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Publisher: Taylor & Francis

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Journal of Vertebrate Paleontology

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/ujvp20>

Redescription of the Skull of *Coloradisaurus brevis* (Dinosauria, Sauropodomorpha) from the Late Triassic Los Colorados Formation of the Ischigualasto-Villa Union Basin, northwestern Argentina

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Published online: 09 Sep 2014.

To cite this article: Cecilia Apaldetti, Ricardo N. Martinez, Diego Pol & Thibaud Souter (2014) Redescription of the Skull of *Coloradisaurus brevis* (Dinosauria, Sauropodomorpha) from the Late Triassic Los Colorados Formation of the Ischigualasto-Villa Union Basin, northwestern Argentina, *Journal of Vertebrate Paleontology*, 34:5, 1113-1132

To link to this article: <http://dx.doi.org/10.1080/02724634.2014.859147>

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REDESCRIPTION OF THE SKULL OF *COLORADISAURUS BREVIS* (DINOSAURIA, SAUROPODOMORPHA) FROM THE LATE TRIASSIC LOS COLORADOS FORMATION OF THE ISCHIGUALASTO-VILLA UNION BASIN, NORTHWESTERN ARGENTINA

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ABSTRACT—The cranial anatomy of the basal sauropodomorph *Coloradisaurus brevis* from the upper levels of the Norian Los Colorados Formation is here redescribed and comparisons made based on the holotype skull and mandible. *Coloradisaurus brevis* is diagnosed by most of the features proposed in the original description and an additional set of autapomorphies, such as presence of circular upper temporal fenestrae, laminae on the ventrolateral margins of a ventral fossa of the basisphenoid and on the ventral region of the parasphenoid, and tab-like medial process at the posteromedial end of the mandible. *Coloradisaurus* is placed within Massospondylidae, as in recent analyses. This position is supported primarily by postcranial characters, but some cranial features identified in this study provide additional evidence supporting this position (e.g., jugal contribution to the antorbital fenestra, frontal proportionately longer than nasals). However, the cranial anatomy of *Coloradisaurus* also bears several characters that are shared with plateosaurids (e.g., low mandibular articulation, broad maxillary wall on the anterior margin of antorbital fossa, broad prefrontals, projection of infratemporal fenestra behind the orbit, stepped braincase, robust septum between basiptyergoid processes). Thus, *Coloradisaurus* is interpreted as a massospondylid that has convergently acquired characters that are otherwise only known in plateosaurids, highlighting the conflicting pattern of character distribution among basal sauropodomorphs.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

INTRODUCTION

The Ischigualasto-Villa Union Basin of northwestern Argentina includes the most diverse dinosaur faunas from the Late Triassic of South America (Bonaparte, 1972, 1978, 1999; Martínez and Alcober, 2009; Ezcurra, 2010; Ezcurra and Apaldetti, 2011), including one of the oldest-known dinosaur assemblages (from the Ischigualasto Formation, ca. 231–226 Ma; Rogers et al., 1993; Martínez et al., 2011). The upper section of the Los Colorados Formation (Late Triassic, Norian; Bonaparte, 1972, 1973) has yielded a remarkably high diversity of basal sauropodomorphs, including *Riojasaurus incertus* (Bonaparte, 1972), *Coloradisaurus brevis* (Bonaparte, 1978), the basal sauropod *Lessemsaurus sauro-poides* (Bonaparte, 1999; Pol and Powell, 2007a), and a recently described medium-sized basal sauropod (Ezcurra and Apaldetti, 2011). Other basal sauropodomorphs have been reported from the Los Colorados Formation, although they have not been yet described (Arcucci and Coria, 1996; Martínez et al., 2004).

Coloradisaurus was one of the first basal sauropodomorphs to be described from the Los Colorados Formation, and was originally named *Coloradia brevis* Bonaparte, 1978, and later renamed *Coloradisaurus brevis* by Lambert (1983). The original publication of the taxon consisted of a brief description that focused mainly on the skull. Bonaparte (1978) provided

comparisons with other basal sauropodomorphs known at that time and considered *Coloradisaurus* as closely related to *Plateosaurus* and *Lufengosaurus*. Based on recent cladistic analyses, some authors reached similar conclusions (Galton and Upchurch, 2004; Upchurch et al., 2007; Martínez, 2009), but other phylogenetic studies have recovered this taxon as more closely related to *Massospondylus* (Leal et al., 2004; Yates, 2004, 2007; Smith and Pol, 2007). Recently, new information on the postcranial anatomy of this taxon was provided based on the description of a referred specimen (Apaldetti et al., 2013). The latter study, based on updated versions of the phylogenetic data sets of Yates et al. (2010) and Upchurch et al. (2007), found strong character support allying *Coloradisaurus* and *Lufengosaurus*. These two taxa were depicted either as part of Massospondylidae (as in Yates et al., 2010) or as closer to *Plateosaurus* (as in Upchurch et al., 2007). The former analysis, however, was preferred because it was based on a larger taxon and character sample and showed stronger character support for the massospondylid affinities of *Coloradisaurus* (and *Lufengosaurus*).

