Zootaxa 3085: 1–33 (2011)
www.mapress.com/zootaxa/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

A new sauropod (Macronaria, Titanosauria) from the Adamantina Formation, Bauru Group, Upper Cretaceous of Brazil and the phylogenetic relationships of Aeolosaurini

RODRIGO M. SANTUCCI[1] & ANTONIO C. DE ARRUDA-CAMPOS[2]
[1]*Universidade de Brasília - Faculdade UnB Planaltina, Brasília-DF, 73300-000, Brazil. E-mail: rodrigoms@unb.com.br*
[2]*Museu de Paleontologia de Monte Alto, Praça do Centenário, s/n. Monte Alto-SP, 15910-000, Brazil.*
E-mail: mpaleo@montealto.sp.gov.br

Table of contents

Abstract . . . 1
Introduction . . . 2
Historical background . . . 2
Geological setting . . . 4
Systematic Palaeontology . . . 4
DINOSAURIA Owen, 1842 . . . 4
SAURISCHIA Seeley, 1887 . . . 4
SAUROPODA Marsh, 1878 . . . 4
MACRONARIA Wilson and Sereno, 1998. . . . 4
TITANOSAURIFORMES Salgado, Coria and Calvo, 1997b. . . . 4
TITANOSAURIA Bonaparte and Coria, 1993 . . . 4
AEOLOSAURINI Franco-Rosas, Salgado, Rosas and Carvalho, 2004 . . . 5
Aeolosaurus Powell, 1987 . . . 5
    Aeolosaurus rionegrinus Powell, 1987 . . . 5
    Aeolosaurus maximus sp. nov. . . . 6
Phylogenetic analysis . . . 17
Comparison and discussion . . . 19
Conclusions . . . 25
Acknowledgements . . . 25
References . . . 26
APPENDIX 1. . . . 29
APPENDIX 2. . . . 29

Abstract

Remains of a new titanosaur, *Aeolosaurus maximus* **sp. nov.**, from the Adamantina Formation (Upper Cretaceous), Bauru Group, São Paulo State of Brazil are described. The new species is represented by a single partially articulated skeleton and is characterized by having a well-developed posterior protuberance below the articular area on the anterior and middle haemal arches and a lateral bulge on the distal portion of the articular process of the mid-posterior haemal arches. It shares with other *Aeolosaurus* species the presence of prezygapophyses curved downward on anterior caudal vertebrae and haemal arches with double articular facets set in a concave posterodorsal surface. These two characteristics are interpreted here as synapomorphies for the genus *Aeolosaurus*. The new diagnosis for the genus *Aeolosaurus* does not support the inclusion of *Gondwanatitan* within *Aeolosaurus* as previously proposed by some authors. The phylogenetic analysis recovered the two *Aeolosaurus* from Argentina as sister groups with *A. maximus* and *Gondwanatitan* as progressively more basal taxa (*Gondwanatitan* (*A. maximus* (*A. rionegrinus*, *A. colhuehuapensis*))). Additionally, according to the results of the phylogenetic analysis performed in this work, the taxa *Panamericansaurus*, *Rinconsaurus*, and *Maxakalisaurus* are also nested within Aeolosaurini, being more basal than *Aeolosaurus* and *Gondwanatitan*. On the basis of the stratigraph-

Accepted by R. Benson: 3 Oct. 2011; published: 31 Oct. 2011

ical range of the *Aeolosaurus* occurrences in Argentina and the age proposals based on microfossils for the Bauru Group, it is assumed a Campanian–Maastrichtian age for the top of the Adamantina Formation for the Monte Alto region in São Paulo State and the bottom of the Marília Formation in Peirópolis, Minas Gerais State—the places where *Aeolosaurus* remains have been reported in Brazil.

Key words: Dinosauria, Sauropoda, Titanosauriformes, Aeolosaurini, *Aeolosaurus*, cladistic analysis

Introduction

The knowledge of titanosaur diversity and geographical distribution has witnessed an extreme increase during the last decades with the description of new material (and species) from Asia (Martin *et al.* 1994; Jain and Bandyopadhyay 1997), Europe (Le Loeuff 1993, 1995; Sanz *et al.* 1999), Africa (Jacobs *et al.* 1993; Curry Rogers and Forster 2001; Gomani 2005), Australia (Molnar and Salisbury 2005; Hocknull *et al.* 2009), and South America (Powell 1986, 2003; Calvo and Bonaparte 1991; Bonaparte and Coria 1993; Salgado and Coria 1993; Salgado and Azpilicueta 2000). In Brazil new forms have also been reported lately such as *Gondwanatitan faustoi* (Kellner and Azevedo 1999), *Baurutitan britoi* (Kellner *et al*. 2005, first reported in Powell, 1986), *Trigonosaurus pricei* (Campos *et al*. 2005, first reported in Powell 1986), *Adamantisaurus mezzalirai* (Santucci and Bertini 2006a), *Maxakalisaurus topai* (Kellner *et al.* 2006), *Uberabatitan ribeiroi* (Salgado and Carvalho 2008), and *Tapuiasaurus macedoi* (Zaher *et al.* 2011). Additionally, fragmentary remains have been described from Minas Gerais State (Santucci and Bertini 2006b; Lopes and Buchmann 2008; Santucci 2008), and Morro do Cambambe, Mato Grosso State (Franco-Rosas *et al*. 2004). Curiously, although well known by numerous remains around the world, the inter-relationships within the clade Titanosauria are not well understood yet.

In 1997 and 1998 the staff of the Museu de Paleontologia de Monte Alto (Monte Alto Paleontological Museum) collected a partially articulated skeleton of a large titanosaur (Fig. 1), here called *Aeolosaurus maximus* **sp. nov.** The skeleton has been found with the cervical vertebrae (only the pairs of the mid-cervical ribs and two posterior cervical vertebrae), caudal vertebrae, humeri, and femora approximately in their anatomical position, whereas some distal caudal vertebrae, ribs, and other limb elements were slightly scattered away. Near the skeleton were also several theropod and crocodylomorph teeth, these were found in close association with the hind limb elements and probably belong to the animals that scavenged the carcass.

In this paper we describe this skeleton as a new species and establish its phylogenetic relationships by using previous data matrices and character lists for sauropods available in the literature. Additionally, a review of the material referred to the genus *Aeolosaurus* together with a phylogenetic approach of the characters that support both the genus *Aeolosaurus* and the clade Aeolosaurini are also addressed in this paper. *Aeolosaurus maximus* **sp. nov.** is the first well-preserved *Aeolosaurus* reported outside Argentina and broadens the geographic distribution of this genus in South America.

Historical background

During the last decades some titanosaurs have been referred to the genus *Aeolosaurus* in Argentina. Although not complete, these specimens preserve anterior caudal vertebrae and, in some instances, several appendicular elements, which allow for good comparison among them. Because anterior caudal vertebrae are present in all these specimens, the diagnosis for the genus is mainly based on the morphology of these axial elements. On the other hand, as different authors have reported new specimens referred to the genus *Aeolosaurus*, the original diagnosis has been emended several times.

Aeolosaurus rionegrinus (Powell 1987) was the first Aeolosaurini to be described. This species is represented by a partial skeleton comprising anterior caudal vertebrae and appendicular elements (MJG-R 1) collected from the Angostura Colorada Formation in Río Negro Province, Argentina (Powell 1986, 1987, 2003). Unfortunately, the original description is part of Powell's PhD, which is not in line with the ICZN rules (item 8.1.3) for naming new taxa. At that time, Powell (1986) accommodated *Aeolosaurus*, together with the genus *Titanosaurus*, within the subfamily Titanosaurinae mainly on the basis of the presence of caudal vertebrae with narrow ventral face, high lateral face, and facets of the prezygapophyses facing laterally. However, this assignment was not supported by subsequent cladistic analyses on titanosaurs. Powell (1987) redescribed *A. rionegrinus*, also providing a diagnosis. This is then considered as the basis of the formal description for *A. rionegrinus*. Among the features listed by Powell (1987) as diagnostic of *A. rionegrinus* are the presence of long prezygapophyses, neural spine directed forward in mid-anterior caudal vertebrae, chevrons with double articular ends set in a concave posterodorsal surface, and other features regarding the appendicular skeleton, such as: broad scapula with expanded distal end, with a short and prominent ridge for muscular attachment near the upper border of its medial face; humerus robust with a prominent apex on the deltopectoral crest; metacarpals short and robust; and pubis broad without longitudinal elevation.

Salgado and Coria (1993) reported new *Aeolosaurus* remains from the Allen Formation, Río Negro Province. These remains comprise caudal vertebrae (MPCA 27174) and appendicular elements (MPCA 27175, MPCA 27176, and MPCA 27177) and were regarded by these authors as *Aeolosaurus* sp. Additionally, Salgado and Coria (1993) proposed an emended diagnosis for the genus which included the presence of large prezygapophyseal articular facets in anterior caudal vertebrae, but excluded the expanded distal end of the pubis from the original diagnosis proposed by Powell (1987).

A third occurrence from the Río Negro Province was described by Salgado *et al.* (1997a). These remains of an incomplete individual were unearthed from the Los Alamitos Formation and comprise anterior caudal vertebrae and limb elements (MPCA 27100), showing some morphological overlap with the remains of *A. rionegrinus* and the material recovered from the Allen Formation (MPCA 27174-27177). Salgado *et al.* (1997a) also provided an emended diagnosis for the genus which was limited to the morphology of the middle and posterior caudal vertebrae (e.g. neural arch located on the anterior half of the centrum and neural spine directed forward on middle and posterior caudal vertebrae).

Gondwanatitan faustoi (Kellner and Azevedo 1999) was reported from the Adamantina Formation, Bauru Basin, in western São Paulo State, Brazil. Among the characteristics listed in the diagnosis of *G. faustoi*, Kellner and Azevedo (1999) included one of the features previously considered as a synapomorphy of *Aeolosaurus*, that is: the presence of neural spine directed forward in caudal vertebrae. Because of that, and because other characteristics originally regarded as diagnostic of *Gondwanatitan* are also present in the previously reported *Aeolosaurus* specimens or even in other titanosaurs, such as deltopectoral crest of the humerus directed medially and cnemial crest of the tibia slightly directed medially, it has been suggested that *Gondwanatitan* could be accommodated within the genus *Aeolosaurus* (Bertini *et al.* 2000; Santucci and Bertini 2001; Almeida *et al*. 2004).

Franco-Rosas *et al.* (2004) assigned some isolated caudal vertebrae (MP 284, 285, 287, and 288) and a fragmentary tibia (MP 286), from the Bauru Group of Mato Grosso State, to the genus *Gondwanatitan* and erected a new clade Aeolosaurini, which was defined as the most inclusive clade comprising *A. rionegrinus* and *G. faustoi*, but not *Saltasaurus loricatus* and *Opisthocoelicaudia skarzynskii*. According to these authors, Aeolosaurini would include the species *A. rionegrinus*, *G. faustoi*, and *Rinconsaurus caudamirus* (Calvo and González Riga 2003). Although Franco-Rosas *et al*. (2004) only depicted a hypothetical diagram of titanosaur relationships, they provided a set of characters that would support the clade Aeolosaurini which mainly encompasses the characteristics for the caudal vertebrae included in the emended diagnosis for *Aeolosaurus* proposed by Salgado and Coria (1993).

A new aeolosaur species was described by Casal *et al.* (2007). *Aeolosaurus colhuehuapensis* Casal *et al.* (2007) is based on several incomplete caudal vertebrae and chevrons (UNPSJB-PV 959/1-959/27) unearthed from the upper member of the Bajo Barreal Formation, Chubut Province. The new diagnosis proposed by these authors for the genus *Aeolosaurus* is similar to that one proposed by Salgado *et al.* (1997a) and also included the presence of haemal arches with double articular facets set in a concave posterodorsal surface.

More recently, Calvo and Porfiri (2010) described another Aeolosaurini, *Panamericansaurus schroederi*, from the Allen Formation, Neuquén Province, Argentina. According to Calvo and Porfiri (2010), *Panamericansaurus* has all the synapomorphies for Aeolosaurini but the presence of the anterior margin of the anterior caudal vertebrae strongly inclined forward (Calvo and Porfiri 2010).

Apart from these descriptions, *Aeolosaurus* has rarely been included in cladistic analyses. In the cladogram presented by Salgado *et al*. (1997b) *Aeolosaurus* is regarded as more related to the clade comprised by *Saltasaurus*, *Neuquensaurus*, and *Alamosaurus* than other titanosaurs. More recently it was either considered as more related to *Rinconsaurus* (Calvo and González Riga 2003) or to *Gondwanatitan* (Calvo *et al.* 2007a; Calvo *et al.* 2007b; González Riga *et al*. 2009). In all these instances, however, the genus *Aeolosaurus* is nested together with other apical titanosaurs. *Aeolosaurus* was also included in the analysis of Curry Rogers (2005), but it falls in a basal polytomy encompassing all Titanosauria.

Martinelli *et al.* (2011) recently published a review of the taxonomic status of the occurrences of the genus *Aeolosaurus* in Brazil and stated they cannot be regarded to this genus because they do not have the articular facets of the postzygapophyses located anteriorly to the edge of the centrum, one of the features proposed by Casal *et al.* (2007) in the emended diagnosis for the genus *Aeolosaurus.*

Geological setting

The Bauru Group (Upper Cretaceous) is comprised by the Araçatuba, Adamantina, São José do Rio Preto, and Marília formations in São Paulo State (Fernandes and Coimbra 2000). Among these units, the Adamantina Formation has the greatest ourcrop area. Mezzalira (1989) and Gobbo-Rodrigues *et al.* (1999) reported well-preserved remains of ostracods, conchostraceans, and molluscs. The vertebrate record is worthy of note and comprises testudines, crocodylomorphs, theropods, sauropods, mammals, and more recently birds (Bertini *et al.* 1993; Kellner and Campos 2000; Alvarenga and Nava 2005).

The Adamantina Formation corresponds to reddish to beige, fine to medium grained massive sandstones. These sandstones gradationally change from beige massive to incipiently laminated siltstones. Locally, conglomeratic and lamitic lenses and cross-bedded sandstones are present (Fernandes and Coimbra 2000).

There is no consensus about the age of the Adamantina Formation. Dias-Brito *et al.* (2001) suggested a Turonian–Santonian age for the Adamantina Formation and a depositional hiatus to the overlaying Marília Formation on the basis of ostracod and charophyte assemblages. Using vertebrates, Bertini *et al.* (1999a), Bertini *et al.* (2000) and Santucci and Bertini (2001) suggested a Campanian–Maastrichtian age for some localities of the Adamantina Formation in São Paulo State mainly based on the occurrence of the titanosaur *Aeolosaurus* in these deposits (see discussion below). The same age was assigned by Gobbo-Rodrigues *et al.* (1999) on the basis of ostracods.

Institutional abbreviations. CPP—Centro de Pesquisas Paleontológicas L. I. Price, Uberaba, Brazil; **LGP**—Laboratório de Geologia e Paleontologia, Fundação Universidade do Rio Grande, Brazil; **MJG**—Museo ‘Jorge Gerhold’, Río Negro, Argentina; **MPCA**—Museo Provincial de Cipolletti, Río Negro, Argentina; **MP**—Museu de Paleontologia da Universidade Federal de Mato Grosso, Mato Grosso, Brazil; **MPMA**—Museu de Paleontologia de Monte Alto, São Paulo, Brazil; **UFRJ**—Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; **UNPSJB**—Universidad Nacional de la Patagonia San Juan Bosco, Comodoro Rivadavia, Argentina.

Morphological abbreviations. acpol, anterior centropostzygapophyseal lamina; **cp**, capitulum; **cpol**, centropostzygapophyseal lamina; **cvr**, cervical rib; **daf**, double articular facets; **dp**, diapophysis; **f**, fossa; **fhd**, femoral head; **fic**, fibular condyle; **ft**, fourth trochanter; **lb**, lateral bulge; **nc**, neural canal; **ns**, neural spine; **pcdl**, posterior centrodiapophyseal lamina; **pf**, pneumatic foramen; **podl**, postzygodiapophyseal lamina; **posl**, postspinal lamina; **poz**, postzygapophysis; **ppt**, posterior protuberance; **pre**, prezygapophysis; **spdl**, spinodiapophyseal lamina; **spol**, spinopostzygapophyseal lamina; **sprl**, spinoprezygapophyseal lamina; **tb**, tuberculum; **tic**, tibial condyle; **tp**, transverse processes; **tpol**, intrapostzygapophyseal lamina. Abbreviations for vertebral laminae follow Wilson (1999).

Systematic Palaeontology

DINOSAURIA Owen, 1842

SAURISCHIA Seeley, 1887

SAUROPODA Marsh, 1878

MACRONARIA Wilson and Sereno, 1998

TITANOSAURIFORMES Salgado, Coria and Calvo, 1997b

TITANOSAURIA Bonaparte and Coria, 1993

AEOLOSAURINI Franco-Rosas, Salgado, Rosas and Carvalho, 2004

Definition. The branch-based clade that corresponds to the most inclusive clade containing *A. rionegrinus* and *G. faustoi*, but not *Saltasaurus loricatus* and *Opisthocoelicaudia skarzynskii* (Franco-Rosas *et al.* 2004).

Temporal range. Late Cretaceous (Campanian–Maastrichtian).

Comments. Although the International Code of Phylogenetic Nomenclature—PhyloCode (Cantino and de Queiroz, 2010) is not in force, the basis of phylogenetic nomenclature has long been established (de Queiroz and Gauthier, 1990, 1992, 1994) and is broadly used in recent papers on vertebrate paleontology (see Padian *et al.*, 1999 and Upchurch *et al.*, 2004, for some examples). According to the original definition provided by Franco-Rosas *et al.* (2004), Aeolosaurini is a branch-based clade that corresponds to the most inclusive clade containing *A. rionegrinus* and *G. faustoi*, but not *Saltasaurus loricatus* and *Opisthocoelicaudia skarzynskii*. Among the elements present in the protologue of this taxon name Franco-Rosas *et al.* (2004) furnished a diagnosis, a list of species (including a third specifier, *Rinconsaurus caudamirus*), a list of assigned materials, and a figure depicting the hypothetical phylogenetic relationships of Titanosauria with the putative position of Aeolosaurini within. Taking into account and the original definition of Aeolosaurini, the elements presented in the protologue by Franco-Rosas *et al.* (2004) pose two main problems. First, since Aeolosaurini is a branch-based clade it does not have a fixed diagnosis because they represent branches that proceed from a node (Padian *et al.*, 1999 pg. 70) or, in other words, because we do not know all the taxa in branch-based taxa, their diagnosis is not possible (Benton, 2004 pg. 7). Second, a third internal specifier, *R. caudamirus*, which does not have its phylogenetic relationships well-established, was included in the protologue. Taking it into account, two scenarios are possible: *Rinconsaurus* is an Aeolosaurini or not. If *Rinconsaurus* is depicted as more related to *Aeolosaurus* and *Gondwanatitan* than any other titanosaur, it will be considered as an Aeolosaurini, according to the definition proposed by Franco-Rosas *et al.* (2004), regardless its inclusion as a specifier in the protologue. On the other hand, if *Rinconsaurus* is depicted as more related to other non-Aeolosaurini (e.g. a Saltasauridae titanosaur) than *Aeolosaurus* and *Gondwanatitan*, the original definition of Aeolosaurini will be violated.

For this reason we propose here to exclude the diagnosis and the third specifier (*Rinconsaurus caudamirus*) from the protologue that establishes the name Aeolosaurini.

Aeolosaurus Powell, 1987

Type species. *Aeolosaurus rionegrinus* Powell, 1987

Geographical and stratigraphical range. Río Negro and Chubut provinces, Argentina, Allen, Angostura Colorada, Bajo Barreal, and Los Alamitos formations; and São Paulo and Minas Gerais states, Brazil, Adamantina and Marília formations.

Emended diagnosis. Titanosaur with the following unique association of characters: prezygapophyses curved downward on anterior caudal vertebrae and haemal arches with double articular facets set in a concave posterodorsal surface on anterior and middle caudal vertebrae.

Comments. In the description of *Aeolosaurus rionegrinus*, Powell (1986, 1987, 2003) mentioned several characteristics that, according to him, would be the autapomorphies of that species. With the description of a new *Aeolosaurus* species from Argentina (Casal *et al.*, 2007) and the proposal of the clade Aeolosaurini by Franco-Rosas *et al.* (2004), many of the autapomorphies of *A. rionegrinus* became the synapomorphies of the genus *Aeolosaurus* or of the clade Aeolosaurini, which also comprises the Brazilian titanosaur *Gondwanatitan*. Additionally, many of the appendicular features seen in *A. rionegrinus* cannot be assessed in these other taxa due to preservation problems. Since only the anterior and middle caudal vertebrae and the haemal arches are preserved in nearly all aeolosaurines known to date, we decided to constrain the diagnosis of the genus to these elements until more complete material are available in order to avoid creating ambiguous characteristics.

Aeolosaurus rionegrinus Powell, 1987

Derivation of name. *rionegrinus*, in reference to the Río Negro Province where the specimen has been found (Powell, 1987).

Holotype. MJG-R 1, seven anterior caudal vertebrae; incomplete scapulae; humeri; right ulna and radius; five metacarpals; nearly complete ischia; right tibia and fibula; astragalus; and incomplete fragments (Powell, 1987).

Locality and Horizon. Angostura Colorada Formation, upper Campanian–lower Maastrichtian, Upper Cretaceous, Casa de Piedra, Río Negro Province, Argentina (Powell, 1987).

Emended diagnosis. Titanosaur with the following unique association of characteristics: prezygapophyses directed mainly upward on anteriormost caudal vertebrae and slightly curved downward on the remaining anterior caudal vertebrae; prezygapophyseal articular facets widened by the presence of both a dorsal and a ventral protuberance on the prezygapophyses of the anterior caudal vertebrae; and apex of the convexity of the posterior articulation strongly displaced upward, so that the apex is flushed to the level of the dorsal margin of the centrum on anterior and middle caudal vertebrae.

Aeolosaurus maximus sp. nov.

