and separated from the crown by a gentle constriction, are present. They slightly curve away from the crown, becoming closely approximated.

Also isolated, another premolariform (Fig. 5M–N) was discovered relatively distant from any tooth-bearing element (Fig. 2), precluding a direct association with the dentary or the maxilla. However, the alveoli count in the left dentary shows that there is no place for this tooth in the lower jaw. Thus, we regard it as an upper premolariform. It is similar to P2; however, differences regarding cusp proportions and relations are present and we regard this premolariform as a right P3. The tooth is broken, the posterior sector being displaced with respect to the rest of the crown. Three well-defined cusps are present on the crown. All of them arise approximately at the same height in the crown. Cusp A is the largest cusp, occupying the mesial half of the crown. This cusp is recumbent, its mesial margin being convex and the distal one nearly straight in lateral view. The lingual face of cusp A is slightly steeper than the labial one. Mesially, a small bulging is present on the base of cusp A. An erect and labiolingually symmetrical cusp C reaches approximately 1/3 of cusp A, from which it is separated by a narrow notch. Distal to cusp C, a small but distinct cusp D is present (although not visible in Fig. 5 due to breakage and distortion of the tooth). It is displaced labially with respect to the midline of the tooth and supported almost entirely

by the posterior root. Two roots were present but unfortunately they are not well preserved.

A tooth, still in its alveolus on the left maxilla (Fig. 6C–D), is damaged and resembles neither the premolariforms found isolated nor molariforms. It is shorter mesiodistally than M1 and bears only three cusps (A, B, and C), which are arranged in line. Cusp A is centered on the crown and distally recumbent with a shorter distal than mesial margin. It is taller but more slender than cusps B and C. Cusp B is erect and very low, and probably did not surpass 1/3 of cusp A when complete. Cusp C is also erect, reaching 2/3 of cusp A height. No cingula or wear can be recognized due to the poor preservation of the tooth. Two almost vertical roots are present, about the same length mesiodistally, but the distal one is longer. Unlike other molariforms, in this tooth cusps B and C are not entirely supported by the roots. Its morphology suggests that this tooth is not a molariform but a complex premolariform, probably the last one. Given the number of isolated teeth interpreted as upper premolariforms, we regard this tooth as the dp4/P4 and thus propose that *Argentoconodon* possessed four upper premolariforms. Whether this is a deciduous or a permanent tooth is uncertain. It is possible that this tooth is a dp4 given its complex morphology; however, *Volaticotherium*, a closely related form, depicts a complex last premolariform that was interpreted as a P4 (Meng et al., 2006) and we therefore consider this issue as unresolved.

**Lower Premolariforms:** Two almost identical teeth (Fig. 5O–P) are regarded as right and left lower premolariforms, because one of them was found very close to the left dentary (Fig. 2). Given the left dentary alveolus count and relative size, we tentatively regard them as p2. Their crowns bear two conspicuous cusps and have a steeper lingual than labial face. The main cusp (a) constitutes approximately 2/3 of the tooth length and its mesial margin is not centered in the midline of the tooth but somewhat displaced lingually. Cusp c is a well-defined conical cusp separated from cusp a by a shallow and wide valley. Basal to cusp c, in the distal margin of the tooth, there is a small bulging displaced lingually that can be interpreted as an additional accessory cusp. A faint constriction marks the end of the crown and the beginning of the root in these teeth. The only root is almost isodiametric, tapering slightly away from the crown, and there is a centrally placed deep and narrow groove labially.

An isolated premolariform (Fig. 5Q–R) was situated very close to the left dentary (Fig. 2) so we provisionally regard it as a left lower premolariform, specifically the p3, because the separation between the roots of this tooth matches with the alveoli for the third premolariform in the left dentary. There are three successive smaller cusps on the crown (a, c, and d). Occupying more than half of the mesiodistal length of the crown, cusp a is recumbent and relatively robust. It is almost symmetrical labiolingually, being slightly more rounded lingually than labially. Cusp a is set apart from a very small cusp c by a shallow and wide notch. Cusp c points distally and, like cusp d, is displaced lingually, the crown being more bulbous labially in the sector distal to cusp a. Cusp d is tiny. It arises basally on the crown and overhangs the posterior root. No cingula or wear are recognizable on this tooth. Two roots are separated from the crown by subtle mesial and distal constrictions. The mesial root is vertically oriented, unlike the distal one, which points distally.