Here, we describe the craniomandibular anatomy of *Coloradisaurus brevis* based on the type specimen (PVL 3967), which includes most of the cranial and mandibular elements, and discuss its diagnostic features. Finally, we evaluate the phylogenetic signal of the cranial characters of *Coloradisaurus*, by discussing the distribution of these traits among basal sauropodomorphs to determine whether they indicate the affinities of this species with either massospondylids or plateosaurids.

*Corresponding author

Institutional Abbreviations—**AMNH**, American Museum of Natural History, New York, U.S.A.; **BP**, Bernard Price Institute, University of the Witwatersrand, Johannesburg, South Africa; **GPIT**, Institut und Museum für Geologie und Paläontologie, Universität Tübingen, Tübingen, Germany; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, People's Republic of China; **LV**, Lufeng Dinosaur Museum, Lufeng, People's Republic of China; **NMQR**, National Museum, Bloemfontein, South Africa; **PULR**, Museo de Ciencias Naturales, Universidad de La Rioja, La Rioja, Argentina; **PVL**, Instituto Miguel Lillo, Universidad de Tucumán, Tucumán, Argentina; **PVSJ**, Instituto y Museo de Ciencias Naturales, Universidad Nacional de San Juan, San Juan, Argentina; **SAM**, Iziko South African Museum, Cape Town, South Africa; **SMNS**, Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany; **UFSM**, Universidade Federal de Santa Maria, Santa Maria, Brazil; **YPM**, Peabody Museum of Natural History, Yale University, New Haven, Connecticut, U.S.A.

Anatomical Abbreviations—**alq**, anterolateral process of the quadrate; **amfe**, anterior margin of the external mandibular fenestra; **amitfe**, anteroventral margin of the infratemporal fenestra; **amq**, anteromedial process of the quadrate; **An**, angular; **anfe**, antorbital fenestra; **Ar**, articular; **B**, basisphenoid; **Bo**, basioccipital; **bp**, basipterygoid process; **bt**, basal tubera; **D**, dentary; **dePmx**, dorsal end of the dorsal process of the premaxilla; **dp**, dorsal process; **dp sp**, dorsal process of the splenial; **dsq**, descending process of the squamosal; **emfe**, external mandibular fenestra; **Eo**, exoccipital; **exn**, external naris; **F**, frontal; **fm**, foramen magnum; **fo**, fenestra ovalis; **grps**, longitudinal ventral groove of the parasphenoid; **icf**, internal carotid foramen; **itfe**, infratemporal fenestra; **J**, jugal; **L**, lacrimal; **lafo**, lacrimal antorbital fossa; **lc**, lateral condyle of the quadrate; **llb**, lateral lamina of the basisphenoid; **llps**, triangular lateral lamina of the

parasphenoid rostrum; **IPmx**, left premaxilla; **Ls**, laterosphenoid; **mc**, medial condyle of the quadrate; **mfb**, median fossa of the basisphenoid; **mfs**, metotic fissure; **mpp**, medial pyramidal process of the articular; **Mx**, maxilla; **mxaf**, maxilla antorbital fossa; **N**, nasal; **nf**, neurovascular foramen; **nfo**, narial fossa; **O**, orbit; **oc**, occipital condyle; **Op**, opisthotic; **P**, parietal; **Pal**, palatine; **Par**, prearticular; **Pf**, prefrontal; **Pmx**, premaxilla; **Po**, postorbital; **popfe**, postparietal fenestra; **ppo**, posterior process of the postorbital; **pptm**, area for the attachment of the M. protractor pterygoideus; **Pra**, proatlas; **Pro**, prootic; **ps**, parasphenoid; **Pt**, pterygoid; **ptfe**, posttemporal fenestra; **Q**, quadrate; **qf**, quadrate foramen; **Qj**, quadratojugal; **qPt**, quadrate wing of the pterygoid; **rap**, retroarticular process; **rN**, right nasal; **rPmx**, right premaxilla; **Sa**, surangular; **saf**, surangular foramen; **sf**, splenial foramen; **shq**, shaft of the quadrate; **So**, supraoccipital; **Sp**, splenial; **Sq**, squamosal; **stfe**, supratemporal fenestra; **stfo**, supratemporal fossa; **tbp**, tabular bony process of the angular; **tmp**, tab-like medial process of the retroarticular process; **vc**, Vidian canal; **vcdf**, vena capitis dorsalis foramen; **vlN**, ventrolateral process of the nasal; **vp**, ventral process; **vp sp**, ventral process of the splenial; **V–XII**, cranial nerves V–XII.