1999a *Aeolosaurus* sp. Bertini *et al.*
1999b *Aeolosaurus* sp. Bertini *et al.*
2001 *Aeolosaurus* sp. Santucci and Bertini, p. 308, Fig. 2A

Derivation of name. *maximus*, in reference to the size of the specimen, meaning large in Latin.

Holotype. MPMA 12-0001-97, two incomplete posterior cervical vertebrae; seven incomplete cervical ribs; a fragmentary anterior dorsal centrum; a probable fragment of a middle dorsal vertebra; a fragmentary posterior dorsal vertebrae; several incomplete diapophysis of dorsal vertebrae; 12 incomplete dorsal ribs; six articulated anterior caudal vertebrae; a mid caudal centrum; two posterior caudal vertebrae; six anterior, one mid, and one posterior haemal arches; a probable fragmentary scapula; an incomplete right humerus; a probably fragmentary left humerus; a probably incomplete radius; incomplete right femur; left femur; left ischium; and several unidentified fragments. The material is housed in the Museu de Paleontologia de Monte Alto (Monte Alto Paleontological Museum), São Paulo, Brazil.

Locality and horizon. Reddish, massive sandstones locally with carbonatic cementation, top of the Adamantina Formation, Campanian–Maastrichtian, Upper Cretaceous, approximately 12 Km SW of the city of Monte Alto, São Paulo State, Brazil (Fig. 1).

Diagnosis. Titanosaur characterized by the following unique association of characteristics: well-developed posterior protuberance below the articular area on the anterior and middle haemal arches and lateral bulge on the distal portion of the articular process of the mid-posterior haemal arches. An additional set of ambiguous synapomorphies includes: presence of posterior centrodiapophyseal lamina (pcdl) at least 50% thicker than the postzygodiapophyseal lamina (podl) in posterior cervical vertebrae; posterior dorsal vertebrae with intrapostzygapophyseal lamina and an oblique anterior centropostzygapophyseal lamina (acpol) which bifurcates from the proximal portion of the centropostzygapophyseal lamina (acpol); mid-thoracic ribs bearing well-developed anterior and posterior crests with a D-shaped cross section. These features are considered ambiguous because they cannot be assessed in other *Aeolosaurus* species so far, and may correspond to a set of synapomorphies of *Aeolosaurus* or even Aeolosaurini.

Taphonomic note. The bones of *A. maximus* were unearthed from a small area of about 100m^2 (Fig. 1) and from the same stratigraphical level. No repeated elements were found. According to their position in the field, they represent a single individual that was lying with its left side down. The two fragmentary posterior cervical vertebrae together with several pairs of cervical ribs were found articulated, with the cervical ribs overlapping at least two consecutive ones. Their position in the field suggests the neck was dorsiflexed, which indicates the skeleton has undergone at least a slightly post-mortem exposure prior its final burial. The same pattern was observed in the recovered anterior caudal series. The high degree of articulation, together with the presence of both large complete bones and small and delicate elements, also suggests the skeleton has undergone little transport.

Several theropod and crocodylomorph teeth have been recovered from the area where both femora were found. The presence of these teeth around this portion of the skeleton suggests that small theropod dinosaurs and crocodylomorphs have fed on the carcass. This pattern has also been reported elsewhere, where teeth of carnivorous dinosaurs are found near the sacral region of articulated or semi-articulated sauropods (Buffetaut and Suteethorn 1989). However, bite marks have not been found in the bones.

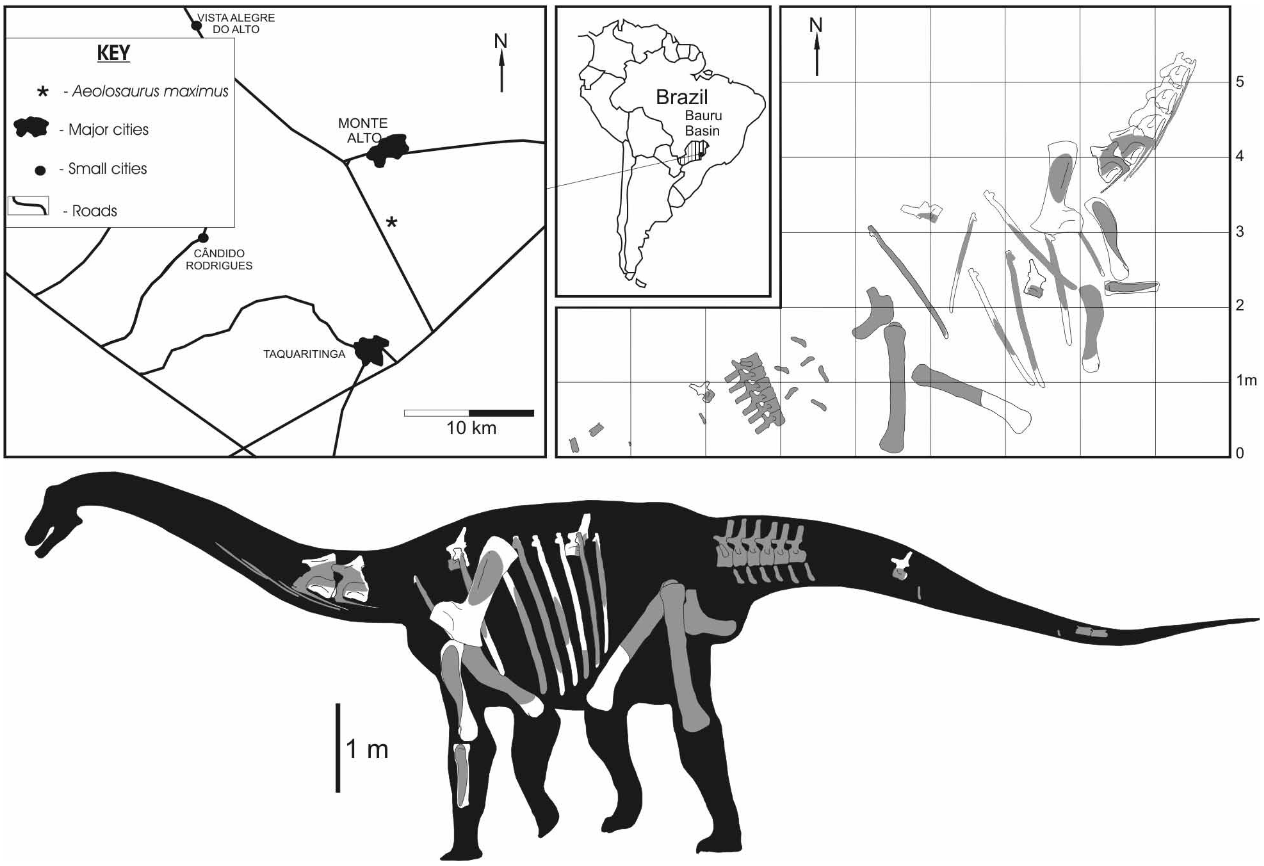

FIGURE 1. *Aeolosaurus maximus* **sp. nov.**, map showing the location of the fossil site and sketches depicting the way the bones were found in the filed and their anatomical position in the skeleton.

Description. Cervical vertebrae. Comparing the cervical vertebrae of *Aeolosaurus maximus* with the nearly complete cervical series of *Malawisaurus dixeyi* (Gomani 2005) and the Series A from Peirópolis (Powell 2003), they seem to correspond to posterior cervical vertebrae, probably the 10th and 11th in the series. The two articulated posterior cervical vertebrae consist of the left lateral portion of the neural arches lacking the centra and the neural spines. Because of their large size (the preserved portion of the posteriormost cervical vertebra is 85 cm in length) and their slender structure, these vertebrae were kept in articulation during preparation. Moreover, they also have signs of dorsoventral deformation (Fig. 2).

According to the preserved portions, the internal bony tissue (camellae) of the centra is composed of subcentimetrical coels circumscribed by thin lamellae. Both vertebrae have the left cervical ribs attached to their centra. The capitulum and tuberculum are thin sheets of bone which are anteroposteriorly wide. However, their contact with the transverse processes is not clear. The tuberculum is internally reinforced by a columnar ridge that extends from the base of the capitulum until the tuberculum. The anterior end of the cervical ribs is shorter than the posterior one and tapers to a point. The posterior end is long and slender, formed by a thin dorsoventrally convex sheet of bone that gradually becomes oval in cross section toward the end. According to the preserved cervical ribs (some of them are 60 cm in length) and their position in the field, they may overlap two or three adjacent cervical vertebrae (Fig. 1).

On both vertebrae the parapophyses are badly damaged and therefore cannot be properly described. The diapophyses are blade-like projections and lay under the level of the prezygapophyses. On the posterior margin of the diapophyses there is a small sheet of bone that projects posteriorly. The most striking feature of these vertebrae is the strong development of the posterior centrodiapophyseal lamina, which is stouter than the postzygodiapophsyeal lamina. Although not completely preserved on both centra, the posterior centrodiapophyseal lamina seems to extend until the posterior margin of the centrum. The postzygodiapophsyeal lamina is thin, well-developed, and extends until the anterior margin of the postzygapophysis. This region is only preserved in the anteriormost cervical vertebra, which is broken and levered forward and upward by the forward displacement of the proceeding cervical vertebra (Fig. 2).

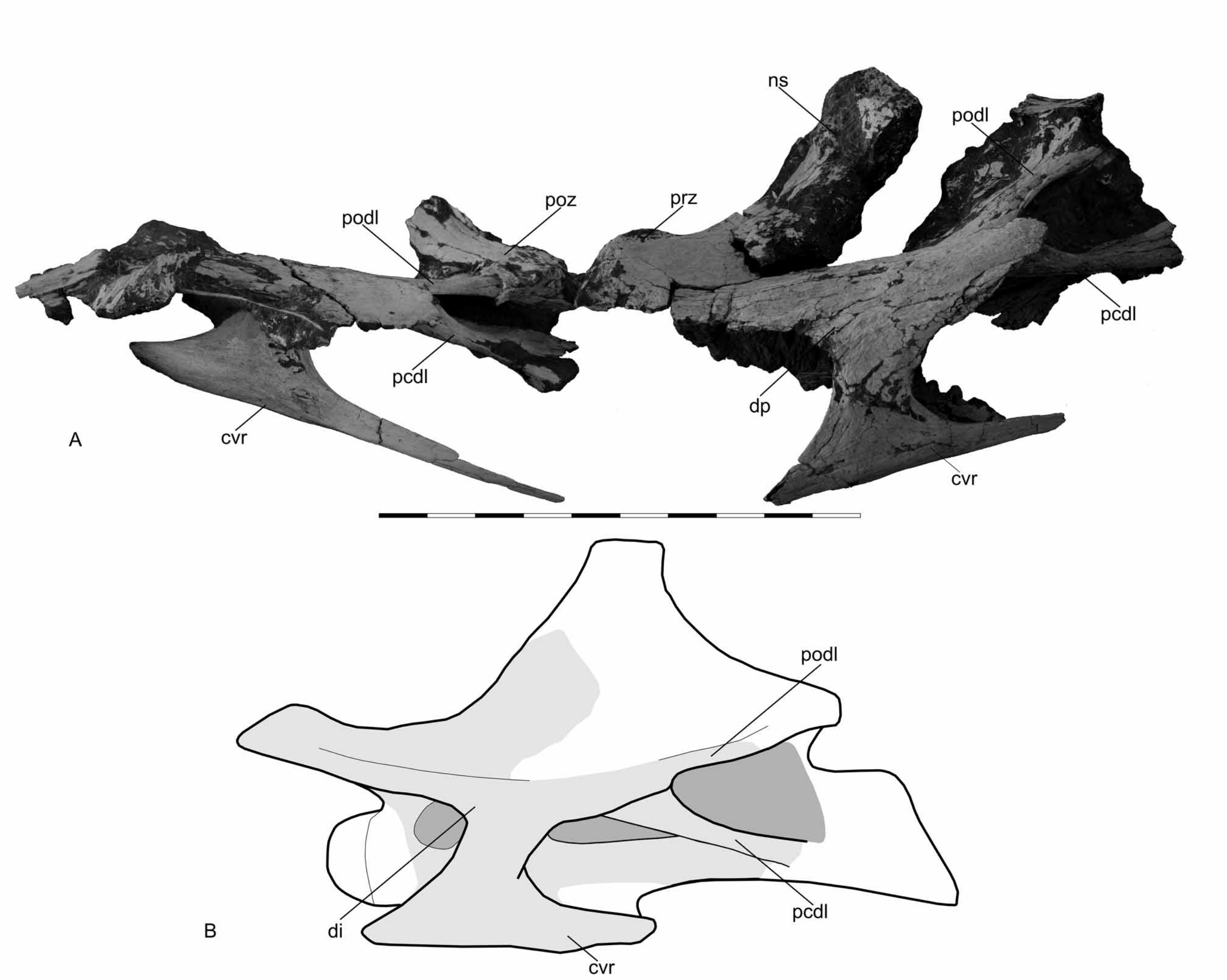

FIGURE 2. *Aeolosaurus maximus* **sp. nov.**, holotype. A, articulated posterior cervical vertebrae (MPMA 12-0001-97) in left lateral view. B, reconstruction of the posteriormost cervical vertebrae (MPMA 12-0001-97) in left lateral view. Shaded areas represent preserved portions. Dark grey corresponds to putative large depressions. Scale bar equals 50 cm.

The prezygapophysis is short and robust, with a wide, flat and elliptical articular facet. The anterior portion of the neural spine (left spinoprezygapophyseal lamina) is preserved. It originates right at the posterior margin of the prezygapophyseal articular facet and extends upward and backward (Fig. 2).

Dorsal vertebrae. Only fragmentary dorsal vertebrae are preserved. A fragmentary neural arch is preserved, comprising a partial neural spine, the right diapophysis, and the right prezygapophysis. According to the height of the neural spine and its shape, this dorsal vertebra is regarded as a middle dorsal vertebra. The neural spine is tall and has an acute triangular shape in anterior view and is anteroporsteriorly short. The diapophysis is robust, short, and directed laterally. The spinodiapophyseal lamina is stout and well developed. The prezygapophysis is broken and seems to be shifted to a more medial position because its articular facet is unusually aligned to the sagittal plane (Fig. 3A). A dorsal centrum (Fig. 3B1-2) is poorly preserved. Its shape cannot be established, but it has well-developed internal coels. In the anterior face of the neural arch there are three fossae that widen into large internal chambers. Between these fossae, on the anterior portion of the neural arch, there are two diagonal shallow ridges that cross each other near their base. Some isolated transverse processes also have spongy bony tissue.

A left postzygapophysis is attributed to an anterior dorsal vertebra. It is robust and has a wide and flat articular facet. On its medial side a thin lamina is attached to it, which seems to be a fragmentary intrapostzygapophyseal lamina.

A large fragmentary posterior dorsal vertebra is preserved and consists of part of the neural arch fused to the centrum, both postzygapophyses, and part of the postzygodiapophsyeal lamina. The dorsal margin of the posterior articulation of the centrum seems to form a large concavity, which indicates that the centrum was opisthocoelous.

The neural canal is large and semi-oval in shape. In lateral view the posterior portion of the neural arch seems to bifurcate distally, where the side that forms the lateroposterior portion of the neural arch (cpol) bifurcates from the base of the postzygapophysis downward. Because of that, an additional oblique lamina, here called anterior centro-postzygapophyseal lamina (acpol), originates from the base of the postzygapophysis and extends forward (Fig. 3C1-2). Unfortunately, its proximal end is not preserved and, therefore, the area where it attaches is not known. The postzygodiapophsyeal lamina is thin and well-developed. The postzygapophyses are robust with large and flat articular facets and face ventrally. They are supported by simple, robust, and well-developed spinopostzygapophyseal laminae. The postspinal lamina consists of a shallow and stout ridge. Although the hyposphene is absent, the postzygapophyses are linked to each other by a thin intrapostzygapophyseal lamina at their bases (Fig. 3C1-2).

Caudal vertebrae. The anterior caudal vertebrae consist of a series of six articulated elements. By comparison with complete caudal series from Brazil (Kellner *et al*. 2005) and other anterior caudal vertebrae of other *Aeolosaurus* specimens (Salgado *et al.* 1997a), they would correspond to the fourth to ninth caudal vertebra (Table 1). All caudal vertebrae are strongly procoelous, with the apex of the convexity of the posterior end slightly displaced above the midline of the centrum, and lack internal spongy bony tissue (Figs. 4–5).

TABLE 1. Measurements of the preserved anterior caudal vertebrae of *A. maximus* (MPMA 12-0001-97). Measurements are in cm. Asteriscs indicate estimated measurements.

	C4	C5	C6	C7	86	C9
Total length including prezygapophises	34,2	35,8	32,2	33,5	33,0	33,5
Length of centrum (with condyle)	26,3	25,5	24,0	20,4	22,0	22,5
Length of centrum (without condyle)	18,5	17,0	17,5	16,0	15,5	16,5
Total height (centrum + neural arch + neural spine)	-	-	42,0*	34,0	36,5	31,5*
Height of neural arch and neural spine	-	-	24,3*	19,5	21,0	16,5*
Height of centrum (posterior view)	17,5	16,7	16,1	15,0	15,5	15,0
Width of centrum (posterior view)	16,5*	17,5	17,0	16,5	16,3	17,0
Width of neural chanal (anterior view)	5,5	5,0	4,7	4,8	4,5	4,4
Heigth of neural chanal (anterior view)	4,5	4,2	3,5	3,3	3,3	2,1
Lenght of neural arch	10,5	10,2	10,1	9,0	9,5	10,0
Length of prezygapophyses	13,5*	11,5	8,5	10,0	9,5	10,0
Distance between the centers of the articular facets of the prezyg.	9,0*	9,1	6,6	6,5	6,4	5,6
Distance between the centers of the articular facets of the postzyg.	8,4	5,9	-	-	5,1	4,6
Distance between the articular facets of the prezyg./postzyg.	21,5	20,7	-	-	17,5	18,0
Width at the tip of transverse processes	-	34,0*	30,4*	30,0*	-	-

The anteriormost preserved caudal vertebra (probably the fourth caudal vertebra) lacks the right transverse process, the right prezygapophysis, and the distal end of the neural spine. The centrum is relatively long and higher than wide. The ventral face is slightly concave and surrounded by shallow lateral ridges. The neural arch is anteroposteriorly short and located on the anterior half of the centrum. The transverse process is stout and directed backward. A large protuberance is located between the anterior margin of the base of the transverse process and the prezygapophysis (Fig. 4B). The prezygapophysis is robust, directed forward, and slightly curved downward when seen in lateral view. The postzygapophyses are large, located at the base of the neural arch, and have elliptical articular facets. At least the base of the neural spine is compressed laterally. The well-developed spinoprezygapophyseal laminae are stout and extend over the preserved portion of the neural spine (Fig. 4A–B).

The fifth caudal vertebra is nearly complete only lacking the distal end of the neural spine. The centrum is higher than wide and the lateral faces are concave anteroposteriorly. The posterior articulation of the centrum has a shallow elliptical groove. The morphology of this caudal vertebra is similar to that of the previous one, except for the curvature of the prezygapophysis, which is less developed, and the distal end of the transverse process, which is slightly expanded dorsoventrally (Fig. 4C–D).

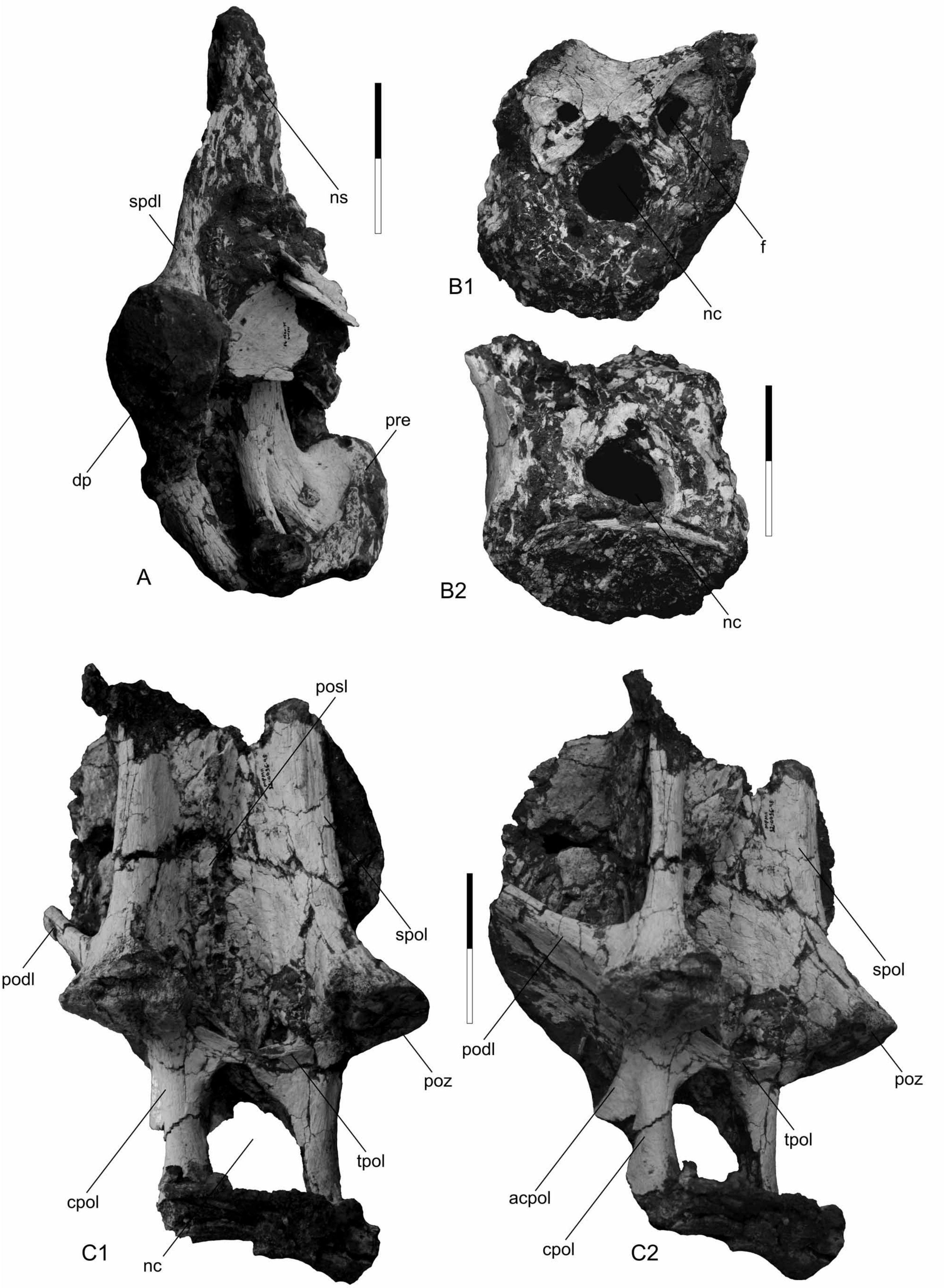

FIGURE 3. *Aeolosaurus maximus* **sp. nov.**, holotype (MPMA 12-0001-97). A, anterior dorsal vertebra in right lateral view. B1-2, dorsal centrum in anterior and posterior views. C1-2, posterior dorsal vertebra in posterior and latero-posterior views. Scale bar equals 10 cm.