An unerupted tooth mesial to the m1 can be seen in place on the substance of the right dentary and partially exposed due to breakage of the alveolar process of the dentary. It is poorly exposed, making a proper description unattainable. Nevertheless, enough is visible to interpret it as representing the last premolariform (i.e., p4). The deciduous p4 is missing. However, two alveoli recognized in the p4 region in the left dentary suggest that the dp4 might have been two-rooted and as mesiodistally long as p3.

Some degree of imbrication was present between premolariforms, because the most mesial and distal edges of the teeth are





not coincident with the long axis of the crown, but displaced labially or lingually.

**Molariforms—Upper Molariforms:** Based on the evidence of both maxillae and isolated elements, we interpret that the number of upper molariforms was likely four. The three mesial upper molariforms bear five conspicuous cusps, three principal (A–C) and two accessory (E and D) ones.

M1 is represented by a partially preserved tooth placed in its alveolus on the right maxilla, which has not been extracted from matrix; thus, only the lingual aspect is accessible for description (Fig. 6M–N). Two roots and three main cusps are recognized. However, cusp B is almost entirely covered by rock and no more than an external cast of the labial face of cusp A is preserved. Only the distal cusp (C) is fully preserved and exposed. The mesial sector of the tooth is not preserved. Although missing, the partial labial impression of cusp A is enough to interpret it as distally pointing. Cusp C is not as tall as cusp A, but is more inclined distally. Cusp C mesial and distal margins are convex. Cusp B seems to be as tall as cusp C but shorter than cusp A. It is more slender than cusps A and C. A distal cusp D is present but it is not visible lingually as M2 overlaps M1 in this view. No cingula or wear can be recognized. The anterior root is missing but represented by the external cast of its labial face. The posterior root is still in the alveolus and only a small portion can be observed due to breakage of the lingual wall of the maxilla. The roots seem to be similar in diameter.

Both right and left M2 were recovered. The right one is preserved in natural position on the unprepared maxilla (Fig. 6M–N), thus only its lingual aspect is accessible. The left tooth was found in such a close association with the left maxilla that it could not be extracted (Fig. 6C–D, I–J). Thus the available information regarding M2 morphology is limited. M2 is mesiodistally longer than M1; it bears mesiodistally aligned cusps and two roots. Cusp A is centered between the two roots and points distally. This cusp is separated from cusp B by a notch that is narrower than the valley separating cusp A from cusp C. Cusp B points distally, similar to cusp A, and slightly labially. Cusp B is approximately 1/2 of cusp A height. Cusp C is only slightly smaller than A and more distally pointing. Both accessory cusps (D and E) are born on the interface between crown and roots projecting mesially and distally from the margin of the anterior and posterior root, respectively. Cusp D emerges from the crown at the same level as the main cusps and is almost 1/2 as high as cusp C. Cusp E is more basally born than cusp D and, although well developed, it does not reach the valley between cusps A and B. No cingula are present on the visible (lingual) side of this molariform. The distal root is slightly more slender and apparently shorter than the mesial one, but these cannot be assured due to breakage and lack of exposure.

The interrelationship between specimen MPEF-PV2363 right M1 and M2 shows unambiguously that the imbrication pattern described for lower molariforms is also present in upper ones, where cusp D of the preceding tooth is labial to cusp E of the succeeding molariform.

The holotype (MPEF-PV1877) was originally described as a lower molariform (Rougier et al., 2007c) but on the basis of the new evidence available is reinterpreted as a left M2 (Fig. 5V–W). This tooth shows slight differences with the above-described M2

and allows us to analyze the structures that cannot be seen in the latter due to the incomplete preparation.