METHODS

A three-dimensional (3D) digital model of the skull of *Coloradisaurus brevis* was produced using photogrammetric software, with 653 photographs of the physical specimen acquired by a Canon EOS 30D 8.2 megapixel camera coupled to a Canon EF 24-105mm f/4 L IS USM lens (see Supplementary Data). We followed the steps of photogrammetric reconstruction (see Falkingham, 2012) to generate sparse and dense 3D point clouds using VisualSFM (software and instructions available from: <http://homes.cs.washington.edu/~ccwu/vsfm>). These point clouds were

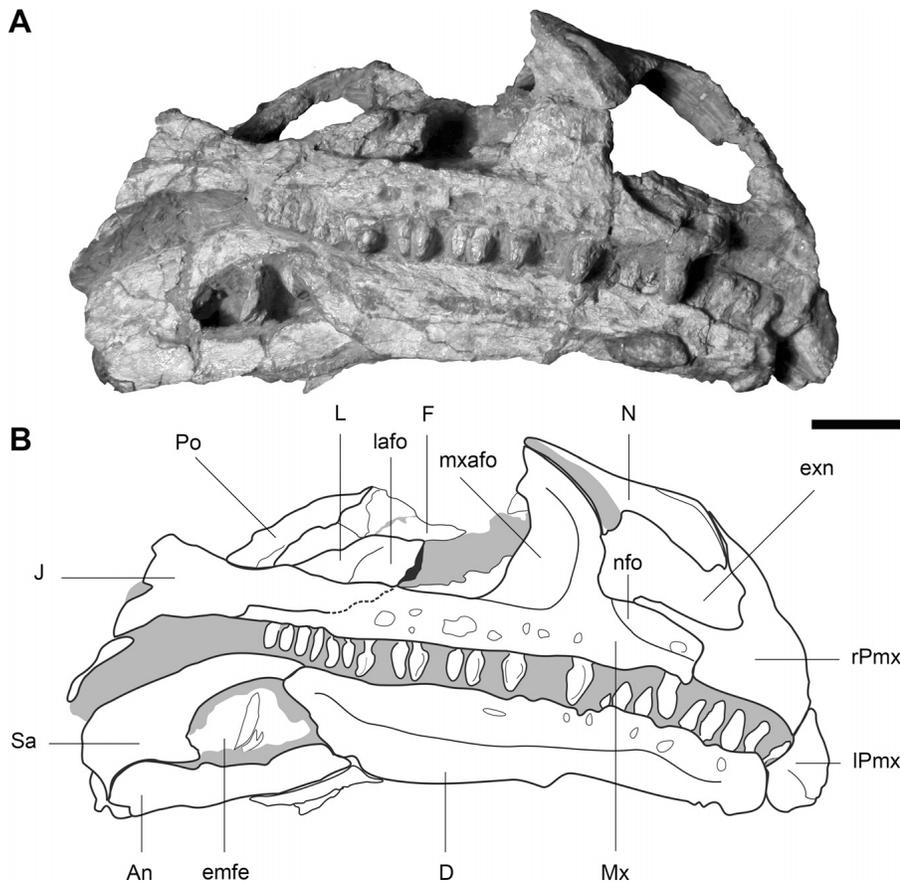


FIGURE 1. Skull of *Coloradisaurus brevis* (PVL 3967) in right lateral view. **A**, photograph; **B**, schematic drawing. See the text for abbreviations. Scale bar equals 20 mm.

then cleaned, triangulated, and processed in Geomagic Studio (version 12; 3D Systems, Rock Hill, South Carolina, U.S.A.) to obtain the final 3D model of the skull, which was subsequently visualized in Maya (version 2011; Autodesk, San Rafael, California, U.S.A.). See Supplementary Data for a video showing the 3D photogrammetric model of the skull of *Coloradisaurus brevis*.

SYSTEMATIC PALEONTOLOGY

DINOSAURIA Owen, 1842
 SAURISCHIA Seeley, 1887
 SAUROPODOMORPHA Huene, 1932
 MASSOPODA Yates, 2007
 MASSOSPONDYLIDAE Huene, 1914
COLORADISAURUS Lambert, 1983

Type Species—*Coloradisaurus brevis* (Bonaparte, 1978).

Diagnosis—As for type and only species.

COLORADISAURUS BREVIS (Bonaparte, 1978)
 (Figs. 1–8)

Holotype—PVL 3967. Skull and mandible found in articulation with the atlas-axis and cervical (C) 3, three other cervical vertebrae (possibly C4–C6), two anterior dorsals, and three isolated caudal vertebrae, fragmentary remains of the scapula, coracoid, humerus, ulna, and radius, incomplete metacarpus and isolated non-terminal manual and ungual phalanges, right astragalus and calcaneum, distal tarsal, and pedal unguals.