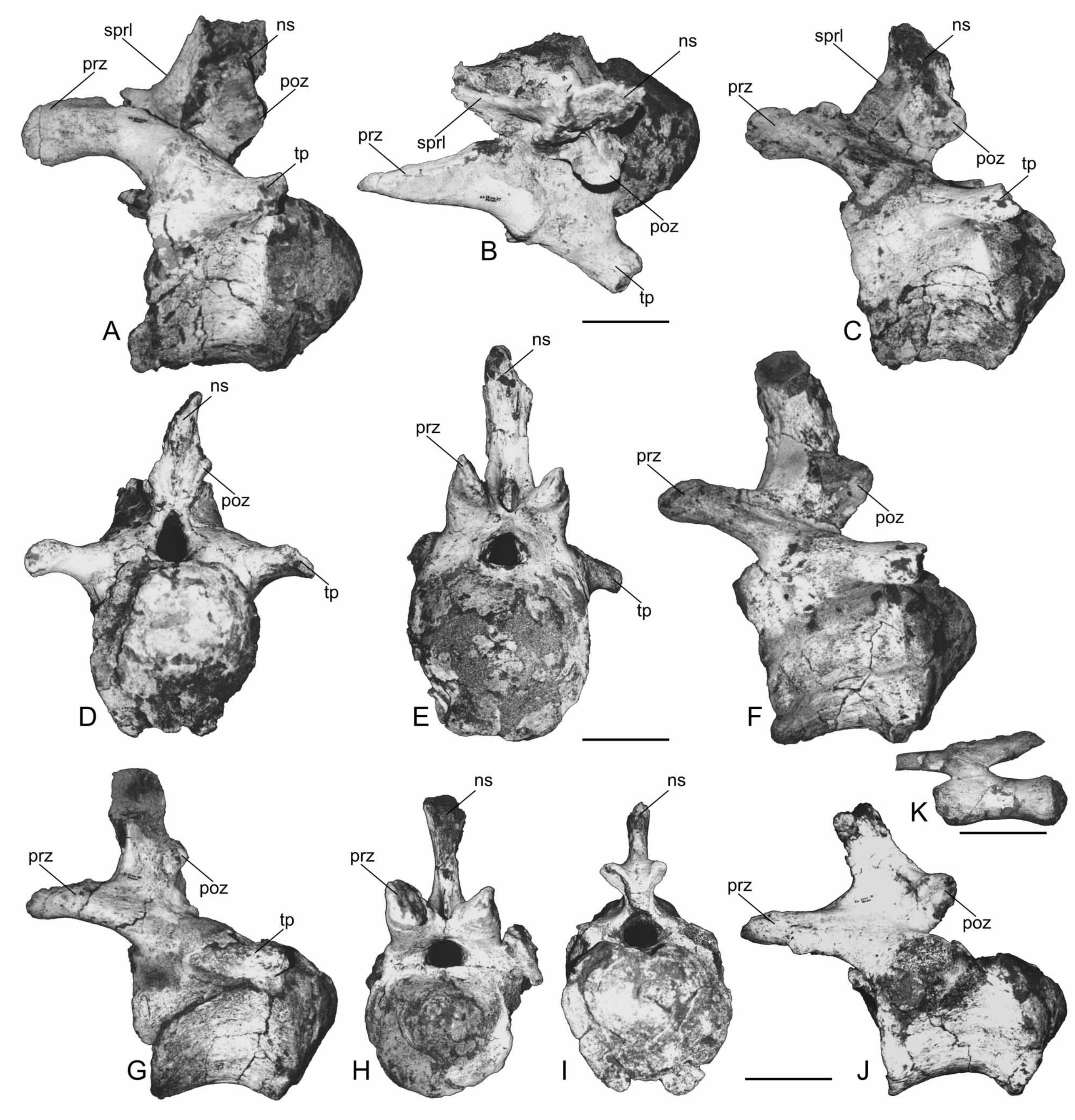

FIGURE 4. *Aeolosaurus maximus* **sp. nov.**, holotype (MPMA 12-0001-97). A–B, anterior caudal in left lateral and dorsal views. C–D, anterior caudal in left lateral and posterior views. E–F, anterior caudal in anterior and left lateral views. G, anterior caudal in left lateral view. H, anterior caudal in anterior view. I, middle anterior caudal in posterior and left lateral views. K, posterior caudal in left lateral view. Scale bar equals 10 cm in A–J and 5 cm in K.

The four remaining anterior caudal vertebrae are well preserved except for the last two vertebrae which lack the transverse processes. The centra are higher than wide and become progressively longer toward the posterior caudal vertebrae. In posterior view, the posterior ends are roughly hexagonal in shape. The articular area for the haemal arches is well-developed, forming a protuberance with a shallow pit at the ventroposterior margin of the centra. The ventral faces are slightly concave anteroposteriorly and laterally compressed, with incipient lateroventral ridges. The transverse processes are robust and strongly directed backward. The neural arches are located on the anterior half of the centra, reaching the anterior margin of the centra of the last two preserved anterior caudal vertebrae. The prezygapophyses become straight and relatively long, with moderately developed articular facets. The spinoprezygapophyseal laminae are well-developed, forming a deep fossa at the base of the neural spine. The postzygapophyses are robust, with concave articular facets and stout spinopostzygapophyseal laminae. The neural spines are laterally compressed at their base and laterally expanded at their distal end. They are directed forward, mainly in the last two anterior caudal vertebrae. The prespinal and postspinal laminae are incipiently developed (Fig. 4E–J).

The partial mid-caudal centrum is poorly preserved and, therefore, cannot provide any further information.

The two posterior caudal vertebrae are well preserved. The centra are procoelous and wider than high. The ventral and lateral faces are gently concave anteroposteriorly. The neural arches are anteroposteriorly short and located on the anterior half of the centra. The transverse processes are absent. The prezygapophyses have rudimentary articular facets and are directed forward. The neural spines are low, anteroposteriorly long, and transversally compressed. The postzygapophyses are poorly developed, consisting of shallow articular facets on the ventral margin of the neural spine (Fig. 4K).

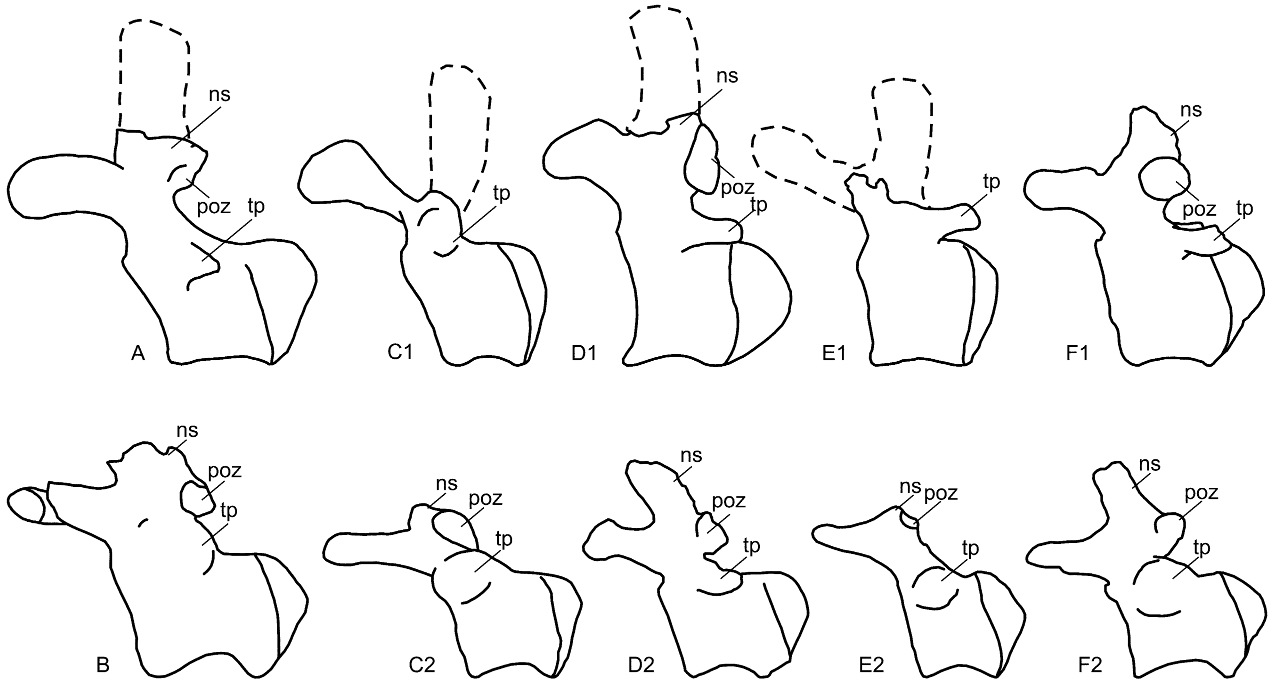

FIGURE 5. Anterior and middle caudal vertebrae of aeolosaurines in left lateral view (D1 reversed). A, *Aeolosaurus* sp. B, *Gondwanatitan faustoi*. C1–2, *Aeolosaurus rionegrinus*. D1–2, *Aeolosaurus* sp. E1–2, *Aeolosaurus colhuehuapensis*. F1–2, *Aeolosaurus maximus*. Redrawn from: A, Salgado *et al.* (1997a); B, Kellner and Azevedo (1999); C1–2, Powell (2003); D1–2, Salgado and Coria (1993); E1–2, Casal *et al.* (2007). Dashed lines indicate broken parts. Not to scale.

Dorsal ribs. Several incomplete dorsal ribs have been recovered. Unfortunately, they were not found in their anatomical position and, therefore, their assignment as anterior or posterior ribs have been made on the basis of better preserved sauropod material such as *Apatosaurus*, *Camarasaurus*, *Brachiosaurus*, and *Opisthocoelicaudia*. The more robust and platelike fragments were regarded as the anterior ribs, whereas the slender ribs were considered as the posterior ones (Fig. 6B–E). None of the anterior ribs have the capitulum and tuberculum well preserved (Fig. 6B–C). In both anterior and posterior dorsal ribs, the proximal portion consists of spongy bony tissue, mainly in a large rib fragment, where the coels open externally forming an elliptical pit. A fragment of proximal end is considered to be the first or second dorsal rib (Fig. 6C). It is a blade-like element with the proximal end directed anteriorly. The posterior portion is damaged and exposes the internal spongy bony tissue and, because of that, it is not possible to determine the shape of the cross section. Other fragments regarded as anterior dorsal ribs have the cross section of the proximal end triangular in shape. The mid-dorsal ribs have shafts with subtriangular cross sections that become blade-like or elliptical toward their distal ends. A mid-thoracic rib has a marked depression between the capitulum and the tuberculum in medial view. The proximal portion of the shaft is D-shaped in cross section with sharp well-developed ridges on both the antero and posterolateral margins (Fig. 6D). The best-preserved rib is about 900 mm in length and is considered to be a posterior one. It only lacks part of the capitulum and the tuberculum and, probably, part of the distal end. It is straight in medial view and gently curved in posterior view. It has the proximal portion of the shaft flat and is anteroposterioly concave in medial view. However, the distal end becomes triangular in cross section as in the middle posterior ones (Fig. 6E).

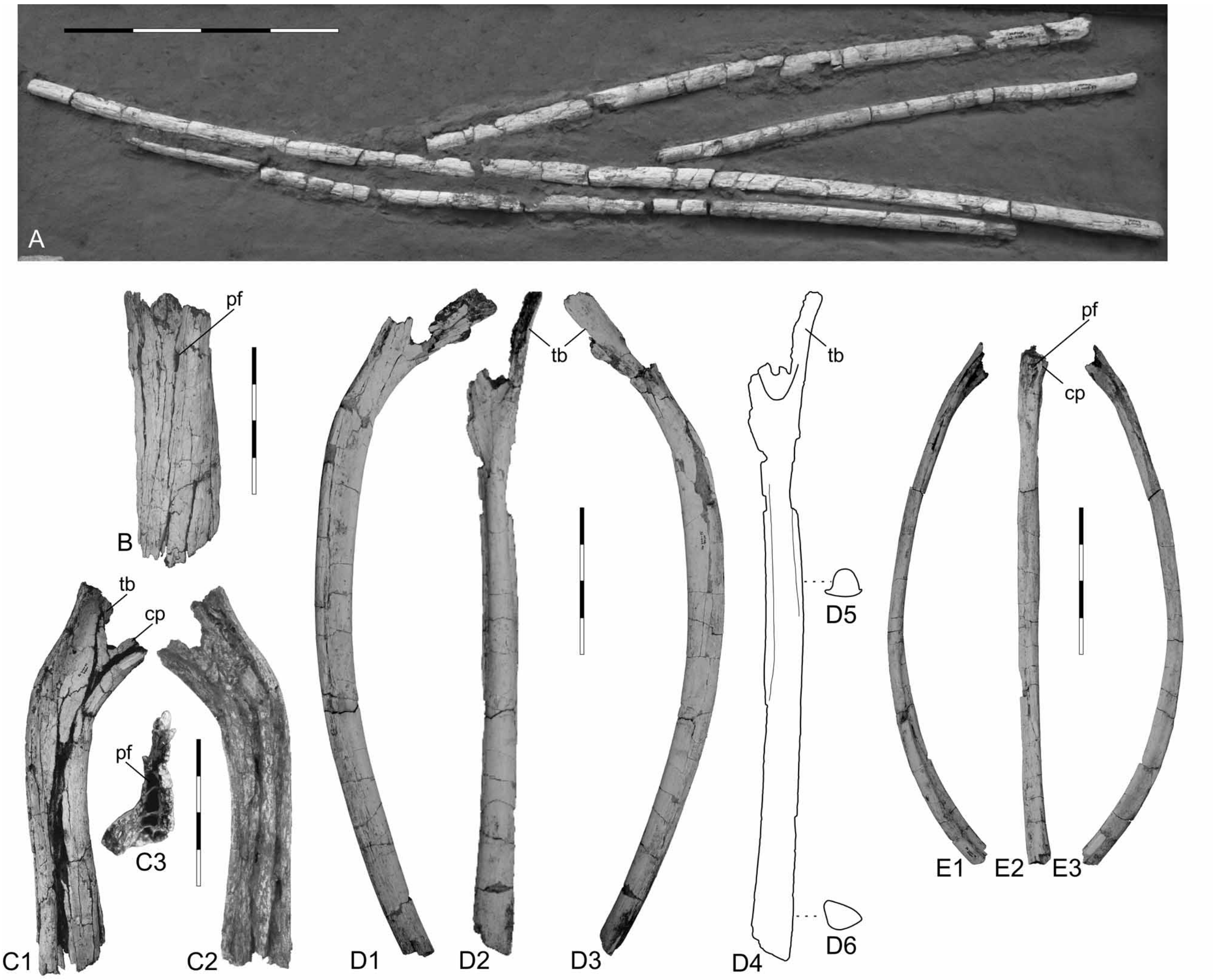

FIGURE 6. *Aeolosaurus maximus* **sp. nov.**, holotype, cervical and dorsal ribs (MPMA 12-0001-97). A, distal portion of the cervical ribs as they were found in the field. B, anterior dorsal rib with pneumatic foramen. C1–3, right anterior dorsal rib in anterior, posterior, and proximal views, respectively. D1–6, right mid-thoracic rib in anterior, medial, posterior, and medial views, and section at the middle diaphysis and distal end, respectively. E1–3, right posterior rib in anterior, medial, and, posterior views, respectively. Scale bars represent 20 cm.

Haemal arches. Six anterior haemal arches are preserved (Fig. 7A–F). Although not found articulated with the six anterior caudal vertebrae, some of them fit exactly in these caudal vertebrae. They are 'Y'-shaped and open proximally, in the proximal chevrons the haemal canal is less than 50% of the length of the whole bone (Table 2). Both proximal and distal processes are laterally compressed (but not laminar) mainly on the distal portion of the distal processes. In lateral view they gently curve backward. The top of the proximal process is nearly flat and has a large concave area in the posterodorsal margin, forming double articular facets. In lateral view this depression is ventrally delimited by a posterior protuberance. The distal process has a rounded distal end in lateral view and is anteroposteriorly expanded. In posterior view the distal process has a thin ridge that runs through its whole posterior aspect (Fig. 7A–F).

A haemal arch from a mid-caudal vertebra is well preserved (Fig. 7G). It is 'Y'-shaped with the haemal canal more than 50% of the length of the whole bone. Only the distal end of the distal process is laterally compressed. In lateral view it is nearly straight with the distal end curved backward. As the anterior haemal arches, the articulation with the centrum has a large posterior concave area which, in lateral view, is ventrally marked by a well-developed protuberance. The proximal process has a lateral protuberance located on its distal half (Fig. 7G).

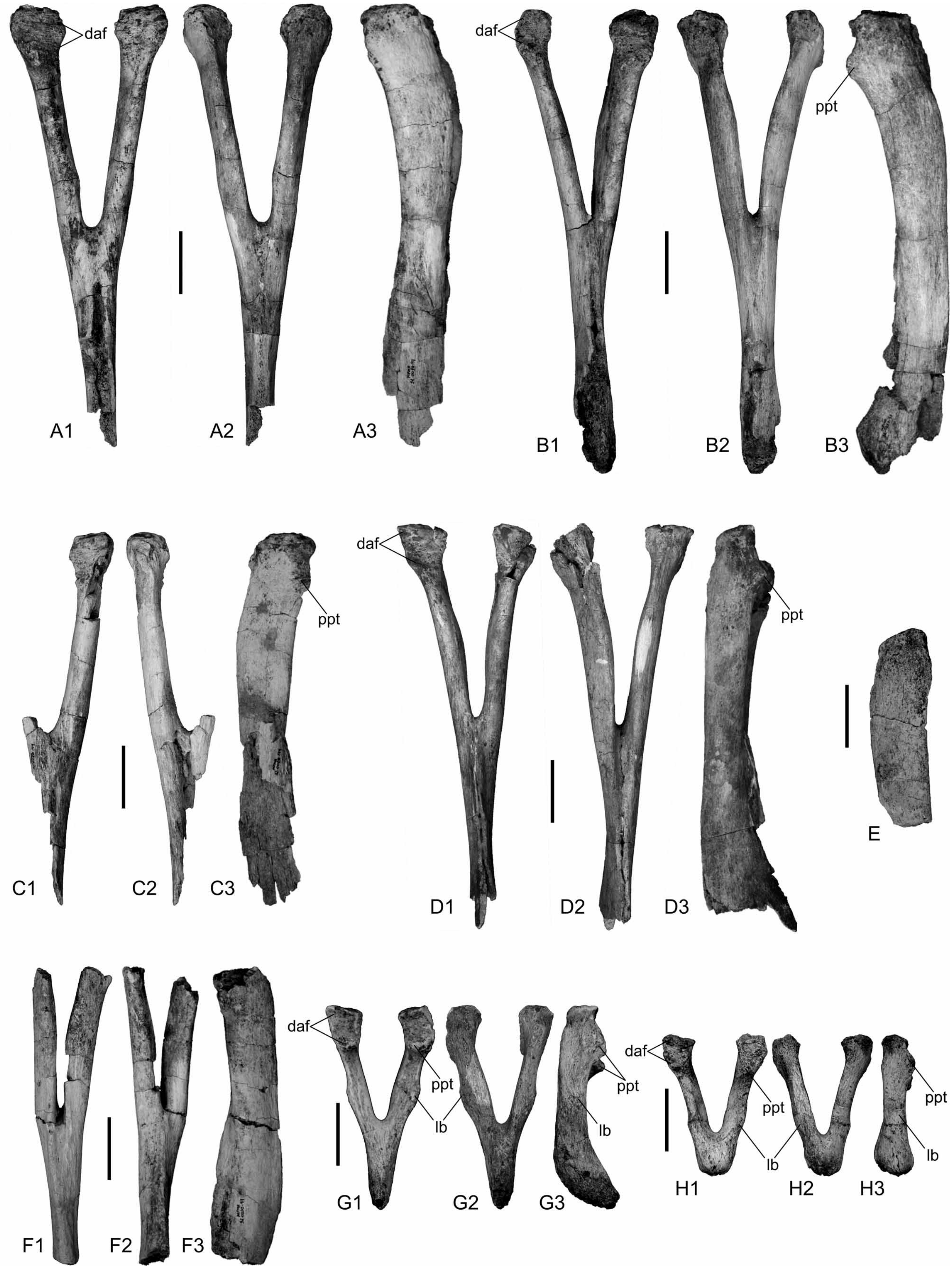

FIGURE 7. *Aeolosaurus maximus* **sp. nov.**, holotype, haemal arches (MPMA 12-0001-97). A–F, anterior haemal arches in posterior, anterior, and lateral views. G, middle haemal arch in posterior, anterior, and left lateral views. H, posterior haemal arch in posterior, anterior, and left lateral views. Scale bar represents 5 cm.