MPEF-PV1877 bears mesiodistally aligned, almost conical cusps that are slightly more rounded lingually than labially. A wear facet is present on the lingual apical portion of cusp B. In the holotype, cusp B is relatively smaller than that of the M2 in the specimen MPEF-PV2363, being approximately 1/3 the height of cusp A, which is clearly the tallest crown cusp. Although slightly shorter, cusp B is significantly more robust than cusp C in the holotype. Furthermore, cusp B of MPEF-PV1877 is slightly asymmetrical, being somewhat labially curved, which may be the consequence of breakage (however, no breakage is apparent). Cusp C is thinner, sharper, and more acute than the other main cusps when compared to that of M2 in MPEF-PV2363. As in MPEF-PV2363, no clear cingula are present in MPEF-PV1877 but a small cusplule is developed lingually between the bases of cusps A and C, its height not being enough to reach the valley separating the latter. There is no evidence of this cusplule in MPEF-PV2363 M1 or M2. Initially, Rougier et al. (2007c) considered this tiny cusplule as homologue to cusp g or kühnecone of some authors (Parrington, 1967); however, under the reinterpretation of this tooth position, this suggestion is unlikely and this cusplule presence may be related to the development of a cingulum, though not connected to any distinctive one. The holotype (MPEF-PV1877) roots are of subcircular section, the mesial one being more expanded mesiodistally than the distal one. They are similar in length but because the anterior root has its tip broken, it is possible that this root was longer than the posterior one.

The M3 is represented by a left tooth found underneath and almost in contact with the left maxilla of the specimen MPEF-PV2363 (Fig. 5S–T) and also by a left tooth of the same size and general morphology present in the attributed maxillary fragment MPEF-PV2362 (Fig. 6O–R). The cusps are not mesiodistally aligned but there is an incipient triangular distribution of them, with the main cusp somewhat lingually displaced with respect to the other main cusps. Main cusps are more labiolingually compressed than those of lower teeth. They are well rounded lingually and steeper labially. No cingula could be recognized. As in M2, cusp A is centered on the crown and slightly taller than cusp C. The valley separating cusp A from cusp C is similar to that between cusps A and B but shallower. Cusp B is about 2/3 as high as cusp A in MPEF-PV2363, but shorter in MPEF-PV2362 (see below). Cusp D overhangs the distal margin of the root, and, although its tip is broken off, it probably reached the first third of cusp C. Cusps A–D are evenly distally pointing. Cusp E is present as a tiny mesially pointing bulge at the interface between crown and root above the level of cusp D base. No wear facets are present in MPEF-PV2363 M3, but in specimen MPEF-PV2362 cusp B shows clear signs of extensive wear, represented by a wear facet on its lingual apical portion. Moreover, wear is also recognizable on cusp A and on the tip of cusp C. Probably as a consequence of wear, cusp B of MPEF-PV 2362 is smaller than the other principal cusps, being approximately 1/3 the height of cusp A. The two vertically oriented roots are oval-shaped in cross-section, the distal one being more slender than the mesial one in lateral view. The mesial root is longer (apicobasally) than the distal root, but as their tips are missing this is uncertain.

← FIGURE 5. Selection of *Argentoconodon fariasorum* isolated teeth. **A–T**, specimen MPEF-PV2363; **U**, specimen MPEF-PV2364; **V–W**, specimen MPEF-PV1877 (holotype). Photograph and outline drawing of **A–B**, right I1 in **(A)** lingual and **(B)** labial views; **C–D**, left I2 in **(C)** labial and **(D)** lingual views; **E–F**, left i1 in **(E)** labial and **(F)** lingual views; **G–H**, left i2 in **(G)** labial and **(H)** lingual views; **I–J**, lower right canine in **(I)** lingual and **(J)** labial views; **K–L**, right P1 in **(K)** lingual and **(L)** labial views; **M–N**, right P3 in **(M)** lingual and **(N)** labial views; **O–P**, right p2 in **(O)** lingual and **(P)** labial views; **Q–R**, left p3 in **(Q)** labial and **(R)** lingual views; **S–T**, left M3 in **(S)** labial and **(T)** lingual views; **U**, right M4 **(U1)** in labial view; **V–W**, left M2 in **(V)** labial and **(W)** lingual views. **Abbreviations:** a/A, b/B, c/C, d/D, E, triconodont cusp nomenclature; cc, cingular cusp; wf, wear facet. Dotted areas indicate rock remains; dashed lines in **I2** and **J2** indicate fractures and in **M2**, **N2**, **S2**, and **T2** indicate incomplete margins.