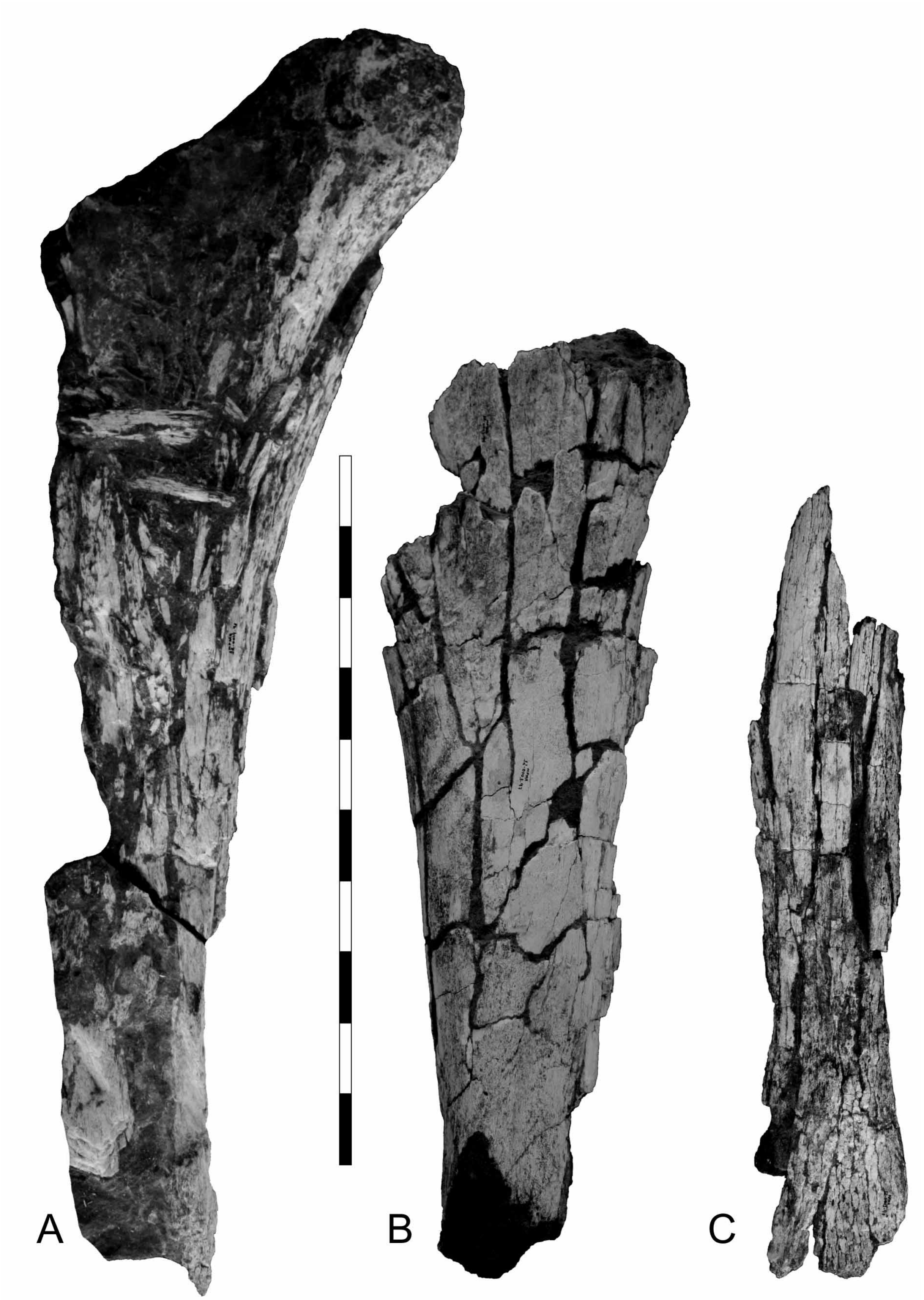

FIGURE 8. *Aeolosaurus maximus* **sp. nov.**, holotype, humeri and radius (MPMA 12-0001-97). A, right humerus in anterior view. B, left humerus in posterior view. C, probable radius. Scale bar represents 50 cm.

The distal haemal arch is a ‘V’-shaped element. The proximal processes have elliptical cross section with a mildly-developed protuberance on their posterolateral margins. The proximal articulations with the centrum have a flat top and a posterior concavity, forming the double articular facets. However, the posterior protuberance that delimitates its ventral margin is less developed than in the previous haemal arches (Fig. 7H).

TABLE 2. Measurements of the preserved anterior (ha1–6), midlle (ha7), and posterior haemal arches (ha8) of *A. maximus* (MPMA 12-0001-97). Measurements are in cm. Asteriscs indicate estimated measurements.

	ha1	ha2	ha3	ha4	ha5	ha6	ha7	ha8
Total height	36,5*	38,2	-	-	-	-	16,5	11,3
Height of haemal canal	18,7	17,7	17,2	16,5	-	-	9,1	7,4
Proximal width	12,5	11,8	10,1	11,4	-	-	9,2	8,1

Scapula. A large platelike fragment is considered to be part of the distal end of a scapula. It has a rounded dorsal margin and its thickness decreases toward the ventral margin.

Humeri. Both humeri are preserved (Fig 8A–B). The right humerus (preserved length of 89 cm) lacks the distal end and the laterodorsal corner (Fig. 8A). The proximal end has a well-developed anterior concavity and is medially expanded. The left one (preserved length of 63 cm) lacks both epiphyses, is anteroposterioly compressed, and is also badly damaged on its anterior portion (Fig 8B).

Radius. A long bone element (preserved length of 56 cm) found near the humerus is interpreted as a radius. Unfortunately, it is badly damaged and strongly compressed, so that nothing can be said about its morphology (Fig 8C).

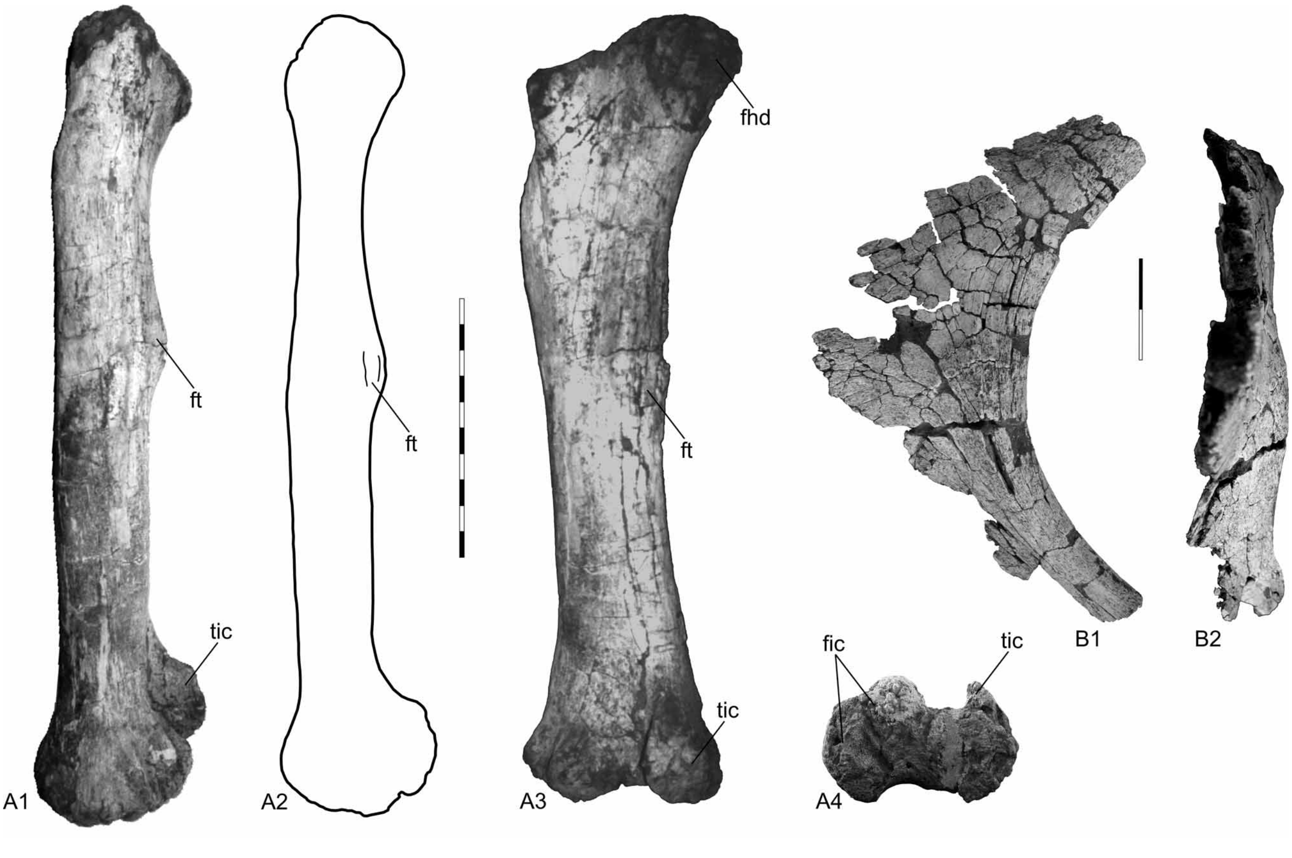

FIGURE 9. *Aeolosaurus maximus* **sp. nov.**, holotype. A1–4, left femur in lateral, posterior, and distal views (MPMA 12-0001-97). B1–2, left ischium in lateral and anteroventral views (MPMA 12-0001-97). Scale bar represents 10 mm.

Ischium. The left ischium is partially preserved (Figs. 9B1–2, 10). It is a platelike element with a concave dorsoposterior margin. Both iliac and pubic pedicles are not completely preserved. However, the pubic articulation seems to be well-developed. The acetabular area is partially preserved, corresponding to a gently concave area between the pubic and iliac articulations, where the bone is thinner than the posterodorsal margin. According to the preserved portion of the distal process, it seems to be relatively long and its thickness decreases from the dorsal margin to the ventral one. The distal process is twisted medially which indicates that when in articulation with its counterpart they should have met in a horizontal plane (Figs. 9B1–2).

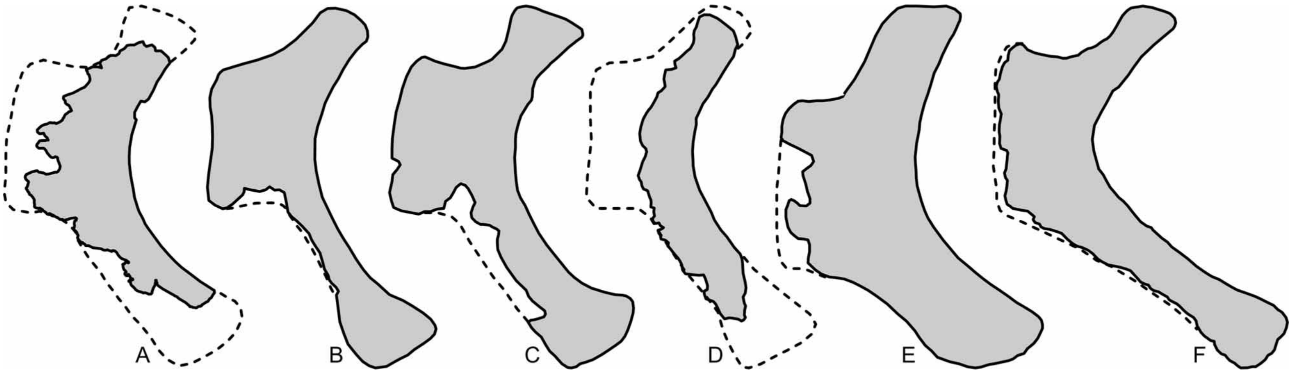

FIGURE 10. Ischia of Aeolosaurines and closely related taxa. A, *Aeolosaurus maximus.* B, *Aeolosaurus* sp. C, *Aeolosaurus rionegrinus* (composite of left and right ischia). D, *Gondwanatitan faustoi*. E, *Rinconsaurus caudamirus*. F, *Muyelensaurus pecheni*. Redrawn from: B, Salgado and Coria (1993); C, Powell (2003); D, Kellner and Azevedo (1999); E, Calvo *et al*. (2007b). Not to scale.

Femur. Both femora were recovered (Fig. 9A1–4), the left one is complete and well preserved, the right one lacks the distal end and part of the shaft. Although large (1.55 m in length), the femur is a relatively slender element. It is straight and strongly compressed anteroposteriorly, so that the shaft has an elliptical shape in cross section. The femoral head is well developed and extends well above the level of the greater trochanter and medially. The femoral head is not aligned with the great trochanter, so that in dorsal view it is slightly directed backward, forming a shallow concave area between both the great trochanter and the femoral head. A lateral bulge is present right under the great trochanter; it is gently convex and extends over the third proximal portion of the shaft. The fourth trochanter is relatively well-developed and located on the posteromedial portion of the shaft at its third upper part. The distal articulation is well-developed and extends from the posterior to the anterior margin of the femur so that in both posterior and anterior view there is a concave area between the tibial and fibular condyles. The same holds true for the distal margin. The tibial condyle is more developed than the fibular one in the way the posterior portion of the former is more developed posteriorly. However, the fibular condyle is stouter and bifurcates into two condyles. The internal (medial) one is more developed and slightly directed laterally. The lateral fibular condyle is less developed and forms part of the lateral corner of the distal end of the femur (Fig. 9A1–4).

Phylogenetic analysis

The phylogenetic relationships of *A. maximus* were inferred by using the data matrix provided by Wilson (2002) which were processed with PAUP 4.0 Beta version 10 (Swofford 2002). The following protocol was used in the heuristic search: random addition sequence with 100,000 replicates, Tree Bisection and Reconnection (TBR) as swapping algorithm, branches collapsed if the minimum branch length is zero, and synapomorphies for the nodes follow DELTRAN character optimization. No topological constrains were used. The characters 8, 37, 64, 66, and 198 were kept ordered as in the original analysis of Wilson (2002). Other titanosaurs previously referred to *Aeolosaurus* or considered to have a close relationship to aeolosaurines have been inserted into the data matrices whenever necessary, such as *A. rionegrinus* (Powell 1986, 1987, 2003), *A. colhuehuapensis* (Casal *et al*. 2007), *Gondwanatitan* (Kellner and Azevedo 1999), *Rinconsaurus* (Calvo and González Riga 2003), *Muyelensaurus* (Calvo *et al*. 2007b), *Maxakalisaurus topai* (Kellner *et al.* 2006), and *Panamericansaurus schroederi* (Calvo and Porfiri, 2010). This procedure aimed to establish the phylogenetic relationships of the taxa within Aeolosaurini.

Additional characters or character states have also been included into the data matrix, namely: apex of the convexity of the posterior articulation on anterior and middle caudal vertebrae; anterior margin of the anterior caudal vertebrae; articular facets of the prezygapophyses on the anterior and middle caudal vertebrae; prezygapophyses curved downward on anterior caudal vertebrae; postzygapophyses located on the anterior half of the centrum on the anterior and middle caudal vertebrae; length proportions of the prezygapophyses with respect to the centrum length in middle caudal vertebrae; neural spine directed forward in anterior caudal vertebrae; and proximal ends of the haemal arches with double articular facets (see Appendix 1 for the character list). This is because these characters are considered as synapomorphies of Aeolosaurini or *Aeolosaurus* (Powell 1986, 1987, 2003; Salgado and Coria 1993; Casal *et al*. 2007) and have not been used in this data matrix.

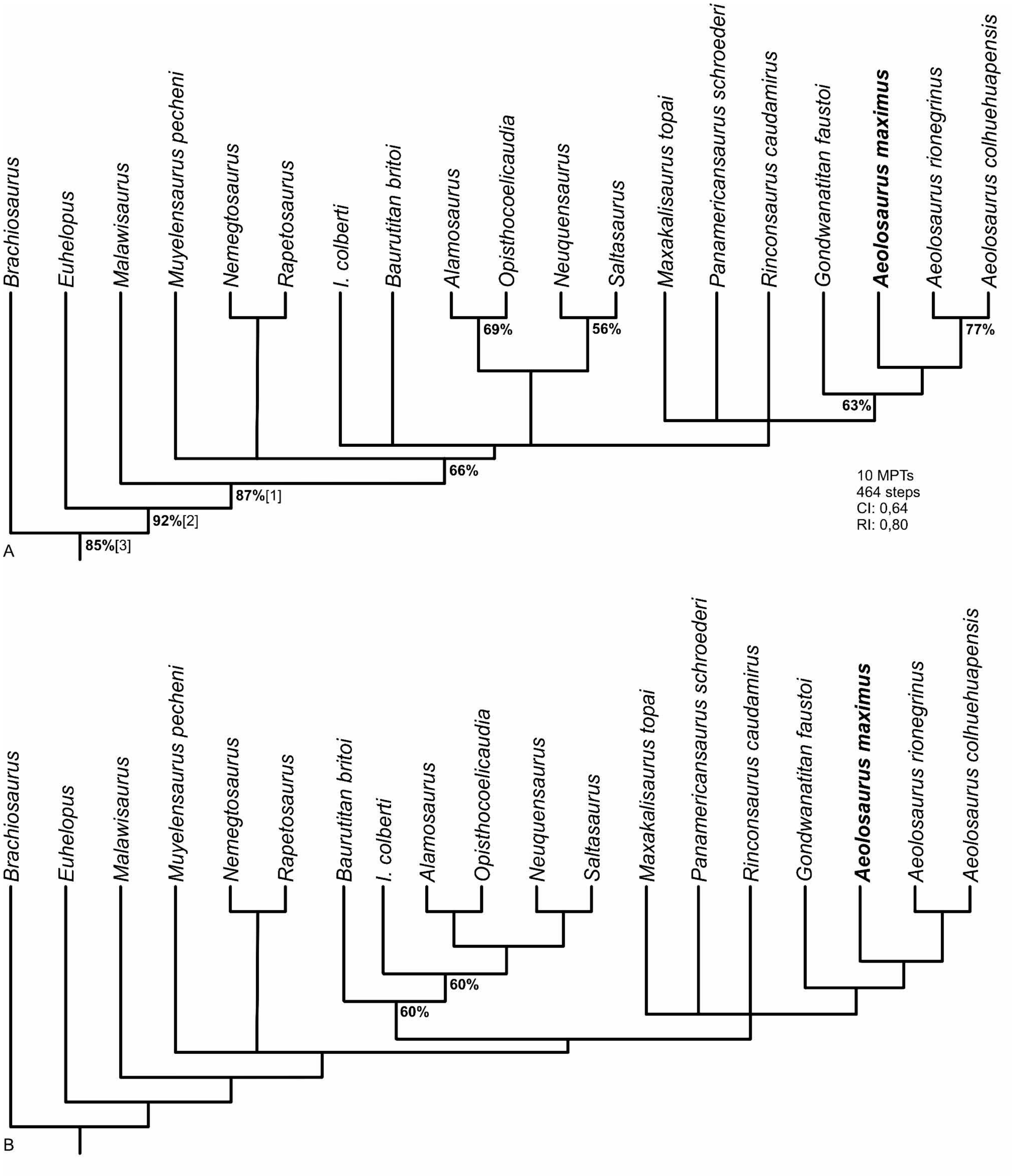

FIGURE 11. Resulting cladogram using the data matrix from Wilson (2002). A, strict consensus of ten most parsimonious trees. B, Major-rule consensus. Bootstrap (percentages in bold type) and Bremer support values are indicated in the strict consensus trees. Percentages in B depict the result of major-rule consensus.

For the data matrix provided by Wilson (2002) a new character state (neural spine directed forward on mid-caudal vertebrae) was added to the character 133 and six new characters were added to the data matrix. The codings for *Euhelopus*, *Andesaurus*, *Malawisaurus*, *Isisaurus*, and *Rapetosaurus* were updated following the new published data of Wilson and Upchurch (2009), Mannion and Calvo (2011), Gomani (2005), Curry Rogers (2009), and personal observations on some of these specimens (see Appendix 1 and 2 for the changes in the matrices).

The analysis retained ten most parsimonious trees of 464 steps, with consistency and retention indexes of 0,64 and 0,80, respectively (Fig.11 A–B). The inclusion of nine more taxa and six new character statements increased the number of most parsimonious trees when compared to the initial results of Wilson (2002). It also caused some changes in the tree topology. *Muyelensaurus* is depicted in a polytomy together with *Rapetosaurus* plus *Nemegtosaurus* and the clade comprising more apical titanosaurs.

The clade Aeolosaurini is nested within a polytomy with *Isisaurus*, *Baurutitan*, and Saltasauridae. *Aeolosaurus rionegrinus* is the sister-taxon of *A. colhuehuapensis*. These two Argentinean *Aeolosaurus* share the following unambiguous synapomorphies: anterior caudal centra with pneumatopores (character 119: 0→1). These pneumatopores are not as developed as the large ones present in the anterior caudal vertebrae of *Diplodocus* and *Barosaurus*. Nevertheless, they refer to the pleurocoel-like depressions reported by Powell (2003, pg. 23) and Casal *et al.* (2007, pg.55) in the anterior caudal vertebrae of these taxa, which is not present in *A. maximus*. The other unambiguous synapomorphy is the presence of wide articular facets (with a dorsal and a ventral expansion or protuberance) at least on the prezygapophyses of the anterior caudal vertebrae (character 237: 0→1). The genus *Aeolosaurus* is supported by one unambiguous synapomorphy: prezygapophyses curved downward on anterior caudal vertebrae (character 238: 0→1); and an ambiguous synapomorphy: haemal arches with double articular facets set in a concave posterodorsal surface (character 240: 0→1). This feature is also present in *Maxakalisaurus* that, according to the analysis performed here, is an Aeolosaurini titanosaur. As this feature cannot be evaluated in *Panamericansaurus*, *Gondwanatitan*, and *Rinconsaurus* due preservation problems, it would represent a synapomorphy for a more inclusive clade or even for Aeolosaurini if were present in one or both taxa. The clade Aeolosaurini (in this analysis the clade comprised by *Aeolosaurus* plus *Gondwanatitan*, *Panamericansaurus*, *Rinconsaurus*, and *Maxakalisaurus*) is supported by the following synapomorphy: posterior caudal centra dorsoventrally flattened (character 135: 0→1). A list of ambiguous and unambiguous synapomorphies for each clade recovered is provided in Table 2.