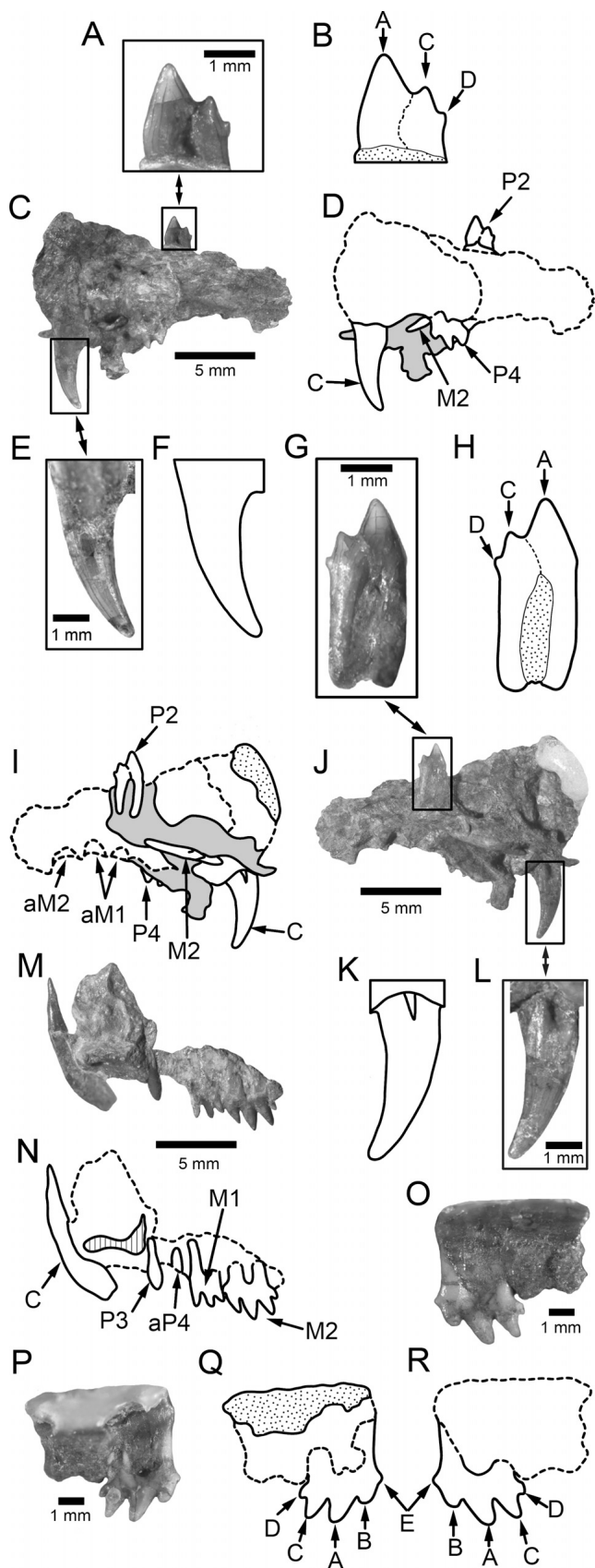


FIGURE 6. Maxillary fragments of *Argentoconodon fariasorum* isolated teeth. A–N, specimen MPEF-PV2363; O–R, specimen MPEF-PV2362. Photograph and outline drawing of A–B, G–H, left P2 in (A,

An isolated tooth (MPEF-PV2364) is proposed to represent the last upper molariform (M4) (Fig. 5U). We provisionally regard it as belonging to *Argentoconodon fariasorum* given its size (approximately 57% the size of M3 of *Argentoconodon*) (Table 1) and cusp morphology. Considering that the imbrication pattern recognized in anterior molariforms would extend to the posterior-most element of the dental row and the lateral displacement of the mesial-most cusp of M4, we propose that MPEF-PV2364 is a right upper last molariform. This labiolingually compressed tooth is still embedded in the matrix, only its labial aspect being available for analysis. It has three cusps interpreted as cusps A, C, and D mesiodistally aligned. Cusp B is lacking. We consider the alternate hypothesis, that the cusps are B, A, and C, as less likely owing to cusp proportions. Cusp A is recumbent with its mesial margin convex and the distal one straight in lateral view. It is as high as cusp C or slightly taller and considerably more robust. Cusp C is not recumbent, because its mesial and distal margins (in lateral view) are both convex. Cusp D is approximately half as tall as cusp C and less recumbent than cusp A, with a mesial margin slightly convex and a distal one straight in lateral view. Cusp D exceeds the distal margin of the root. A minute but distinct cusp E is developed basally at the mesiolingual margin of cusp A. Cusp E and the mesial portion of cusp A are not supported by the root. The only root is labiolingually compressed and ovoidal in cross-section, tapering away from the crown.