The robustness of the results were evaluated under both bootstrap and Bremer support (Fig. 11A). Bootstrap analysis was performed from 10,000 replicates. The support for Aeolosaurini and its internal nodes are relatively low: only 77% for the clade comprised by *A. rionegrinus* plus *A. colhuehuapensis*; and 63% for the clade corresponding to the genus *Aeolosaurus* plus *Gondwanatitan*. For the other nodes within Aeolosaurini the Bootstrap values are less than 50%. In this analysis the Bremer support equals zero for all nodes within Titanosauria including Aeolosaurini.

Comparison and discussion

Several phylogenetic analyses regarding titanosaurs have been published (e. g. Salgado *et al.* 1997b; Sanz *et al.* 1999; Curry Rogers and Forster 2001; Curry Rogers 2005, Calvo and González Riga 2003; Calvo *et al.* 2007a; González Riga *et al.*, 2009). Moreover, broader cladistic studies on sauropods have also considered titanosaurs in their data matrices (Wilson 2002; Upchurch 1998; Upchurch *et al.* 2004, Mannion and Calvo, 2011). As a result, a well-established set of characteristics can be used to support the phylogenetic relationships of *Aeolosaurus maximus* within Titanosauria. On the other hand, with few exceptions, these studies disagree with regard the inter-relationships of more apical taxa within Titanosauria. However, according to the results of the cladistic analysis performed here, the monophyly of the genus *Aeolosaurus* and the clade Aeolosaurini is mainly supported by features (see Table 3 and the section Phylogenetic Analysis) regarding the anterior caudal vertebrae and the haemal arches. Although these characters have long been considered to be diagnostic for the genus *Aeolosaurus* and/or Aeolosaurini (Powell, 1987, 1987, 2003; Salgado *et al.* 1993, 1997b; Franco-Rosas *et al.*, 2004) this is the first time that they were tested under the cladistic point of view. Additionally, Aeolosaurini is grouped as a distinct clade to Saltasauridae (*sensu* Wilson, 2002).

Comparison to other Aeolosaurini and Brazilian titanosaurs. Together with *A. maximus*, *Gondwanatitan* is the only Aeolosaurini in which dorsal vertebrae are preserved and, because of that, comparisons within this clade are restricted. As in *A. maximus* the preserved posterior dorsal vertebrae of *Gondwanatitan* also bear well-developed postzygodiapophyseal lamina. However, the most striking feature of the posterior dorsal vertebra of *A. maximus* is the presence of an oblique and stout anterior centropostzygapophysal lamina (acpol, see Fig. 3C1, C2) that originates at the base of the postzygapophysis together with the column that forms the posterior margin of the neural arch (cpol) and probably would have been attached to the upper middle portion of the centrum. This lamina is not present in any other known titanosaur but is not considered here as an autapomorphy of *A. maximus* because dorsal vertebrae are not known in other species of the genus *Aeolosaurus*.

TABLE 3. Monophyletic groups recovered from the analysis of the data matrix of Wilson (2002) with the inclusion of the *Aeolosaurus* species and closely related taxa. All synapomorphies supporting each clade and their respective transformations are listed. Characters in bold face refer to unambiguous synapomorphies.

Taxa	Species included	Synapomorphies
Unnamed	*A. rionegrinus* + *A. colhuehuapensis*	**119 (0→1)**, **237 (0→1)**
Aeolosaurus	(*A. rionegrinus* + *A. colhuehuapensis*) + *A. maximus*	**238 (0→1)**, 240 (0→1)
Unnamed	*Gondwanatitan* (*A. maximus* + *A. rionegrinus* + *A. colhuehuapensis*)	**236 (0→1)**, **239 (0→1)**, **241 (1→2)**
Aeolosaurini	*Panamericansaurus Rinconsaurus Maxakalisaurus* (*Gondwanatitan* (*A. maximus* + *A. rionegrinus* + *A. colhuehuapensis*))	**135 (0→1)**

The caudal vertebrae provide useful information for comparison with other titanosaurs, mainly aeolosaurines, since their most significant characters are based on the caudal vertebrae morphology. The anteriormost preserved caudal vertebra in *A. maximus*, which is considered to be the fourth one, is quite similar to the fourth caudal vertebra of *Aeolosaurus* sp. (MPCA 27100), reported by Salgado *et al.* (1997). In MPCA 27100 an abrupt change in the prezygapophyseal morphology of the anterior caudal vertebrae is observed between the third and fourth caudal vertebrae, where they change from short and straight to long and curved downward. However, this feature seems to be constrained to the 4th and 5th caudal vertebrae. Curved prezygapophyses on anteriormost caudal vertebrae are present in *A. maximus*, *Aeolosaurus* sp. (MPCA 27100, Salgado *et al.* 1997a), *A. colhuehuapensis*, and *A. rionegrinus* (the curvature in this species is less pronounced). Because of that, this character is considered as a synapomorphy for the genus *Aeolosaurus*. Additionally, as far as comparisons are possible, the shape of the prezygapophysis on the anteriormost caudal vertebrae of *A. rionegrinus* (probably the 2nd and 3rd) is similar to the anterior caudal vertebra of *Aeolosaurus* sp. (MPCA 27174), reported by Salgado and Coria (1993) from the Allen Formation, where they are straight and more directed upward, bearing both a dorsal and a ventral protuberance which makes their articular facets seem to be wider.

The anterior caudal vertebrae of *A. maximus* have the distal end of the neural spine expanded laterally. This feature is also present in *Aeolosaurus* sp. (MPCA 27174) from the Allen Formation. However, it is also seen in other Brazilian titanosaurs such as *Adamantisaurus* (Santucci and Bertini 2006) and *Trigonosaurus* (Campos *et al.* 2005). The neural spine on the middle-anterior and middle caudal vertebrae of *A. maximus* is directed forward as in other aeolosaurines (*Aeolosaurus* and *Gondwanatitan*). Moreover, this feature was also reported in *Trigonosaurus* by Campos *et al.* (2005). Because of that, Campos *et al.* (2005) suggested that *Trigonosaurus* might be closely related to *Aeolosaurus* and *Gondwanatitan*; however, they stated that *Trigonosaurus* differs from *Aeolosaurus* by having shorter prezygapophyses and from *Gondwanatitan* by lacking caudal centra with a 'heart-shaped' outline in posterior view. These differences also holds true for *A. maximus*.

Except for *A. colhuehuapensis*, the Patagonian *Aeolosaurus* have the apex of the posterior articulation of the anterior caudal centra strongly displaced upward, almost reaching the level of the dorsal margin of the centrum (see Fig. 5). Because of that *A. maximus* differs from these taxa by having the apex of the posterior convexity of the centrum closer to the centrum midline as in *A. colhuehuapensis*. The mid-anterior caudal vertebrae of *A. maximus* have shallow depressions for the haemal arch attachment as in *A. rionegrinus* (Powell 2003), *A. colhuehuapensis* (Casal *et al*. 2007), *Aeolosaurus* sp. (Salgado and Coria 1993), and *Panamericansaurus* (Calvo and Porfiri 2010). This feature, however, does not seem to be a synapomorphy for the genus, since it is also present in other titanosaurs such as *Trigonosaurus* (Campos *et al*. 2005), *Baurutitan* (Kellner *et al.* 2005), and *Adamantisaurus* (Santucci and Bertini 2006a).

The posterior caudal vertebrae of *A. maximus* provide few characters for comparison. The dorsoventrally compressed posterior caudal centra with no signs of lateral ridge differs *A. maximus* from *Gondwanatitan* (Kellner and Azevedo 1999), *Rinconsaurus* (Calvo and González Riga 2003), *Baurutitan* (Kellner *et al.* 2005), and *Maxakalisaurus* (Kellner *et al.* 2006), and *Muyelensaurus* (Calvo *et al.* 2007b). However, the dorsoventral compression and the absence of lateral ridges or transverse processes on posterior caudal vertebrae of *A. maximus* can be due to the fact they represent more posterior caudal vertebrae in the series.

Haemal arches are known in some titanosaurs including most Aeolosaurini. Titanosaurs, other than Aeolosaurini, generally have chevrons with single articular facets or anteroposteriorly convex proximal ends with two distinct articular surfaces (Mannion & Calvo, 2011). Therefore, the presence of haemal arches with double articular facets set in a concave posterodorsal surface in *A. maximus* differs this Aeolosaurini from other Brazilian titanosaurs like *Adamantisaurus* and *Baurutitan*. However, double articular ends set in a concave surface have also been reported for the haemal arches of *A. rionegrinus*, *A. colhuehuapensis*, the basal titanosaur *Mendozasaurus* (González Riga 2003), and the recently described titanosaur *Maxakalisaurus topai* (Kellner *et al.* 2006) from the Adamantina Formation of Minas Gerais State. The presence of a well-developed posterior protuberance that delimitates the ventral rim of the articular facet on both anterior and middle haemal arches differs *A. maximus* from all other known titanosaurs, including those ones that have double proximal articular facets (e. g. other aeolosaurines, *Mendozasaurus*, and *Maxakalisaurus*). Additionally, the lateral bulge present in the middle haemal arches of *A. maximus* has already been reported in other Brazilian titanosaur, namely *Baurutitan* (Kellner *et al.* 2005), and on the haemal arches of *Alamosaurus* (Gilmore, 1946, pg. 33). According to the phylogenetic analysis, however, these two taxa are not closely related to Aeolosaurini (Fig. 11A–B) as are interpreted as independently acquired in these taxa. Additionally, this lateral bulge on haemal arches is neither present in *A. rionegrinus* nor in *A. colhuehuapensis*. The laterally compressed distal end of the haemal arch with a marked posterior crest contrasts *A. maximus* from *Adamantisaurus*, but is similar to that one seen in *A. rionegrinus.*

The humerus of *Aeolosaurus maximus* is poorly preserved and, therefore, comparisons with other titanosaurs are limited to the proximo-medial portion of the bone. As in other titanosaurs the proximo-medial border of the humerus is well-developed and expanded medially. Unfortunately, the presence of a relatively well-developed deltopectoral crest medially oriented, as in *A. rionegrinus* and *Gondwanatitan*, cannot be observed in *A. maximus.*

The ischium of *A. maximus* seems to have a blade-like distal axis, which is twisted medially as in other titanosaurs, so that the distal shaft of both ischia must have been coplanar. The posterodorsal margin has a gently curvature as in other aeolosaurines contrasting with that of the *Muyelensaurus* where the angle between the iliac peduncle and the distal blade is acute (Fig. 10). The ischia of *A. rionegrinus* and *Aeolosaurus* sp. (Salgado & Coria, 1993) seems to be less blade-like than in other titanosaurs (e. g. the distal shaft is relatively narrow when compared to its length), unfortunately this feature cannot be assessed in *A. maximus* since the distal end of this bone is badly damaged in this taxon.

General comparison to other titanosaurs. Among the axial skeleton, the cervical vertebrae are the least known in titanosaurs and are not preserved in other *Aeolosaurus* specimens previously reported. Although not well preserved, the posterior cervical vertebrae of *Aeolosaurus maximus* differ from all other titanosaurs by having well-developed posterior centrodiapophyseal laminae, which are more robust than the postzygodiapophyseal laminae. So far, this feature is only known in *A. maximus.* The relatively long prezygapophysis (inferred by the distance between its articular facet and the base of the diapophysis) is similar to that of *Malawisaurus* (Gomani 2005 fig. 9, pg. 11), *Rinconsaurus* (Calvo & González Riga 2003), *Trigonosaurus* (Campos *et al.* 2005), and *Uberabatitan* (Salgado and Carvalho 2008), and contrasts with the condition seen in *Saltasaurus* (Powell 2003), *Neuquensaurus* (Powell 2003), and *Isisaurus* (Jain and Bandyopadhyay 1997), where it is short. Because the articular facet of the prezygapophysis is faced anterodorsally, the prezygapophysis has a flat anterodorsal surface in lateral view, contrasting with the rounded profile of the prezygapophysis in posterior cervical vertebrae of other titanosaurs. The neural spine of the posterior cervical vertebrae of *A. maximus* slopes steeply upward as in *Malawisaurus* (Jacobs *et al.* 1993), *Rinconsaurus* (Calvo and González Riga 2003), and *Rapetosaurus* (Curry Rogers and Forster 2001). The posterior portion of the cervical ribs is long as in *Malawisaurus* (Gomani 2005) and *Uberabatitan* (Salgado and Carvalho 2008), differing from the short ones as in *Isisaurus.*

Because it is badly damaged, the anterior dorsal vertebra of *A. maximus* provides little information that can be used for comparisons. However, it contrasts with those of other titanosaurs by having three openings in the anterior portion of the neural arch. These apertures lead to a large chamber in the centrum.

The fragmentary posterior dorsal vertebra of *A. maximus* has a thin and well-developed intrapostzygapophyseal lamina (tpol), contrasting with all other known titanosaurs. A slender and well-developed postzygodiapophyseal lamina is also present on the posterior dorsal vertebra. This lamina is not present in *Opisthocoelicaudia* (Borsuk-Bialynicka 1977), *Ampelosaurus* (Le Loeuff 1995), and *Lirainosaurus* (Sanz *et al.* 1999). *Trigonosaurus* only has postzygodiapophyseal laminae on the last two dorsal vertebrae (Campos *et al.* 2005); however, they are poorly developed.

The dorsal ribs of *A. maximus* greatly vary in shape. Unfortunately, dorsal ribs are rare or poorly illustrated in other titanosaurs. As far as comparisons are possible, the mid-thoracic ribs of *A. maximus* differ from other titanosaurs by having the anterior half of the shaft with a conspicuous D-shaped cross section. Additionally, the anterior half of the shaft of these mid-posterior dorsal ribs also bears well-developed anterior and posterior ridges.

Aeolosaurus maximus has subcentimetrical pneumatocoels in the proximal end of both anterior and posterior ribs as in *Euhelopus*, *Malawisaurus* (Gomani 2005), and *Opisthocoelicaudia*. Janensch (1950) recorded the presence of centimetrical oval-shaped pneumatocoels only in the anterior dorsal ribs of *Brachiosaurus brancai*. Although being present in both the anterior and posterior dorsal ribs of *A. maximus*, the pneumatocoels in the anterior dorsal ribs are larger than in the posterior ribs. Additionally, the suboval pneumatocoels of *A. maximus* differs from those ones present in *Malawisaurus*, which are quadrangular in shape and open externally in the posterior portion of the ribs (Gomani 2005). The pneumatocoels in the dorsal ribs of *Euhelopus* also seem to open externally in the posterior aspect of the bone (Wilson and Upchruch 2009).

The femur of *A. maximus* has the proximal third deflected medially with a well-developed lateral bulge, which is a feature seen in all other Titanosauriformes. It contrasts with the femur of *Epachthosaurus* (Martínez *et al.* 2004) and *Opisthocoelicaudia* (Borsuk-Bialynicka 1977) by being more slender. Regarding the position of the fourth trochanter, it differs from *Opisthocoelicaudia* where it is located on the distal half of the femur and flushed to its midline (Borsuk-Bialynicka 1977). It also differs from the femur of *Rapetosaurus* which shows an extreme constriction on the distal portion of the shaft.

Other putative *Aeolosaurus* occurrences in Brazil. Besides *A. maximus*, other titanosaur occurrences have been attributed to the genus *Aeolosaurus* in Brazil. All these materials, however, comprise scattered and incomplete elements, mainly caudal vertebrae.

A middle caudal vertebra from the Serra da Galga Member (Marília Formation) was reported by Bertini *et al.* (1999b) and Santucci and Bertini (2001, fig. 2B). Although previously reported, this caudal vertebra (CPP 248) from Peirópolis (Minas Gerais State) has never been described in detail. The centrum is as higher than wide and procoelous, with the apex of the convexity of the posterior end slightly displaced above the centrum midline. The lateral and ventral faces are strongly concave anteroposteriorly. Because of that, the mid-portion of the centrum is strongly constricted in ventral view. The transverse processes are stout and directed backward. The neural arch is located on the anterior portion of the centrum so that its upper anterior rim lies anterior to the anterior margin of the centrum. The prezygapophyses are long with no broad articular facets. The postzygapophyses have concave articular facets and are located near the base of the neural arch. The neural spine lacks its distal end but the preserved portion indicates it is directed forward (Fig. 12). Although comprised by a single middle caudal vertebra, CPP 248 has the synapomorphies of Aeolosaurini, namely: neural spine directed forward on mid-anterior caudal vertebrae; postzyagpophyses located on the anterior half of the centrum; and middle caudal vertebrae with long prezygapophyses (more than 50% of the centrum length). Unfortunately, according to the new diagnosis of *Aeolosaurus* presented in this paper (e. g. prezygapophyses curved downward on anterior caudal vertebrae and haemal arches with double articular facets set in a concave posterodorsal surface), none of these features can be accessed in CPP 248, but since this caudal vertebra does not show the heart-shaped centrum contour in posterior view as in *Gondwanatitan*), CPP 248 is assigned to the genus *Aeolosaurus*, instead of *Gondwanatitan*.

Almeida *et al.* (2004) and Candeiro *et al.* (2006) attributed a mid-posterior caudal vertebra and a haemal arch (UFRJ-DG 270-R), unearthed from the Adamantina Formation near the city of Prata, Minas Gerais State, to the genus *Aeolosaurus*. The haemal arch lacks the proximal ends and, therefore, it is not possible to know if double articular facets were present. On the other hand, it lacks the lateral protuberance present in *A. maximus*. The mid-posterior caudal vertebra has the neural spine directed backward (Almeida *et al.* 2004, fig. 2A; Candeiro *et al.* 2006, fig. 5A). Therefore, none of the synapomorphies of the genus *Aeolosaurus* are present and at least one synapomorphy for Aeolosaurini is absent in UFRJ-DG 270-R. Because of that, this material cannot be assigned to *Aeolosaurus*. The presence of heart-shaped posterior articulation suggests, however, it might be related to *Gondwanatitan*.

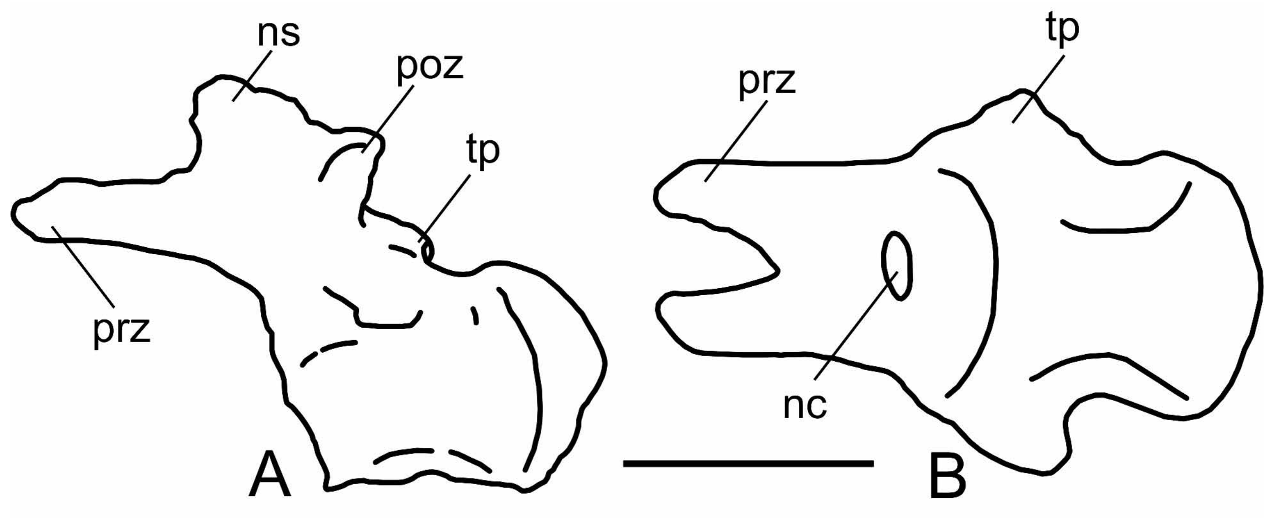

FIGURE 12. *Aeolosaurus* sp. (CPP 248). A, middle caudal in left lateral view. B, ventral view. Scale bar equals 5 mm.

Lopes and Buchmann (2008) tentatively assigned two badly damaged caudal centra (LGP-D0002 and LGP-D0003) to the genus *Aeolosaurus*. These caudal vertebrae do not share any synapomorphy with *Aeolosaurus*, but could be related to *Gondwanatitan* due the presence of heart-shaped centra.

In a recent paper Martinelli *et al.* (2011) suggested that all *Aeolosaurus* specimens in Brazil were incorrectly assigned to this genus based on two main points: first, the lack of a well-established phylogenetic reconstruction for Brazilian titanosaurs precludes good taxonomic assignments; second, the Brazilian specimens do not have postzygapophyses located anteriorly to the edge of the caudal centrum. Regarding the first point, Martinelli *et al.* (2011) misinterpreted the meaning of taxonomy and systematics. In this case taxonomy (naming species) does not necessarily require a phylogenetic tree to be accomplished (see de Queiroz and Gauthier 1990; Cantino and de Queiroz 2010; and the International Code of Zoological Nomenclature, for further discussion). Additionally, although their criticism, Martinelli *et al.* (2011) did not use any apomorphy to perform their review, since the features they used were not evaluated under the scope of a phylogenetic analysis. Concerning the second point, the character postzygapophyses located anteriorly to the edge of the centrum, which was included in the emended diagnosis of the genus *Aeolosaurus* by Casal *et al.* (2007), seems to vary along the caudal series. In *A. rionegrinus* the anterior margin of the postzygapophysis is only located anteriorly to the anterior edge of the centrum in one mid-anterior caudal vertebra (Powell, 2003, plate 11, fig. 2a), while in the preceding anterior caudal vertebrae it is located slightly posteriorly to the anterior edge of the centrum (Powell, 2003, plate 11, fig. 1a). Similarly, in *A. colhuehuapensis* only one mid-anterior caudal vertebra has the postzygapophyses located anteriorly to the anterior edge of the centrum (Casal *et al.* 2007, figs. 2 and 3). Although not located anteriorly to the edge of the centrum, the position of the prezygapophyses varies along the series in *A. maximus* as well. In the anteriormost caudal vertebrae the postzygapophyses are located more posteriorly. They almost reach the anterior edge of the centrum only in the fifth preserved caudal vertebra (Fig. 4G). From this caudal vertebra toward the tip of the tail the postzygapophyses are located more posteriorly again (Fig. 4J). Additionally, the other Argentinean specimens assigned to the genus *Aeolosaurus* by Salgado and Coria (1993) and Salgado *et al*. (1997a) do not have this feature, although being quite similar to *A. rionegrinus* in all other aspects. Because of that, we consider the two specimens described here (*A. maximus* and CPP 248) as belonging to the genus *Aeolosaurus*. Moreover, the character concerning the position of the postzygapophyses on the caudal centrum proposed by Salgado *et al*. (1997b) was used in the data matrix because it encompasses this kind of variation in the caudal series.