**Lower Molariforms:** Three molariforms were present on the lower jaw of *Argentoconodon*; however, only right and left m1 and m2 were recovered. Molariforms are labiolingually compressed, bear two roots, and their crowns are dominated by three main cusps mesiodistally aligned.

On the right dentary (not figured), only the basal portion of m1 in its alveoli and an associated tooth interpreted as a very damaged m2 are preserved. The purported right m2 lacks the posterior root and cusp c is lost to weathering but has been casted from its impression on the matrix, further posteriorly the roots of the right m3 are recognized. The lower left molariforms are better preserved and still found in their alveoli (Fig. 3).

First and second lower molariforms are extremely labiolingually compressed and four mesiodistally aligned cusps are present on the crown: three principal—a, b, and c—and an accessory one—d. The crown is almost flat lingually whereas it is slightly more rounded labially. No wear facets are present. All the cusps arise at the same level of the crown. Main cusps are recumbent, a trait that increases slightly distally. Cusp a is centrally located between the two roots of the molariform. This cusp is slightly larger than cusps b and c, which are subequal in m2 but cusp b is more robust than cusp c in m1. The distal singular cusp (d), only clearly exposed in lateral view in the left m2, is conical and reaches 1/3 of the height of cusp c. No mesial accessory cusp is present; only a small recess can be recognized in the mesial margin of lower molariforms near the base of cusp b; as such, the mesial slope of cusp b forms a rounded eminence projecting mesially from the root, defining a conspicuous, almost

← B) lingual and (G, H) labial views; E–F, K–L, left upper canine in (E, F) labial and (K, L) lingual views; C–D, I–J, partial left maxilla in (C–D) lateral and (I–J) medial views; M–N, partial right maxilla in medial view; O–R, partial left maxilla in (O, R) lateral and (P, Q) medial views. **Abbreviations:** A, B, C, D, E, triconodont cusp nomenclature; aM1, first upper molariform alveoli; aM2, second upper molariform alveoli; aP4, fourth upper premolariform alveoli; M1, first upper molariform; M2, second upper molariform. Dotted areas indicate rock remains; hatched areas in N indicate broken surfaces; dashed lines in B and H indicate fractures and in D, I, N, Q, and R indicate incomplete bone margins.

blade-like surface. In labial view, the m2 is partially covered by the ascending process of the dentary. The interlocking between these two teeth was imbricated; that is, cusp d of the preceding tooth is labial to cusp b of the posterior molariform.

Despite the similarities between m1 and m2, there are differences: in the m2, cusp b is slightly displaced labially compared to cusp c, whereas in the m1 the opposite situation is observed. On the labial side of the m1, the valley separating cusps a and b is not as deep as that present in the m2, and whereas in the m1 the labiolingual width of the crown is constant, in the m2 it narrows distally. The m2 is wider labiolingually and longer mesiodistally (approximately 25% longer) than m1 (Table 1). Furthermore, m1 is labially placed and arises in a lower position from the dentary than the other molariform.

A third lower molariform is represented only by two roots in the right dentary; the anterior root is broader than the distal one. The corresponding alveoli are also present in the left dentary. The lower m3 was considerably smaller than either m1 or m2 and it was probably almost completely hidden from labial view by the coronoid process.

### PHYLOGENETIC RESULTS AND DISCUSSION

Our analysis of triconodont interrelationships is based on the data matrix first developed by Rougier et al. (2001) and the modifications introduced in 2007 (Rougier et al., 2007a) to accommodate new taxa. We also considered some of the characters introduced to this matrix by Gao et al. (2010). In addition, we incorporated into the analysis nine extra taxa (*Acinacodus tagaricus*, *Argentoconodon fariasorum*, *Bocaconodon tamaulipensis*, *Ichthyoconodon jaworowskorum*, *Juchilestes liaoningensis*, *Jugulator amplissimus*, *Meiconodon* sp., *Victoriaconodon inaequalis*, *Volaticotherium antiquus*), and 29 characters (characters 63 to 92), as well as minor modifications to several of the original characters (see Supplementary Data 1; supplementary data available online at [www.vertpaleo.org/jvp/JVPcontents.html](http://www.vertpaleo.org/jvp/JVPcontents.html)).

The resultant data matrix of 92 characters and 37 taxa (see Supplementary Data 2) was analyzed using TNT version 1.1 (Goloboff et al., 2003, 2008). Some of the characters were treated as ordered (following Rougier et al., 2007a). Heuristic searches started from 100 random addition sequences, keeping up to 100 trees in memory for each one of them, and applying the TBR algorithm. The search yielded four most parsimonious trees (MPTs) of 296 steps with a CI of 0.378 and a RI of 0.687. These MPTs differ in the alternative positions of *Juchilestes* and *Bocaconodon*, but the consensus remains well resolved (Fig. 7).

The cladograms support a close relationship of *Argentoconodon* with *Ichthyoconodon* and *Volaticotherium*, a clade here recognized as the tribe Volaticotherini, deriving from the monotypic recognition of the order Volaticotheria and the family Volaticotheridae by Meng et al. (2006). Hence, Volaticotherini is defined here as the common ancestor of *Argentoconodon*, *Ichthyoconodon*, and *Volaticotherium* plus all its descendants. Volaticotherini are nested within the traditional triconodontid subfamily, Alticonodontinae, which also includes a monophyletic grouping of Cretaceous triconodonts (Alticonodontini) with tall crowns and recurved cusps. Affinities of *Argentoconodon*-*Ichthyoconodon*-*Volaticotherium* are supported by four unambiguous synapomorphies: presence of symmetrical or slightly labiolingually compressed lower molariform cusps in cross-section (character 35:0; paralleled in *Arundelconodon*, *Jugulator*, *Meiconodon*, *Astroconodon*, *Corviconodon*, and *Alticonodon*; unknown in *Volaticotherium*), presence of cusp d overhanging distal root in lower molariforms (character 71:1; also occurring in more basal triconodonts, but with the cusp less projected distally), presence of compressed molariform cusps, oval in cross-section (character 83:0), and lower molariforms extremely compressed labiolingually (character 84:2).

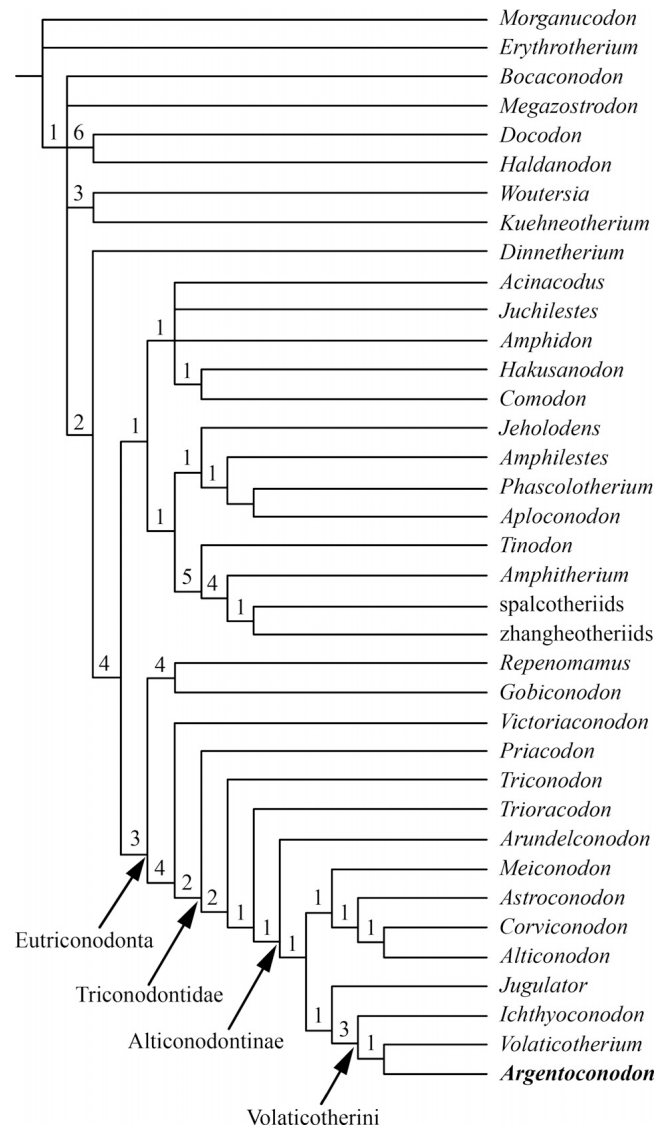


FIGURE 7. Strict consensus of the four most parsimonious trees found. Numbers represent the Bremer support.