The stratigraphic significance of the genus *Aeolosaurus*. The occurrence of *Aeolosaurus* remains together with hadrosaurs in Argentina was claimed to be of significant chronostratigraphic value (Bonaparte 1992; Powell 1987; Salgado *et al.* 1997a) mainly because the presence of Late Cretaceous hadrosaurs in Argentina is considered to be the result of the establishment of the land bridge between North and South America landmasses during the Campanian-Maastrichtian.

The age of the Los Alamitos Formation, which is considered to be Campanian–Maastrichtian (Papú and

Sepúlveda 1995), was mainly established on the basis of palynological evidence, based on the presence of the pollen *Tricolpites reticulatus* (Papú and Sepúlveda 1995; Prámparo *et al.* 2007). This genus is also present in Campanian rocks of the Otway Basin, Australia (Prámparo *et al.* 2007). Additionally, the vertebrate fauna is consistent with this assignment. Bonaparte *et al.* (1984) argued that the presence of North American Campanian–Maastrichtian genera such as the hadrosaur *Kritosaurus* (*K. australis*), which is considered as the junior synonym of *Secernosaurus koerneri* by Prieto-Marquez and Salinas (2010), and the mammal *Mesungulatum* (*M. houssayi*) resulted from the physical connection between North and South America during the Campanian–Maastrichtian.

The age of the Allen Formation was established on the basis of the microfossil evidence, where its upper member was considered to be upper Maastrichtian in age on the basis of its ostracod assemblage (Ballent 1980). The Allen Formation has also produced a mixture of Gondwanan and Laurasian vertebrates (Martinelli and Forasiepi 2004), the latter corresponding to Hadrosauridae and Nodosauridae dinosaurs, which could be also related to the connection between North and South America at the end of the Cretaceous (Bonaparte 1986; Martinelli and Forasiepi 2004). Finally, Dingus *et al*. (2000), based on paleomagnetic data, assigned a Campanian age to the underling Río Colorado Formation, which would indicate that the Allen Formation cannot be older than Campanian.

Regarding the Bajo Barreal Formation, Archangelsky *et al.* (1994), on the basis of its palynological content, assigned a Cenomanian–Coniacian age to the lower member of this unit, which also provided the titanosaur *Epachthosaurus sciuttoi* (Martínez *et al.* 2004). On the other hand, Casal *et al.* (2006) stated that the presence of the dinosaurs *Secernosaurus koerneri* and *Notoceratops bonarelli* is also the result of the connection between North and South America at the end of the Cretaceous and, therefore, assigned a Campanian–Maastrichtian age for the Upper Member of the Bajo Barreal Formation near the Lake Colhué Huapi.

Curiously, for the Angostura Colorada Formation, where *A. rionegrinus* was found, there is no biostratigraphical information available. However, Manassero (1997) tentatively assigned a late Campanian age based on its stratigraphical position.

In Brazil, the Adamantina Formation provided some microfossils of biostratigraphic value. Gobbo-Rodrigues *et al.* (1999) assigned a Campanian–Maastrichtian age for the lower portion of the Adamantina Formation on the basis of the presence of the ostracods *Ilyocypris argentiniensis* and *I. riograndensis*. On the other hand, Dias-Brito *et al.* (2001) argued for a Turonian–Santonian age for the Adamantina Formation, suggesting the existence of a depositional hiatus between Adamantina and Marília formations. However, in several instances a gradational contact between these formations is observed (Batezelli *et al.* 2003), which weakens the hiatus hypothesis.

Additionally, Tamrat *et al.* (2002) analysed the magnetostratigraphy of the Uberaba and Marília formations. The reversed polarity of these rocks indicates that the age of both units are younger than the Cretaceous normal polarity quiet zone (125–83.5Ma), which means that they cannot be older than latest Santonian.

Therefore, considering the existing evidence, it seems reasonable to suggest that the temporal distribution of the genus *Aeolosaurus*, in both Argentina and Brazil, is limited to the Campanian–Maastrichtian interval (see Table 4).

TABLE 4. Different *Aeolosaurus* occurrences and their respective geological unit and assigned age.

Taxon (cathalogue number)	Unit	Age	Author
A. rionegrinus (MJG-R 1)	Angostura Colorada Fm	?late Campanian	Powell (1987)
A. colhuehuapensis (UNPSJB-PV 959/1-27)	Bajo Barreal Fm	?Campanian-Maastrichtian	Casal *et al.* (2006)
Aeolosaurus sp. (MPCA 27174-7)	Allen Fm	Campanian-early Maastrichtian	Ballent (1980); Bonaparte (1986); Dingus *et al.* (2000); Martinelli and Forasiepi (2004)
Aeolosaurus sp. (MPCA 27100)	Los Alamitos Fm	Campanian-Maastrichtian	Papú & Sepúlveda (1995); Prámparo *et al.* (2007)
A. maximus	Adamantina Fm	Campanian-Maastrichtian	Gobbo-Rodrigues *et al.* (1999)

Conclusions

A cladistic evaluation of the diagnostic characters claimed to be the synapomorphies for Aeolosaurini and the genus *Aeolosaurus* was performed. Considering the taxa nested within Aeolosaurini, only the caudal vertebrae and haemal arches are preserved in all these titanosaurs. Because of that, the diagnosis of both the genus *Aeolosaurus* and Aeolosaurini is constrained to the morphology of these elements. The inclusion of these characters and taxa into the data matrix of Wilson (2002) resolves the relationships within Aeolosaurini grouping *Gondwanatitan* as the sister-taxon of the genus *Aeolosaurus* and place *Panamericansarus, Rinconsaurus*, and *Maxakalisaurus* as more basal Aeolosaurini.

According to the analysis performed here, Aeolosaurini is supported by the following synapomorphy: posterior caudal centra dorsoventrally flattened. This change in the diagnosis of the clade Aeolosaurini (when compared to the original diagnosis proposed by Franco-Rosas *et al*., 2004) is due to the inclusion of three new titanosaurs within this branch-based clade (*Panamericansarus, Rinconsaurus*, and *Maxakalisaurus*). In this case, they show a close relationship with *Gondwanatitan* and *Aeolosaurus*, but have no the diagnostic features originally proposed for this clade.

The genus *Aeolosaurus* is supported by the following synapomorphies: prezygapophyses curved downward on anterior caudal vertebrae and haemal arches with double articular facets set in a concave posterodorsal surface on anterior and middle caudal vertebrae. The analysis suggests that the new species described here, *A. maximus*, is the most basal *Aeolosaurus* known to date. Furthermore, *A. rionegrinus* and *A. colhuehuapensis* are sister-taxa. Additionally, the inclusion of *Gondwanatitan faustoi* within *Aeolosaurus* is not supported, contrasting to what was previously stated by Bertini *et al.*, (2000) and Santucci and Bertini (2001), because *Gondwanatitan* does not bear the prezyagapophyses curved downward on anterior caudal vertebrae (Kellner and Azevedo, 1999, figs. 6 and 11). Whether the haemal arches with double articular facets are present in *Gondwanatitan* cannot be observed because the proximal ends of the haemal arches are not preserved in this species.

A re-evaluation of the diagnostic features of *A. rionegrinus* showed that many of the characteristics once claimed to be autapomorphies of this species are actually the synapomorphies of more inclusive clades within Aeolosaurini. Therefore, a new diagnosis for *A. rionegrinus* is proposed here encompassing the unique association of the following characteristics: prezygapophyses directed mainly upward on anteriormost caudal vertebrae and slightly curved downward on the remaining anterior caudal vertebrae; prezygapophyseal articular facets widened by the presence of both a dorsal and a ventral protuberance on the prezygapophyses of the anterior caudal vertebrae; and apex of the convexity of the posterior articulation strongly displaced upward, so that the apex is flushed to the level of the dorsal margin of the centrum on anterior and middle caudal vertebrae.

Aeolosaurus maximus is diagnosed only by the morphology of its haemal arches as follows: well-developed posterior protuberance below the articular area on the anterior and middle haemal arches and lateral bulge on the distal portion of the articular process of the mid-posterior haemal arches. Additionally, *A. maximus* differs from *A. rionegrinus* by the absence of the apex of the posterior articulation on caudal vertebrae strongly displaced upward and differs from both *A. rionegrinus* and *A. colhuehuapensis* by the absence of prezygapophyses with wide articular facets.

Finally, *A. maximus* is the first well-preserved *Aeolosaurus* to be formally described outside Patagonia. Together with the probable presence of this genus from the Serra da Galga Member (CPP 248) of the Marília Formation, Minas Gerais State, this genus would have been present from southern Patagonia in Argentina to the southeastern region of Brazil. In contrast to the previous records for this group, *A. maximus* is a relatively large Aeolosaurini, also differing from the general record for most of Brazilian titanosaurs.

Acknowledgements

The authors are indebted to Ademir Frare, Aldirene Costa Franco, Fabiano V. Iori, Itapotiara Vilas Bôas, Ismar S. Carvalho, Pedro Nobre, R. José Bertini, Silvia Gobbo, William Nava, Sirlei, Pepe, Cledinei A. Francisco, and Sandra Tavares for their help during the field sessions in 1997–1998. Special thanks to Sandra Tavares for her preparation work. We also thank D. Unwin and W.-D Heinrich (Museum für Naturkunde der Humboldt Universität); L. Salgado and J. Calvo (Universidad Nacional del Comahue); R. Coria (Museo Carmen Funes); S. Bandyopadhyay and D. Sengupta (Indian Statistical Institute); J. Le Loeuff (Museé des Dinosaures); A. Milner, S. Chapman and P. Barrett (The Natural History Museum); A. Kellner and D. Henriques (Museu Nacional); M. Borsuk-Bialynicka (Polish Academy of Sciences); J. Powell (Instituto Miguel Lillo); M. Regero (Museo de La Plata); J. Bonaparte (Museo Argentino de Ciencias Naturales); Luiz C. B. Ribeiro (Centro de Pesquisas Paloentológicas L. I. Price) for kindly facilitate the access to collections in their care. Mr. Dalmo and the Municipality of Monte Alto provided equipments and personnel for the collection work. RMS thanks R. José Bertini for previous discussions on the specimen described in this paper. A previous draft of the manuscript was reviewed by L. Salgado and J. Wilson; however it does not imply they agree with everything herein. We also thank Michael D'Emic and Philip Mannion whose comments greatly improved this paper. RMS was supported by Fundação de Auxílio à Pesquisa do Estado de São Paulo (FAPESP), scholarship numbers 00/00190-4 and 02/00574-2.

References

Almeida, E.B., Avilla, L.S. & Candeiro, C.R.A.(2004) Restos caudais de Titanosauridae da Formação Adamantina (Turoniano–Santoniano), Sítio do Prata, Estado de Minas Gerais, Brasil. *Revista Brasileira de Paleontologia*, 7, 239–244.

Alvarenga, H.M.F. & Nava, W.R. (2005) Aves Enantiornithes do Cretáceo Superior da Formação Adamantina do Estado de São Paulo, Brasil. *Abstracts of the II Congresso Latino-Americano de Paleontologia de Vertebrados*, Rio de Janeiro, Brazil, 20 pp.

Archangelsky, S, Bellosi, E.S., Jalfin, G.A. & Perrot, C. (1994) Palynology and alluvial facies from the mid-Cretaceous of Patagonia, subsurface of San Jorge Basin, Argentina. *Cretaceous Research*, 15, 127–142.

Ballent, S.C. (1980) Ostrácodos de ambiente salobre de la Formación Allen (Cretácico Superior) en la Provincia de Río Negro (República Argentina). *Ameghinana*, 17, 67–82.

Batezelli, A., Saad, A.R., Etchebehere, M.L.C., Perinotto, J.A.J. & Fulfaro, V.J. (2003) Análise estratigráfica aplicada à Formação Araçaatuba (Grupo Bauru—KS) no Centro-Oeste do Estado de São Paulo. *Geociências*, 22, 5–19.

Benton, M. J. (2004) Origin and relationships of Dinosauria. *In*: Weishampel D.B., Dodson P. & Osmólska H. (Eds.), *The Dinosauria.* Second Edition, University of California Press, Berkeley, pp. 7–24.

Bertini, R.J., Marshall, L.G., Gayet, M. & Brito, P.M. (1993) The vertebrate fauna from the Adamantina and Marília formations, Upper Cretaceous of the Paraná Basin, Southeast Brazil. *Neues Jahrbuch für Geologie und Paläontologie. Abhandlungen*, 188, 71–101.

Bertini, R.J., Santucci, R. M. & Arruda-Campos, A.C. (1999a) First occurrence of *Aeolosaurus* (Sauropoda, Titanosauridae) in Bauru Group of the Paraná Basin, Brazil. *Abstracts of the XVI Congresso Brasileiro de Paleontologia*, Crato, Brazil, 27–28 pp.

Bertini, R.J., Santucci, R.M. & Ribeiro, L.C.B. (1999b) O Titanosaurido *Aeolosaurus* sp. (Saurischia, Sauropoda) no Membro Serra da Galga da Formação Marília, Grupo Bauru do Triângulo Mineiro. *Abstracts of the VI Simpósio de Geologia do Sudeste*, São Pedro, Brazil, 72 pp.

Bertini, R.J., Santucci, R. M. & Ribeiro, L.C.B. & Arruda-Campos, A.C. (2000) *Aeolosaurus* (Sauropoda, Titanosauria) from Upper Cretaceous of Brazil. *Abstracts of the XVI Jornadas Argentinas de Paleontologia de Vertebrados*, San Luis, Argentina, 6 pp.

Bonaparte, J.F. (1986) History of the terrestrial Cretaceous vertebrates of Gondwana. *Report of the IV Congreso Argentino de Paleontologia y Bioestratigrafia*, Mendoza, Argentina, 2, 63–95 pp.

Bonaparte, J.F. (1992) Uma neuva especie de Triconodonta (Mammalia) de La Formación Los Alamitos, Provínvia de Río Negro y comentarios sobre su fauna de mamiferos. *Ameghiniana*, 29, 99–100.

Bonaparte, J.F. & Coria, J.O. (1993) Un nuevo y gigantesco saurópodo titanosaurido de la Formación Río Limay (Albiano–Cenomaniano) de la Provincia de Neuquén, Argentina. *Ameghiniana*, 30, 271–282.

Bonaparte, J.F., Franchi, M.R., Powell, J.E. & Sepulveda, E.G. (1984) La Formación Los Alamitos (Campaniano–Maastrichtiano) del sudeste de Rio Negro, con description de *Kritosaurus australis* sp. nov. (Hadrosauridae). Significado paleogeográfico de los vertebrados. *Revista de la Asociación Geológica Argentina,* 39, 259–265.

Borsuk-Bialynicka, M. (1977) A new camarasaurid sauropod *Opisthocoelicaudia skarzynskii* gen. n. sp. n. from the Upper Cretaceous of Mongolia. *Paleontologica Polonica*, 37, 5–64.

Buffetaut, E. & Suteethorn, V. (1989) A sauropod skeleton associated with theropod teeth in the Upper Jurassic of Thailand: Remarks on the taphonomic and paleoecological significance of such associations. *Palaeogeography, Palaeoclimatololy, Palaeoecology,* 73, 77–83.

Calvo, J.O. & Bonaparte, J.F. (1991) *Andesaurus delgadoi* gen. et sp. nov. (Saurischia, Sauropoda), dinosaurio Titanosauridae de la Formación Río Limay (Albiano–Cenomaniano), Neuquén, Argentina. *Ameghiniana*, 28, 303–310.

Calvo, J.O. & Gonzalez Riga, B. J. (2003) *Rinconsaurus caudamirus* gen. et sp. nov., a new titanosaurid (Dinosauria, Sauropoda) from the Late Cretaceous of Patagonia, Argentina. *Revista Geológica de Chile*, 30, 333–353.

Calvo, J.O. & Porfiri, J.D. (2010) *Panamericansaurus schroederi gen. nov. sp. nov.*Un neuvo Sauropoda (Titanosauridae-Aeolosaurini) de la Provìncia del Neuquén, Cretácico Superior de Patagonia, Argentina. *Brazilian Geographical Journal,* 1, 100-115.

Calvo, J.O., Porfiri, J.D., González Riga, B.J. & Kellner, A.W.A. (2007a) A new Cretaceous terrestrial ecosystem from Gondwana with the description of a new sauropod dinosaur. *Anais da Academia Brasileira de Ciencias*, 79, 529–541.

Calvo, J.O., González Riga, B.J. & Porfiri, J.A. (2007b) A new titanosaur sauropod from the Late Cretaceous of Neuquén, Patagonia, Argentina. *Arquivos do Museu Nacional*, 65, 485–504.

Campos, D.A., Kellner, A.W.A., Bertini, R.J. & Santucci, R.M. (2005) On a titanosaur (Dinosauria, Sauropoda, Titanosauridae) vertebral column from the

Bauru Group, Late Cretaceous of Brazil. *Arquivos do Museu Nacional*, 63, 565–593.

Candeiro, C.R.A., Santos, A.R., Rich, T., Marinho, T.S. & Oliveira, E.C. (2006) Vertebrate fossils from the Adamantina Formation (Late Cretaceous), Prata paleontological district, Minas Gerais State, Brazil. *Geobios*, 39, 319–327.

Cantino, P.D. & Queiroz, K. de (2010) PhyloCode: a phylogenetic code of biological nomenclature. <http://www.ohio.edu/phylocode/>.

Casal, G., Luna, M., Martínez, R.D., Lamanna, M.C., Sciutto, J.C. & Ivany, E. (2006) La fauna Campaniana–Maastrichtiana? de la Formación Bajo Barreal en el E-SE del Lago Colhué Huapi, Provincia de Chubut, Argentina. *Ameghiniana* (*Supplement*), 43, 28R.

Casal, G., Martinez, R.D., Luna, M., Sciutto, J.C. & Lamanna, M.C. (2007) *Aeolosaurus colhuehuapensis* sp. nov. (Sauropoda, Titanosauria) de la Formacion Bajo Barreal, Cretacico superior de Argentina. *Revista Brasileira de Paleontologia*, 10, 53–62.

Cope, E.D. (1869) Synopsis of the extinct Batrachia, Reptilia and Aves of North America. *Transactions of the American Philosophical Society*, 14, 1–252.

Curry Rogers, K. (2009) The postcranial anatomy of *Rapetosaurus krausei* (Sauropoda: Titanosauria). *Journal of Vertebrate Paleontology*, 29, 1046-1086.

Curry Rogers, K. (2005) Titanosauria: A Phylogenetic Overview. *In*: Curry Rogers, K. & Wilson J.A. (Eds). *The Sauropods: Evolution and Paleobiology.* University of California Press, Berkley, pp 50–103.

Curry Rogers, K. & Forster, C.A. (2001) The last of the dinosaur titans: a new sauropod from Madagascar. *Nature*, 412, 520–534.

Dias-Brito, D., Musacchio, E. A., Castro, J.C., Maranhão, M.S.A.S., Suarez, J.M. & Rodrigues, R. (2001) Grupo Bauru: uma unidade continental do Cretáceo no Brasil—concepções baseadas em dados micropaleontológicos, isotópicos e estratigráficos. *Reviue de Paleobiologie*, 20, 245–304.

Dingus, L., Clarke, J., Scott, G. R., Swisher, C., Chiappe, L.M. & Coria, R.A. (2000) Stratigraphy and magnetostratigraphic/faunal constraints for the age of sauropod embryo-bearing rocks in the Neuquén Group (late Cretaceous, Neuquén Province, Argentina). *American Museum Novitates*, 3290, 11 pp.

Fernandes, L.A. & Coimbra, A.M. (2000) Revisão estratigráfica da parte oriental da Bacia Bauru (Neocretáceo). *Revista Brasileira de Geociências*, 30, 717–728.

Franco-Rosas, A.C., Salgado, L., Rosas, C.F. & Carvalho, I.S. (2004) Nuevos materiales de titanosaurios (Sauropoda) en el Cretácico Superior de Mato Grosso, Brasil. *Revista Brasileira de Paleontologia*, 7, 329–336.

Gilmore, C.W. (1946) Reptilian fauna of the North Horn Formation of central Utah. *Uunited States Geological Survey Professional Paper*, 210-C, 29–51.

Gobbo-Rodrigues, S.R., Petri, S. & Bertini, R.J. (1999) Ocorrências de ostrácodes na Formação Adamantina do Grupo Bauru, Cretáceo Superior da Bacia do Paraná e possibilidades de correlação com depósitos isócronos argentinos. Parte I - Família Ilyocyprididae. *Acta Geológica Leopoldensia*, 23, 3–13.

Gomani, E.M. (2005) Sauropod Dinosaurs from the Early Cretaceous of Malawi, Africa, *Palaeontologia Electronica*, 8, 1–37.

González Riga, B.J. (2003) A new titanosaur (Dinosauria, Sauropoda) from the Upper Cretaceous of Mendoza Province, Argentina. *Ameghiniana*, 40, 155–172.

González Riga, B.J. Previtera, E. & Pirrone, C.A. (2009) *Malarguesaurus florenciae* gen. et sp. nov., a new titanosauriform (Dinosauria, Sauropoda) from the Upper Cretaceous of Mendoza, Argentina. *Cretaceous Research*, 30, 135–148.