A sister-group relationship between *Argentoconodon* and *Volaticotherium* is recovered in all the most parsimonious cladograms, unambiguously supported by the absence of lingual lower molariform cingulum (character 66). Other characters provide ambiguous support to this clade: mesial lower incisor larger than distal ones but not hypertrophied (character 2:1); last lower premolariform shorter or subequal than the first molariform (character 8:1); absence of locking mechanism between posterior lower cheek teeth (character 14:0); cusps b and c of similar size (character 21:1); three or more large mental foramina (character 41:1); presence of an angular process (character 57:1); absence of flat labial surface on upper molariforms (character 59:0); absence of anterior accessory cusps at least in posterior lower molariforms (character 64:0); cusp E in upper molariforms (character 75:1); upper molariforms lacking cingula (character 77:1); recumbent principal cusps on upper molariforms (character 80:1); and high angle of the symphysis with respect to the ventral margin of the dentary posterior to it (character 87:1). Meng et al. (2006) considered the presence of an angular process as a distinctive feature of *Volaticotherium* to the exclusion of any other

triconodont, implying that it was apomorphic of Volaticotheria (tribe Volaticotherini of the present contribution). The angular process is shared as a derived feature by *Argentoconodon* and *Volaticotherium* but unknown in *Ichthyoconodon*, thus this character is ambiguous at the base of Volaticotherini.

In our cladogram the monophyly of the family Triconodontidae, defined as the less inclusive group containing *Priacodon* and *Triconodon*, their common ancestor and all its descendants, is supported, as well as that of the subfamily Alticonodontinae, defined as the last common ancestor of *Arundelconodon* and *Alticonodon* plus all its descendants. On the other hand, the classical subfamily Triconodontinae is shown as a paraphyletic array of triconodontids representing successive stem-taxa to the monophyletic alticonodontines.

Gobiconodontids are recognized as a well-supported monophyletic grouping more closely related to triconodontids than to 'amphilestids,' but the pruning and relocation to the base of the clade that includes amphilestids is only four steps longer.

*Jeholodens* and taxa regarded as amphilestids (see Kielan-Jaworowska et al., 2004, for a review; Rougier et al., 2007a; Gao et al., 2010; Lopatin et al., 2010) are nested in a group that also includes 'symmetrodontans' (*Amphidon*, *Tinodon*, spalcotheriids, and zhangheotheriids) and *Amphitherium*, the sole cladotherian of this study. Although this group has been recovered previously by many authors (Rougier et al., 2001, 2007a; Montellano et al., 2008; Gao et al., 2010), it has remained unnamed. Therefore, we define the clade Amphilestheria nov. as the most inclusive group including those taxa more closely related to Cladotheria than to *Triconodon*.

It is worth pointing out that whenever multituberculates are considered in dental, cranial, and postcranial character analyses (Luo et al., 2002, 2007; Meng et al., 2006; Rougier et al., 2007b), the results show multituberculates (not represented in our data matrix given their extremely apomorphic dentition) as more closely related to therians than triconodonts. Some of these results recover a monophyletic Eutriconodonta (in the sense of Kermack et al., 1973). If these topologies prove to be correct, the Amphilestheria clade would include multituberculates but exclude amphilestids as well as triconodonts. The present study shows Eutriconodonta in its traditional sense to be an unlikely grouping, suggesting that the recovery of this entity in other analyses could be related to a large number of inapplicable entries concerning triconodont anatomy and a poor representation of triconodont taxa.

Although not always recovered as synapomorphies in our analysis, the following unique and shared characteristics of the molariforms of *Argentoconodon* stand out.

*Argentoconodon* lower molariforms differ from those of the other members of the subfamily Alticonodontinae in that they lack well-developed cingula (characters 66 and 67) and four subequal cusps (a–d) fused or set apart by very narrow valleys (character 85). *Argentoconodon* shares with the Alticonodontinae the presence of a tall cusp d incorporated in the crown (character 27:1).

As in *Argentoconodon*, lower molars of *Volaticotherium* have four distally recumbent cusps (a–d) (character 17:1), no mesial accessory cusp e (character 30:1), and an imbricated interlocking mechanism (character 65:1). Moreover, there is a reduction in the number of lower molariforms in both genera when compared with other triconodonts (character 10:0). On the other hand, unlike the Argentinean taxon, *Volaticotherium* has lower molariforms with narrower valleys separating main cusps and well-developed cingula. Furthermore, the size of the lower molariforms of *Volaticotherium* decrease posteriorly, whereas in *Argentoconodon* m2 is larger than m1 (character 37); cusp proportions are also different between the lower molariforms of these taxa.

*Ichthyoconodon* is a monospecific taxon from the Lower Cretaceous of Morocco represented by two isolated teeth. Initially

described by Sigogneau-Russell (1995) as lower molariforms, they were re-interpreted as upper ones by Meng et al. (2006) who recognized resemblance with the upper molariforms of *Volaticotherium*. When compared with *Argentoconodon*, the teeth of *Ichthyoconodon* resemble lower molariforms, because they lack mesial accessory cusps. Thus, based on this feature, also shared by *Volaticotherium*, we tentatively consider *Ichthyoconodon* to be represented by lower teeth, as originally interpreted by Sigogneau-Russell (1995).

Contrasting with upper molariforms of *Argentoconodon*, classical alticonodontine upper molariforms (known from *Corviconodon* and *Astroconodon*) lack cusp E (character 75) and bear poorly separated cusps (character 85), show labial cingula (character 77), and a cusp D proportionately taller with respect to the main cusps and not overhanging the distal root.

Unlike *Argentoconodon*, cusp B of *Volaticotherium* upper molariforms is as recumbent as the remaining principal cusps. Moreover, in *Volaticotherium* cusps D and E are reduced or absent (except for M2, where cusp D is well developed), whereas they are present in all the known upper molariforms of *Argentoconodon*. Other differences between *Argentoconodon* and *Volaticotherium* upper molariforms correspond to variation in relative sizes of cusps.

## CONCLUSIONS

As previously mentioned, *Argentoconodon* was found in rocks that are close to Toarcian in age (Cuneo and Bowring, 2010). Its sister taxon, *Volaticotherium*, has been reported from the Daohugou beds in China (Meng et al., 2006), whose age could range between the Middle Jurassic (164 Ma) and the Early Cretaceous (125 Ma). *Ichthyoconodon*-bearing rocks are of Early Cretaceous age (Berriasian) on the basis of calcareous nannofossils found in adjacent marine strata (Sigogneau-Russell et al., 1998). Accepting these dates, ghost lineages for *Ichthyoconodon* and *Volaticotherium* lineages must extend back at least to the Early Jurassic. The protracted ghost lineage also applies to the whole Alticonodontinae subfamily, given the highly nested position of *Argentoconodon*. The presence of Middle or perhaps Early Jurassic alticonodontines in the southern continents underscores an early radiation of triconodonts toward more faunivorous diets characterized by relatively large animals for Mesozoic standards. The alticonodontines do not appear to reach the Late Cretaceous in South America but are moderately diverse and common in particular North American localities from the Early and Late Cretaceous (Patterson, 1951; Fox, 1969, 1976; Winkler et al., 1990; Jacobs et al., 1991; Cifelli et al., 1997, 1998, 1999; Cifelli and Madsen, 1998; Turnbull and Cifelli, 1998).

Meng et al. (2006) interpreted *Volaticotherium* to have been a gliding animal based on the exceptional preservation of a purported patagium in combination with other osteological traits. Some postcranial characteristics of *Argentoconodon* are similar to those described for *Volaticotherium*, suggesting similar locomotory habits (Gaetano and Rougier, 2010). These similarities include the orientation and morphology of the proximal portion of the femur, with a poorly differentiated head in line with the main shaft of the femur and greater and lesser trochanters confluent with the femoral head. Hence, a sister-group relationship between these two taxa might imply the existence of a widely distributed gliding clade of mammals at least as old as the Early Jurassic, but the preservation of *Argentoconodon* is insufficient to go beyond these tantalizing possibilities.

The peculiar composition of the mammalian fauna from Queso Rallado, with australosphenidans, derived triconodonts, and an allothere, has no ready parallel among other Mesozoic localities and bears credence to the common notion that much is yet to be discovered in the Mesozoic of southern continents.

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