Hocknull, S.A., White, M.A., Tischler, T.R., Cook, A. G., Calleja, N.D. Sloan, T. & Elliott, D. A. (2009) New mid-Cretaceous (latest Albian) dinosaurs from Winton, Queensland, Australia. *PLoS ONE*, 4, e6190.doi:10.1371/journal.pone.0006190.

Jacobs, L.L., Winkler, D.A., Downs, W.R. & Gomani, E.M. (1993) New material of an Early Cretaceous titanosaurid sauropod dinosaur from Malawi. *Palaeontology*, 36, 523–534.

Jain, S.L. & Bandyopadhyay, S. (1997) New titanosaurid (Dinosauria: Sauropoda) from the Late Cretaceous of central India. *Journal of Vertebrate Paleontology*, 17, 114–136.

Janensch, W. (1950) Die Wirbelsäule von *Brachiosaurus brancai*. *Palaeontographica* (*Supplement 7*), 3, 27–93.

Kellner, A.W.A. & Azevedo, S.A.K. (1999) A new sauropod dinosaur (Titanosauria) from the Late Cretaceous of Brazil. 111–142. *In*: Tomida, Y., Rich, T.H. & Vickers-Rich, P. (Eds). *Proceedings of the Second Gondwana Dinosaur Symposium.* National Science Museum Monographs, Tokyo, 296 pp.

Kellner, A.W.A. & Campos, D.A. (2000) Brief review of dinosaur studies and perspectives in Brazil. *Anais da Academia Brasileira de Ciências*, 72, 509–538.

Kellner, A.W.A., Campos, D.A. & Trotta, M.N. (2005) Description of a titanosaurid caudal series from the Bauru Group, late Cretaceous of Brazil. *Arquivos do Museu Nacional*, 63, 529–564.

Kellner, A.W.A., Campos, D.A., Azevedo, S.A.K., Trotta, M.N.F., Henriques, D.D.R., Craik, M.M.T. & Silva, H.P. (2006) On a new titanosaur sauropod from the Bauru Group, Late Cretaceous of Brazil. *Boletim do Museu Nacional, Nova Série, Geologia*, 74,1–31.

Le Loeuff, J. (1993) European titanosaurids. *Revue de Paléobiologie (Supplement)*, 7, 105–117.

Le Loeuff, J. (1995) *Ampelosaurus atacis* (nov. gen., nov. sp.), un nouveau Titanosauridae (Dinosauria, Sauropoda) du Crétacé Superieur de la Haute Vallée de l'Aude (France). *Compte Rendus de l'Académie des Sciences de Paris*, 321, 693–699.

Lopes, R.P. & Buchmann, F.S.C. (2008) Fossil of titanosaurs (Dinosauria, Sauropoda) from a new outcrop in Triangulo Mineiro, Southeastern Brazil. *Revista Brasileira de Paleontologia*, 11, 51–58.

Manassero, M.L. (1997) Sedimentology of the Upper Cretaceous red beds of Angostura Colorada Formation in the western sector of the Northpatagonian Massif, Argentina. *Journal of the South American Earth Sciences*, 10, 81–90.

Mannion, P.D. Calvo, J.O. (2011) Anatomy of the basal titanosaur (Dinosauria, Sauropoda) *Andesaurus delgadoi* from the mid-Cretaceous (Albian–early Cenomanian) Río Limay Formation, Neuquén Province, Argentina: implications for titanosaur systematics. *Zoological Journal of the Linnean Socciety*, doi: 10.1111/j.1096-3642.2011.00699.x.

Marsh, O.C. (1878) Principal characters of American Jurassic dinosaurs. Part 1. *American Journal of Science*, 16, 411–416.

Martin, V., Buffetaut, E. & Suteethorn, V. (1994) A new genus of sauropod dinosaur from the Sao Khua Formation (Late Jurassic or Early Cretaceous) of northeastern Thailand. *Comptes Rendus de l'Academie des Sciences Paris (série II)*, 319, 1085-1092.

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

Martinelli, A.G., Riff, D & Lopes, R.P. (2011) Discussion about the occurrence of the genus *Aeolosaurus* Powell 1987 (Dinosauria, Titanosauria) in the Upper Cretaceous of Brazil. *Gaea*, 7, 34–40.

Martínez, R.D., Giménez, O., Rodríguez, J., Luna, M. & Lamanna, M.C. (2004) An articulated specimen of the basal titanosaurian (Dinosauria: Sauropoda) *Epachthosaurus sciuttoi* from the early Late Cretaceous Bajo Barreal Formation of Chunut Province, Argentina. *Journal of Vertebrate Paleontology*, 24, 107–120.

Mezzalira, S. (1989) *Os fósseis do Estado de São Paulo*. Instituto Geológico, São Paulo, 142 pp.

Molnar, R.E. & Salisbury, S.W. (2005) Observations on Cretaceous sauropods from Australia. *In*: Tidwell, V. & Carpenter, K. (Eds), *Thunder-Lizards: the Sauropodomorph Dinosaurs*. Indiana University Press, Bloomingon, pp 454–465.

Padian, K., Hutchnson, J.R. & Holtz, T.R. (1999) Phylogenetic definitions and nomenclature of the major taxonomic categories of the carnivorous Dinosauria (Theropoda). *Journal of Vertebrate Paleontology*, 19, 69–80.

Papú, O.H. & Sepúlveda, E.G. (1995) Datos palinológicos de la Formación Los Alamitos en la localidad de Montonilo, Departamento 25 de Mayo, Río Negro, Argentina, sus relaciones con unidades colindantes coetáneas. *VI Congreso Argentino de Paleontología y Bioestratigrafía*, Trelew, pp. 195–200.

Powell, J.E. (1986) *Revisión de los titanosáuridos de América del Sur*. PhD Dissertation, Universidad Nacional de Tucumán, Argentina, 340 pp.

Powell, J.E. (1987) The Late Cretaceous fauna of Los Alamitos, Patagonia, Argentina. Part VI. The titanosaurids. *Revista del Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia'*, 3, 147–153.

Powell, J.E. (2003) Revision of South American titanosaurid dinosaurs: palaeobiological, palaeobiogeographical and phylogenetic aspects. *Records of the Queen Victoria Museum*, 111, 173 pp.

Prámparo, M.B., Quattrocchio, M., Gandolfo, M.A., Zamaloa, M.C. & Romero, E. (2007) Historia evolutiva de las angiospermas (Cretáceo-Paleógeno) em Argentina a través de los registros paleoflorísticos. *Ameghiniana, Especial Publication*, 11, 157–172.

Prieto-Marquez, A. & Salinas, G.C. (2010) A re-evaluation of *Secernosaurus koerneri* and *Kritosaurus australis* (Dinosauria, Hadrosauridae) from the Late Cretaceous of Argentina. *Journal of Vertebrate Paleontology*, 30, 813–837.

Queiroz, K. de & Gauthier, J.A. (1990) Phylogeny as a central principle in taxonomy: Phylogenetic definitions of taxon names. *Systematic Zoology*, 39, 307–322.

Queiroz, K. de & Gauthier, J.A. (1992) Phylogenetic taxonomy. *Annual Reviews of Ecology and Systematics*, 23, 449–480.

Queiroz, K. de & Gauthier, J.A. (1994) Toward a phylogenetic system of biological nomenclature. *Trends Ecology and Evolution*, 9, 27–31.

Salgado, L. & Azpilicueta, C. (2000) Un nuevo saltasaurino (Sauropoda, Titnosauridae) de la Provincia de Río Negro (Formación Allen, Cretácico Superior), Patagonia, Argentina. *Ameghiniana*, 37, 259–264.

Salgado, L. & Carvalho, I.S. (2008) *Uberabatitan ribeiroi*, a new titanosaur from the Marília Formation (Bauru Group, Upper Createaceous), Minas Gerais, Brasil. *Palaeontology*, 51, 881–901.

Salgado, L. & Coria, R.A. (1993) El género *Aeolosaurus* (Sauropoda-Titanosauridae) en la Formación Allen (Campaniano–Maastrichtiano) de la Província de Río Negro, Argentina. *Ameghiniana*, 30, 119–128.

Salgado, L., Coria, R.A. & Calvo, J.O. (1997a) Presencia del gênero *Aeolosaurus* (Sauropoda, Titanosauridae) en La Formación Los Alamitos, Cretácico Superior de La Província de Rio Negro, Argentina. *Revista Universidade de Guarulhos*, 2, 44–49.

Salgado, L., Coria, R.A. & Calvo, J.O. (1997b) Evolution of titanosaurid sauropods. I: Phylogenetic analysis based on the postcranial evidence. *Ameghiniana*, 34, 3–32.

Santucci, R.M. (2008) First titanosaur (Saurischia, Sauropoda) axial remains from the Uberaba Formation, Upper Cretaceous, Bauru Group, Brazil. *Historical Biology*, 20, 165–173.

Santucci, R.M. & Bertini, R.J. (2001) Distribuição paleogeográfica e biocronológica dos titanossauros (Saurischia, Sauropoda) do Grupo Bauru, Cretáceo Superior do sudeste brasileiro. *Revista Brasileira de Geociências*, 31, 307–314.

Santucci, R.M. & Bertini, R.J. (2006a) A new titanosaur from western São Paulo State, Upper Cretaceous Bauru Group, South-east Brazil. *Palaeontology*, 49, 59–66.

Santucci, R.M. & Bertini, R.J. (2006b) A large sauropod titanosaur from Peirópolis, Bauru Group, Brazil. *Neues Jahrbuch für Geologie und Paläontologie. Monatshefte*, 6, 344–360.

Sanz, J. L., Powell, J.E., Le Loeuff, J., Martinez, R. & Suberbiola, X.P. (1999) Sauropod remains from the Upper Cretaceous of Laño (north-central Spain). Titanosaur phylogenetic relationships. *Estudios del Museu de Ciencias Naturales de Alava*, 14, 235–255.

Seeley, H.G. (1888) The classification of the Dinosauria. *British Association for the Advancement of Science, Report*, 1887, 698–699.

Swofford, D.L. (2000) *PAUP*. Phylogenetic Analysis Using Parsimony (*and other methods)*, Version 4b10. Sinauer Associates, Sunderland, MA.

Tamrat, E., Ernesto, M., Fulfaro, V.J., Saad, A.R., Batezelli, A. & Oliveira, A.F. (2002) Magnetoestratigrafia das Formações Uberaba e Marília (Grupo Bauru) no Triângulo Mineiro. *VI Simpósio sobre o Cretáceo Brasileiro e II Simpósio sobre el Cretácico de America del Sur*, São Pedro, p. 323–327.

Upchurch, P. (1998) The phylogenetic relationships of sauropod dinosaurs. *Zoological Journal of the Linnean Society*, 124, 43–103.

Upchurch P., Barret P.M. & Dodson P. (2004) Sauropoda. *In*: Weishampel D.B., Dodson P. & Osmólska H. (Eds.), *The Dinosauria.* Second Edition, University of California Press, Berkeley, pp. 259–322.

Wilson, J.A. (1999) A nomenclature for vertebral laminae in sauropods and other saurischian dinosaurs. *Journal of Vertebrate Paleontology*, 19, 639–653.

Wilson, J.A. (2002) Sauropod dinosaur phylogeny: critique and cladistic analysis. *Zoological Journal of the Linnean Society*, 136, 217–276.

Wilson, J.A. & Sereno, P.C. (1998) Early evolution and higherlevel phylogeny of sauropod dinosaurs. *Society of Vertebrate Paleontology*, Memoir 5, 1–68.

Wilson, J.A. & Upchurch, P. (2009) Redescription and reassessment of the phylogenetic affinities of *Euhelopus zdanskyi* (Dinosauria: Sauropoda) from the Early Cretaceous of China. *Journal of Systematic Palaeontology*, 7, 199–239.

Zaher, H., Pol, D., Carvalho, A.B., Nascimento, P., Riccomini, C., Larson, P., Juarez-Valieri, R., Pires-Domingues, R., Silva, N. & Campos, D. A. (2011). A complete skull of an Early Cretaceous sauropod and the evolution of advanced titanosaurians. *PLoS ONE*, 6, e16663. doi:10.1371/journal.pone.0016663.

APPENDIX 1. Character statements added to the data matrices of Wilson (2002).

235. Apex of the convexity of the posterior articulation on anterior and middle caudal vertebrae: (0) concentrical or slightly displaced above the centrum midline; (1) strongly displaced upward, so that the apex of the posterior articulation is flushed to the level of the dorsal margin of the centrum (Powell, 1986, 1987, 2003).
236. Anterior margin of the anterior caudal vertebrae: (0) vertical; (1) strongly inclined forward (Franco-Rosas *et al*., 2004).
237. Articular facets of the prezygapophyses on anterior and middle caudal vertebrae: (0) normal, not expanded; (1) wide, with a dorsal and a ventral expansion or protuberance (Powell, 1986, 1987, 2003).
238. Prezygapophyses curved downward on anteriormost caudal vertebrae: (0) absent; (1) present.
239. Postzygapophyses located on the anterior half of the centrum on anterior and middle caudal vertebrae: (0) absent; (1) present (Salgado *et al*., 1997b).
240. Haemal arches with double articular facets set in a concave posterodorsal surface: (0) absent; (1) present (Powell, 1986, 1987, 2003).
241. Length proportions of the prezygapophyses with respect to the centrum length in middle caudal vertebrae: (0) less than 40%; (1) between 40-50%; (2) more than 50% (Powell, 1986, 1987, 2003; Calvo *et al.*, 2007a).

APPENDIX 2. Codings for the data matrix of Wilson (2002).

PROSAUROPODA
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 9 9 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 9
0 0 0 0 0 0 0 0 0 0 0 1 1 0 9 0 0 0 0 0 0 9 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 9 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
9 9 0 0 0 0 0 9 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 9 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 ? 0 0 0 0 0 0

THEROPODA
0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 9 9 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 9
0 0 0 0 0 0 0 0 0 0 0 0 1 0 9 0 0 0 0 0 0 9 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 9 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
9 9 0 0 0 0 0 9 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 9 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
0 0 0 0 0 0 0 0 0 0 0 0 0 0 9 9 0 0 0 0 0 0 0 0 0 0 0 0 0 0 ? 0 0 0 0 0 0

Vulcanodon
? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 0 ?
? ? ? ? 0 ? ? ? ? 9 ? 1 ? ? ? ? 0 ? ? 0 ? 0 0 ? ? ? ? ? ? ? 1 0 0 0 0 1 ? ? ? ? ? ? ? ? ? ? ? ? 0
0 ? ? 1 0 ? ? ? ? ? ? ? ? ? 1 0 1 0 ? 1 1 1 0 1 0 0 1 ? ? ? ? 0 ? ? ? ? ? ? ? 1 ? ? ? 0 0 0 1 0 1 0 1 0 1 0 ? ? ? 0 0 0 ? 0 0 0 0 1 0 0 0 0
1 0 ? 1 0 0 1 0 0 1 0 0 ? 0 1 1 0 0 0 ? 0 0 0 0 0 0

Barapasaurus
? 1 ? 0 ?
? ? ? 0 0 ? ? 0 1 9 ? ? 0 1 0 0 9 ? 1 0 1 0 1 1 0 1 1 1 0 1 0 0 0 0 1 1 0 0 ? 0 ? ? 0 ? 0 0 ? ? ? ? ? ? ? 1 0 0 0 0 0 0 0 0 0 9 9 ? ? ? 0 1
? 0 0 ? 0 1 1 0 0 0 0 0 0 0 ? 0 1 0 1 0 1 1 1 1 0 1 0 0 ? ? ? ? ? ? ? ? ? ? ? ? 0 1 1 0 0 0 1 0 1 0 1 0 1 1 1 0 1 0 0 0 1 0 1 1 1 1 ? 1 ?
1 0 ? ? ? 0 1 0 ? ? ? ? ? ? ? 1 ? ? 1 1 ? 0 ? 0 0 0 0 0 0

Omeisaurus
1 1 1 0 0 0 1 1 0 1 1 ? 0 0 0 ? 0 1 0 1 1 0 0 0 0 1 0 1 1 1 ? 1 1 ? 0 ? 1 ? ? 1 1 1 0 0 ? 0 ? 0 ? 0 ? 0 0 1 1 0 0 0 0 ? 1 ? ? ? 1 1 1 0 1
1 1 1 1 ? 0 0 0 1 0 4 0 1 1 1 0 1 0 ? 0 9 3 1 0 1 ? 1 1 0 1 1 1 0 0 0 0 0 0 2 1 1 0 1 ? 0 1 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 ? 0 0 0 ? ? ?
1 0 0 ? 1 1 0 0 0 0 1 1 0 0 0 ? 0 0 0 0 0 1 0 1 0 1 1 0 1 0 1 0 0 1 0 1 0 0 0 0 0 0 1 1 1 ? 1 1 0 0 0 1 0 1 0 1 0 1 ? 1 0 0 0 ? 0 1 0 1
1 ? ? 0 1 0 1 0 0 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 0 ? 0 0 0 0 0 0

Shunosaurus
0 1 1 0 0 0 1 1 0 1 1 0 0 0 0 0 0 0 0 1 ? ? 0 0 0 0 0 1 1 1 0 1 1 0 0 0 1 0 0 1 1 0 0 0 0 0 0 0 0 ? 0 0 0 1 1 0 0 0 0 ? 1 0 1 ? 1 1 1 0
1 1 1 2 0 ? 0 0 0 0 0 3 1 1 9 1 0 0 1 0 0 9 2 1 0 0 0 0 ? 0 0 0 0 0 0 0 0 ? 0 1 0 9 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 ? 0 0 0 9
9 9 0 ? 0 0 1 1 1 0 1 0 1 0 0 0 0 0 0 0 0 0 0 1 0 1 0 1 1 0 1 0 1 0 0 1 0 1 0 0 0 0 0 1 1 0 1 0 1 1 0 0 0 1 0 1 0 ? 0 1 1 1 0 1 0 0 ? 1
0 1 ? 1 0 0 1 0 ? 0 0 1 1 1 1 0 1 1 1 0 1 1 1 ? 1 1 1 1 1 0 ? 0 0 0 0 0 0

Patagosaurus
1 ? 1 0 0 ? 1 1 ? ? ? ? ? ? ? ? 0 ? 1 ? ? ? ? ? ? ? ? ? ? ? ? ? 0 ? ? ? ? ? ? ? ? 1 ? 1 0 1 1 1 ?
? ? 0 0 0 1 ? ? 0 1 1 ? 0 0 1 0 0 9 ? 1 0 1 0 1 1 0 1 ? ? 0 1 0 0 0 0 2 ? ? 0 ? ? ? ? ? ? 0 0 ? ? ? ? ? ? ? 1 ? ? ? 0 ? 0 0 0 ? ? ? 1 ? 0 0
? ? 0 0 ? ? 1 1 0 ? 0 ? 0 0 0 ? 0 1 0 1 1 1 1 1 1 0 1 0 0 ? ? ? ? ? ? ? ? ? ? ? ? ? 1 1 0 0 0 1 0 1 0 1 0 1 1 1 0 1 0 0 0 0 0 1 ? ? ? ? ? ?
? ? ? ? 1 0 1 0 1 1 ? ? ? ? ? ? ? ? ? ? ? 0 ? 0 0 0 0 0 ?

Mamenchisaurus
? 1 1 0 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 1 0 0 0 0 ? 1 0 1 1 1 ? 1 ? 1 1 1 1
0 0 0 0 1 1 ? 4 0 1 ? 1 0 1 0 1 1 0 3 1 0 1 0 ? 1 ? 1 ? 1 0 ? 0 0 0 0 2 ? ? ? ? ? 0 1 1 0 1 0 0 0 0 0 0 0 0 1 0 0 0 0 ? 0 0 0 ? ? ? 1 0 0
0 1 1 0 0 ? 0 1 ? ? ? ? ? ? ? ? ? 0 1 0 1 0 1 1 1 1 0 1 0 0 1 ? ? ? ? ? ? ? ? ? ? ? ? 1 1 0 0 ? ? ? ? 0 1 0 1 1 1 0 1 0 0 1 1 0 1 ? 1 1 0 1
1 1 0 ? 1 1 ? ? ? ? ? 1 ? 1 1 ? 1 ? ? 1 ? ? 0 0 0 0 0 0 0 0

Apatosaurus
0 0 1 1 1 1 1 2 0 1 1 ? 1 1 1 ? 0 1 0 1 1 1 ? 1 0 1 0 1 1 1 1 1 1 0 0 0 2 0 ? 1 ? 0 0 0 0 1 0 0 0 0 0 0 1 1 ? ? ? ? ? ? ? ? ? ? 2 2 1 2 0
2 1 2 1 ? ? ? 0 1 1 4 0 1 1 0 1 0 1 1 1 1 5 1 0 1 1 1 1 1 1 1 1 0 0 0 0 0 0 2 1 ? 1 1 0 0 1 1 0 0 0 0 1 1 1 1 0 1 1 1 1 1 0 0 0 0 0 1 1
1 1 1 0 0 1 1 0 0 1 0 1 1 0 0 1 1 0 0 0 0 0 1 0 1 0 1 1 0 1 0 1 0 0 1 1 1 1 1 0 0 0 0 1 1 1 1 1 1 0 0 1 1 0 1 0 0 0 1 1 1 0 1 0 0 1 1 0
1 1 1 0 1 1 1 1 0 1 1 1 1 1 1 1 1 1 1 ? 1 1 1 1 ? 1 1 1 0 0 0 0 0 0 0 0

Barosaurus
? ?
? ? 0 1 ? ? 0 1 1 ? 1 1 1 ? 1 1 ? 1 0 1 ? ? ? ? 1 1 1 0 0 0 0 0 0 0 ? ? ? ? ? 0 ? 1 1 0 1 1 1 1 1 1 1 0 1 1 1 1 1 1 1 1 0 0 1 1 ? ? ? ? 0 1 ?
0 0 ? 0 1 ? ? ? ? ? ? ? ? 0 ? 1 1 ?
? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 0 ? 0 0 0 0 0 0

Brachiosaurus
1 1 1 1 0 0 1 1 1 1 1 1 0 0 0 1 0 1 0 1 1 0 0 0 0 1 0 1 1 1 1 1 1 1 0 0 1 0 1 1 1 1 0 0 0 0 0 0 0 1 1 0 0 1 1 0 0 1 1 1 1 1 1 2 1 1 1 0
0 1 1 2 1 0 0 0 1 1 0 3 0 1 1 0 0 1 1 0 0 9 3 1 0 1 0 1 1 1 1 1 1 1 0 0 1 0 0 2 1 1 0 1 0 ? 1 0 0 0 0 0 0 0 1 1 0 0 1 0 0 0 0 0 0 0 0 ?
? ? 1 0 1 1 ? ? 1 0 ? ? 1 1 0 1 0 1 0 0 0 0 0 1 0 1 0 1 1 1 1 0 1 0 0 1 1 1 1 1 1 1 1 1 1 0 1 1 1 1 0 1 0 1 1 1 0 1 1 1 1 1 1 1 0 0 1 1
0 1 1 1 1 1 1 1 1 0 0 1 1 1 1 0 1 1 1 ? 1 1 ? 1 ? ? 1 1 ? 0 ? 0 0 0 0 0 0

Camarasaurus

1 1 1 1 0 0 1 1 1 1 1 1 0 0 0 1 0 1 0 1 1 0 0 1 0 1 0 1 1 1 0 0 1 1 0 1 1 0 1 1 1 1 0 0 0 0 0 0 0 0 1 0 0 1 1 0 0 1 1 1 1 1 1 1 1 1 0
1 1 1 2 1 0 0 0 0 1 0 2 0 1 1 0 1 0 1 0 1 0 3 1 0 1 0 1 1 0 1 1 1 1 0 0 1 0 0 2 1 1 0 1 0 0 1 0 0 0 0 0 0 0 1 1 0 1 1 0 0 0 0 0 0 0 0 0
9 9 1 0 0 ? 1 0 1 0 1 0 1 1 0 1 0 1 0 0 0 0 0 1 0 1 0 1 1 1 1 0 1 0 0 1 1 1 1 1 1 1 0 0 1 1 1 1 1 1 0 0 0 1 1 1 0 1 1 1 1 1 0 1 0 0 1 1
0 1 1 1 0 1 1 1 1 0 0 1 1 1 1 0 1 1 1 1 1 1 1 1 1 1 1 1 1 0 ? 0 0 0 0 0 0

Dicraeosaurus
0 0 ? 1 1 ? ? ? ? ? 0 ? ? 0 0 ? 0 1 1 1 1 1 1 1 0 1 1 1 1 1 ? ? ? ? ? 1 ? 0 ? ? 1 0 0 0 1 1 1 0 1 0 1 0 1 1 1 1 0 ? ? ? ? ? ? ? 2 2 1 2 0 2
1 2 1 ? 0 0 0 1 1 2 0 1 1 0 1 0 1 0 1 1 3 1 1 1 1 1 0 0 1 1 1 0 0 0 0 0 1 2 1 ? 1 ? 0 ? 1 1 0 0 0 0 1 0 1 1 0 1 1 1 0 0 0 0 0 0 0 1 1 ?
1 1 0 0 1 ? 0 0 ? ? 1 1 0 0 0 1 0 0 0 ? 0 1 0 1 0 1 1 1 1 0 ? ? ? 1 ? ? ? ? ? ? ? ? ? ? ? 1 1 1 0 0 1 1 0 1 0 0 0 1 1 1 0 1 0 0 1 1 0 1 1
1 0 1 1 1 1 0 ? ? 1 1 1 1 1 1 ? 1 1 ? ? ? ? 1 1 ? ? 0 ? 0 0 0 0 0 0

Diplodocus
0 0 1 1 1 1 1 2 0 1 1 1 1 1 1 1 0 1 0 1 1 1 0 1 0 1 0 1 1 1 1 1 1 0 0 0 2 0 1 1 1 0 0 0 0 1 0 0 0 0 1 0 1 1 1 1 0 1 0 1 1 0 1 ? 2 2 1 2
0 2 1 2 1 1 1 0 0 1 1 4 0 1 1 0 1 1 1 1 1 1 5 1 0 1 1 1 1 1 1 1 1 0 0 0 0 0 0 2 1 1 1 1 0 0 1 1 0 1 1 1 1 1 1 1 0 1 1 1 1 1 1 1 1 1 0 0 1
1 1 1 1 0 0 1 1 0 0 1 0 1 1 0 0 0 1 0 0 0 0 0 1 0 1 0 1 1 1 1 0 1 0 0 1 ? ? ? ? ? ? ? ? ? ? ? 1 1 1 0 0 1 1 0 1 0 0 0 1 1 1 0 1 0 1 1 1 0
1 ? 1 0 1 1 1 1 0 0 1 1 1 1 1 1 1 1 1 1 1 1 1 ? 1 1 1 1 0 0 0 0 0 0 0 0

Haplocanthosaurus
? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 0 ? 0 ?
? ? ? 0 1 ? 3 0 1 1 0 0 0 1 0 0 9 2 1 0 1 0 1 1 0 1 1 1 1 0 0 0 0 0 2 1 1 0 1 0 ? 1 0 0 0 0 0 0 0 1 1 0 0 1 0 0 0 0 0 0 0 ? ? ? ? 1 1 0 0
? ? 1 0 ? ? 1 0 0 0 0 1 0 0 0 ? 1 1 1 0 0 0 1 0 1 0 1 1 1 1 0 1 0 0 ? ? ? ? ? ? ? ? ? ? ? ?
? 0 ? 0 0 0 0 0 ?

Amargasaurus
? ? ? ? ? ? ? ? ? ? 1 ? ? 0 0 1 0 1 1 1 1 ? 1 1 0 1 1 1 1 ? ? ? ? ? ? ? ? ? ? ? ? ? 0 0 1 1 1 0 1 1 ? 0 1 1 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?
? ? ? ? ? 0 0 1 3 0 1 9 ? 1 0 1 0 1 0 5 1 1 1 ? ? ? ? 1 ? ? 0 0 0 0 ? 1 2 ? ? 1 ? ? ? ? 0 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 0 ? ? ? ? ? ? ? 0
? ? ? ? ? ? 1 ? ? 0 ? 1 ? ? ? ? 0 1 0 1 0 1 1 0 1 0 ? 0 0 1 ? ? ? ? ? ? ? ? ? ? ? ? 1 1 0 0 ? ? ? ? ? ? ? 1 1 1 0 ? 0 0 ? ? ? ? ? ? ? ? ? ? ?
? 0 ? ? 0 ? 0 0 0

Euhelopus
0 1 1 1 0 ? 1 1 ? ? 1 ? ? ? ? 1 0 ? ? ? ? ? ? ? 0 ? ? ? ? ? ? ? 1 1 ? ? ? 0 1 1 ? ? ? ? ? ? ? ? ? ? ? ? ? ? 1 0 0 1 ? ? ? ? ? ? 1 1 1 0 1 1 1
2 1 ? 1 0 1 1 ? 4 0 1 1 1 0 1 1 0 1 1 2 1 0 1 0 1 1 1 1 0 1 1 0 0 1 ? 0 3 ? ? 0 1 ? 1 0 1
1 ? ? ? ? ? ? 1 1 0 0 1 0 0 0 0 ? 1 1 0 1 0 1 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 1 1 1 ? ? 0 1 ? ? 0 1 1 1 1 1 1 1 0 0 1 1 0 1 ? 1 0 1 1
1 ? 0 0 ? 1 1 1 0 1 ? 1 1 ? 1 ? ? ? 1 1 ? ? 0 ? ? ? ? ? ? ?

Jobaria
1 1 1 1 0 0 1 1 1 1 1 1 0 0 0 1 0 1 0 1 1 0 0 0 0 1 0 1 1 1 0 1 1 1 0 ? 1 0 ? 1 1 ? 0 0 0 ? ? 0 0 0 ? 0 0 1 0 0 0 ? ? ? ? ? ? ? 1 1 1 0 1
1 1 0 0 0 0 0 0 1 ? 3 0 1 1 0 0 0 1 0 0 9 3 1 0 1 0 1 1 1 1 1 1 1 0 0 0 0 0 2 1 1 0 1 0 0 1 0 0 0 0 0 0 0 1 1 0 0 1 0 0 0 0 0 0 0 ? ?
? 1 0 0 0 1 ? 0 0 1 0 1 1 0 1 0 1 0 0 0 0 0 1 0 1 0 1 1 1 1 0 1 0 0 1 0 1 1 1 0 0 0 0 1 1 1 1 1 1 0 0 0 1 0 1 0 1 1 1 1 1 0 1 0 0 1 1 0
1 1 1 0 1 1 1 1 0 0 1 1 1 1 0 1 1 1 1 1 ? ? ? ? ? ? ? ? 0 ? 0 0 0 0 0 0

Malawisaurus
1 1 ? ? ? ? ? 1 ? ? 1 ? 1 0 0 ? ? ? ? ? ? ? 1 ? 1 ? ? 1 1 2 1
0 ? 0 1 1 ? ? 1 1 0 0 0 1 1 ? 0 9 ? 1 0 1 0 1 ? 0 1 ? 1 1 0 1 1 1 0 ? ? ? ? ? ? ? 1 ? ? 1 0 ? 0 0 1 1 1 0 1 0 0 0 0 1 0 0 0 ? ? ? 1 0 1 ? 0
9 1 1 ? ? 1 ? ? ? ? ? 0 0 0 1 1 1 0 1 0 1 1 0 0 0 1 0 0 ? ? ? 1 ? ? 1 1 1 ? ? ? ? ? ? ? ? ? ? ? ? 1 1 1 ? 1 1 1 ? ? ? ? ? 1 1 1 1 0 ? ? ? ? ?
? ? 1 ? ? ? ? ? ? ? ? ? ? ? ? ? 1 ? ? 1 1 0 0 0 0 0 1

Nigersaurus
0 0 1 1 ? ? 1 1 0 0 ? ? ? 0 0 1 1 9 0 0 1 ? ? 9 1 9 9 9 9 1 ? 1 1 1 0 ? ? ? ? ? ? ? 0 0 0 1 ? 0 0 ? ? 0 1 1 1 0 9 1 0 0 ? ? ? ? 2 2 1 1 0 2
1 2 0 1 0 1 0 1 ? ? 0 1 1 0 0 0 1 ? 0 9 ? 1 1 0 0
? ? ? ? ? ? ? 1 0 2 0 ? 0 ?
? 0

Rayososaurus
? ? ? ? ? ? ? ? ? 0 1 ? ? 0 0 1 1 9 0 0 1 1 0 9 1 9 9 9 1 1 0 ? 1 1 0 ? ? 0 ? ? ? ? 1 0 0 1 0 1 0 1 1 0 1 1 ? ? ? ? ? ? ? ? ? ? ? ? 1 ? ? 2
1 2 ? ? ? 1 0 1 ? ? 0 1 1 0 0 0 1 0 0 9 ? 1 ? 1 0 ? ? ? 1 1 1 0 0 0 0 ? 1 ? ? ? ? ? 0 0 1 0 0 0 0 0 0 0 1 1 0 1 1 0 0 0 0 0 0 0 0 1 1 ? 1
? ? ? ? ? 1 ? ? ? 1 1 0 2 0 ? 0 0 0 1 0 1 0 0 0 1 1 1 0 1 0 0 1 ? ? ? ? ? ? ? ? ? ? ? ? ? 1 1 ? ? 0 1 0 1 0 1 1 1 1 1 0 ? 0 0 ? 1 0 ? ? 1 ?
1 ? ? ? 0 ? ? 1 0 0 0 1 1 1 1 ? ? ? ? ? ? ? ? ? 0 ? 0 0 0 0 0 ?

Rebbachisaurus

? ?
? ? ? 1 ? ? ? ? ? ? ? ? ? ? 0 9 ? 1 1 ? ? 1 1 1 1 1 1 0 0 0 0 1 1 ?
? ? 1 1 0 2 0 1 ? ? ? ? ? 1 ? 0 ? 0 1 1 ?
? ? ? ? ? ? ? ? ? ? ? ? ? ? 0 ? ? ? ? ? ? ?

Alamosaurus
? ?
? ? 1 1 ? ? 1 1 0 0 0 0 1 ? 0 9 ? 1 0 1 0 1 1 0 1 0 1 1 0 1 1 1 0 ? ? ? ? ? ? 1 2 3 1 1 0 0 0 0 1 1 0 1 1 0 0 0 0 1 0 1 0 ? ? ? ? ? ? ? 0
9 1 1 1 1 1 1 1 0 1 1 1 1 ? 1 1 1 1 1 1 0 1 1 0 0 1 1 1 ? 9 9 1 1 1 1 1 1 2 9 9 ? ? ? ? ? ? ? ? 0 1 1 1 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?
? 0 0 0 0 0 0 0 0

Nemegtosaurus
0 1 ? 1 9 0 1 1 ? 1 0 1 0 0 0 1 0 1 0 1 0 1 0 1 0 1 0 1 0 1 0 1 0 1 1 1 1 2 1 1 1 1 1 ? 1 1 0 0 0 1 0 0 0 1 0 1 1 0 1 1 1 ? ? 0 1 ? 1 1 1 ? 0
2 1 2 1 0 0 0 ?
? ?
? ?

Neuquensaurus
? ?
? ? 1 1 ? ? 0 1 0 ? 0 0 1 ? 0 9 ? 1 0 1 ? ? ? ? 1 ? 1 ? 0 1 1 1 0 3 1 ? 0 ? 1 ? ? 3 0 1 0 ? 0 0 1 1 ? 1 1 0 0 0 0 1 0 1 1 1 0 ? ? ? ? ? ? ?
? ? ? ? 1 1 1 0 1 0 1 1 1 1 1 1 1 1 1 0 1 1 0 1 1 1 1 ? ? ? ? ? ? ? ? ? ? ? ? ? 1 1 1 1 0 1 ? 0 1 1 1 1 1 2 1 1 1 1 1 1 1 1 ? 1 0 1 1 1 0
1 ? ? 1 1 1 0 ? ? ? ? ? 1 ? ? ? ? ? ? ? 1 0 0 0 0 0 ? 0

Opisthocoelicaudia
? ?
? ? ? 1 ? ? ? ? ? ? ? ? ? 0 1 0 4 1 0 1 0 1 1 1 1 0 1 1 0 1 1 1 0 3 1 ? 0 ? ? 1 2 2 1 2 0 0 0 0 1 1 0 1 1 0 0 0 0 1 0 2 0 1 0 0 ? ? 1 1 0
9 1 1 1 1 1 1 0 0 1 1 1 1 1 1 1 1 1 1 1 0 1 1 0 1 1 1 1 1 9 9 1 1 1 1 1 1 2 9 9 1 1 1 1 ? 0 1 1 0 1 1 1 1 1 2 1 1 1 0 1 1 1 1 1 1 0 1 1
1 0 1 1 1 1 1 1 0 1 1 1 1 1 1 1 1 1 0 1 1 1 1 0 ? 0 0 0 0 0 0

Rapetosaurus
0 0 1 1 ? 1 1 1 ? 1 0 ? 0 0 0 ? 0 0 0 1 0 1 0 1 0 1 0 1 0 1 0 ? 1 1 1 2 1 1 1 ? ? ? 1 1 ? 0 1 0 0 ? 1 1 0 1 0 0 1 1 1 ? ? ? ? ? 1 1 1 1 0
2 1 2 1 0 0 0 1 1 ? ? 1 1 0 ? 0 1 1 ? 0 9 ? 1 0 1 0 1 ? 0 1 0 1 1 0 1 1 1 0 3 ? ? ? ? ? ? ? ? ? 1 ? ? 0 ? ? ? ? ? ? ? 0 0 ? ? ? 1 ? ? ? ? 1
? ? ? ? ? ? ? ? ? 1 1 1 0 ? ? 1 0 0 1 1 1 0 1 1 0 1 ? 0 0 1 1 0 ? ? ? ? ? 1 ? 1 ? ? ? ? 1 1 1 0 1 0 1 1 0 1 1 1 1 1 ? 1 1 0 1 ? ? ? ? ? ? ?
? 1 0 1 0 0 0 ? ?

Saltasaurus
? ? ? ? ? ? ? ? ? ? ? ? ? 0 0 ? ? 1 0 1 ? 0 0 1 0 1 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 0 1 0 0 0 1 0 1 ? ? ? 1 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?
? ? ? ? 1 1 ? ? 0 1 1 0 0 0 1 1 0 9 ? 1 0 1 0 1 ? 1 1 0 1 1 0 1 1 1 0 3 1 2 0 1 1 ? ? ? ? 1 0 ? 0 0 1 1 1 1 1 0 0 0 0 1 0 1 1 1 0 ? 1 ? ?
? ? ? 1 1 ? 0 1 1 1 0 1 0 1 1 1 1 1 1 1 1 1 0 1 1 0 1 1 1 1 ? ? ? ? ? ? ? ? ? ? ? ? 1 1 1 1 1 0 1 1 0 1 1 1 1 1 2 1 1 1 1 1 1 1 1 1 1 0 ?
? 1 0 0 0 0 0 0 0

I. colberti
? ?
? ? ? 1 ? ? 1 1 0 0 0 0 1 0 0 9 ? 1 0 1 0 1 1 0 1 0 1 0 0 ? 1 1 0 3 1 2 0 ? ? ? ? ? ? 1 0 ? 0 0 1 1 0 1 1 0 0 0 0 1 0 1 0 ? ? ? 1 ? ? 1 0
9 1 1 ? 0 1 0 1 0 1 0 ? ? ? ? 1 1 0 1 1 1 1 1 0 1 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 1 1 1 1 1 0 1 1 0 1 1 1 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?
? 0 0 0 0 0 0 ?

Baurutitan britoi
? ?
? 1 3 1 1 0 0 0 0 1 1 0 0 1 0 0 ? 0 1 0 1 ? ? ? ? ? ? ? ? 0 9 1 1
? ?
? ? ? ? ? ? ? ? ? ? ? ? ? ? 0 0 0 0 0 0 1

Maxakalisaurus topai
? 0 0 2 ?
? ? 0 ? ? ? ? 1 1 ? ? ? ? 1 ? 0 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 1 ? ? ? ? ? ? ? ? ? ? ? 1 0 ? ? ? ? ? ? ? ? 0 0 ? 0 1 ? 1 1 ? ? ? 1 ? ? ? 0 9 1
1 ? ? ? ? ? ? ? ? ? ? ? 1 ? 1 0 ?
? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 1 0 0 ? ? ? 1 ?

Aeolosaurus maximus

? ?
? ? 1 ? ? ? 0 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 0 ? ? ? ? 1 1 ? ? ? ? ? ? 0 ? ? ? ? 1 0 ? 0 0 0 0 0 0 1 0 0 ? 0 1 2 1 1 ? ? ? ? 0 1 1 0 9 1
1 ? 0 1 ? ? ? ? ? ? ? ? ? ? ? ? 1 ? 1 ? 1 1 2 1 1 0 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ?
? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 0 1 0 1 1 1 2

Aeolosaurus rionegrinus
? ?
? 1 1 ? 0 0 ? 1 ? ? 1 0 0 ? 0 1 2 ? ? ? ? ? ? ? ? ? ? 0 9 1 0
? ? 1 1 ? 0 ? 0 ? ? ? ? ? 1 ? 1 1 1 1 ? 0 1 ? ? ? ? ? ? ? ? 1 0 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 1 ? 1 ?
? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 1 1 1 1 1 1 2

Aeolosaurus colhuehuapensis
? ?
? 0 ? 1 ? ? 1 1 0 0 0 1 ? ? ? 1 0 0 ? 0 1 2 1 ? ? ? ? ? ? ? ? 0 9 1 ?
? 0 1 ?
? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 0 1 1 1 1 1 2

Gondwanatitan faustoi
? ?
? ? 1 1 ? ? ? ? ? ? ? ? ? ? ? ? ? 1 0 1 ? ? ? 0 ? ? ? 0 0 1 1 1 0 3 ? ? ? ? 0 ? ? 0 ? 1 0 0 0 0 ? 1 ? 0 1 0 0 ? 0 1 2 1 1 ? ? ? ? ? 1 ? 0 9 1
? ? ? 1 ? ? ? 1 ? ? ? ? ? 1 1 0 1 1 ? 1 ? ? ? ? ? ? 1 1 ? ? ? ? ? ? ? 0 0 1 ? ? ? ? ? ? ? ? ? ? ? ?
? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 0 1 0 0 1 ? 2

Rinconsaurus caudamirus
? ? ? ? ? ? ? ? ? ? ? ? ? ? 0 ? 2 ?
? ? 0 ? 1 ? ? 0 1 0 ? 0 0 1 1 0 ? ? 1 0 ? ? ? ? ? ? ? ? ? ? ? 1 1 0 ? ? ? ? ? ? ? ? ? ? 1 0 ? ? ? ? ? ? ? ? 0 ? ? 0 0 0 1 1 ? ? ? ? ? ? ? 0 9
1 ? ? ? 1 ? ? ? ? 0 ? 1 ? 1 ? 1 0 1 ? 1 ?
? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 0 0 0 0 0 0 1

Muyelensaurus pecheni
? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 0 ? ? 0 0 ? 0 0 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 0 1 ? ? ? ? 0 ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 1 ? 1 ? ? ?
? ? ? 1 1 ? ? 1 1 0 ? ? 1 1 ? 0 ? ? 1 0 1 0 1 1 0 1 0 0 0 0 ? 1 1 0 ? ? ? ? ? ? ? ? ? ? 1 0 ? 0 0 1 1 ? 0 ? ? ? ? ? ? 0 1 ? ? ? ? 1 1 ? ? ? ?
? ? ? ? 1 1 0 0 ? ? ? ? ? 1 1 1 ? 0 1 1 0 1 1 1 1 1 ? 1 1 ? ? ? 1 ? ? ? ? ? 1 ? ? ? ? ? ?
? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 0 1 0 0 0 ? 1

Panamericansaurus schroederi
? ?
? 1 0 0 ? ? ? ? ? ? ? 0 0 ? 0 ? 2 1 ? ? ? ? ? ? ? ? 0 9 1 ? ?
? ? ? ? ? ? ? ? ? ? ? 1 1 0 ? ? 1 ?
? ? ? ? ? ? ? ? ? ? ? ? ? ? 0 0 1 0 0 ? 1