Referred Specimen—PVL 5904, a partially articulated postcranial skeleton including an anterior cervical vertebra, an almost complete dorsal series, an isolated anterior caudal, and two fused middle caudals, complete left scapula and coracoid,

isolated right coracoid, right humerus, metacarpal III, partial left ilium, articulated pubes, right ischium, both femora, both tibiae, both fibulae, left astragalus, a medial left distal tarsal, and complete left pes (see Apaldetti et al., 2013).

Horizon and Locality—Both specimens were found by José Bonaparte in the upper section of the Los Colorados Formation (Groeber and Stipanovic, 1953), which is commonly regarded as Norian–Rhaetian age (Bonaparte, 1972), falling within the tetrapod-based late Coloradian biochron (Bonaparte, 1973). The holotype (PVL 3967) and the referred specimen (PVL 5904) were found at the La Esquina locality, located south of Paganillo village, La Rioja Province, Argentina.

Revised Diagnosis—A medium-sized basal sauropodomorph diagnosed by the following unique combination of characters (autapomorphies are indicated by an asterisk): preorbital region shorter than in *Lufengosaurus* and *Plateosaurus*, with frontals longer than nasals; posteroventral corner of antorbital fossa projecting underneath the orbit; broad ascending process of the maxilla; circular upper temporal fenestrae*; tall and thin bony laminae forming the ventrolateral margins of a deep, ventrally opening fossa on the basisphenoid*; triangular bony laminae extend from the basipterygoid processes to the ventrolateral margins of the parasphenoid rostrum*; low mandibular articulation; tab-like medial process on the medial border of the retroarticular process of the mandible*; low and elongated cervical vertebrae; deep depression with a sharply defined distal margin facing proximally on anterior surface of pubic apron*; semicircular cross-section of pubic apron, creating a deep trough along posterior surface of pubic apron*; posteromedial region of the distal surface of the tibia deflected and facing posterodistally*; and pyramidal dorsal process of the posteromedial corner of astragalus almost as high as ascending process*.

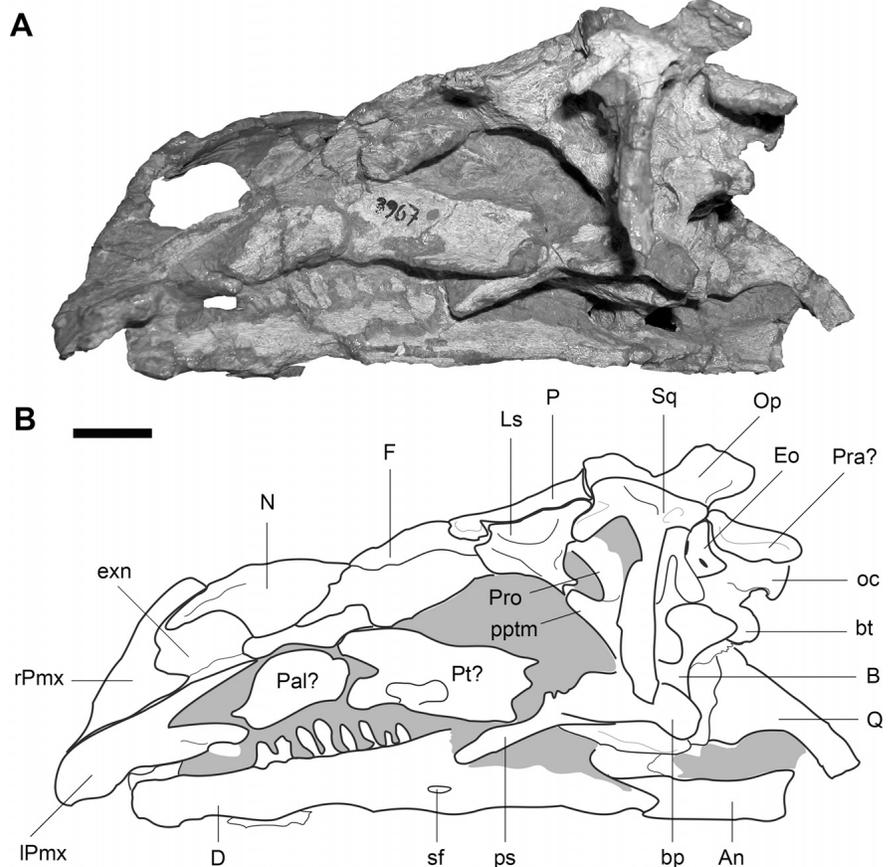


FIGURE 2. Skull of *Coloradisaurus brevis* (PVL 3967) in left lateral view. **A**, photograph; **B**, schematic drawing. See the text for abbreviations. Scale bar equals 20 mm.

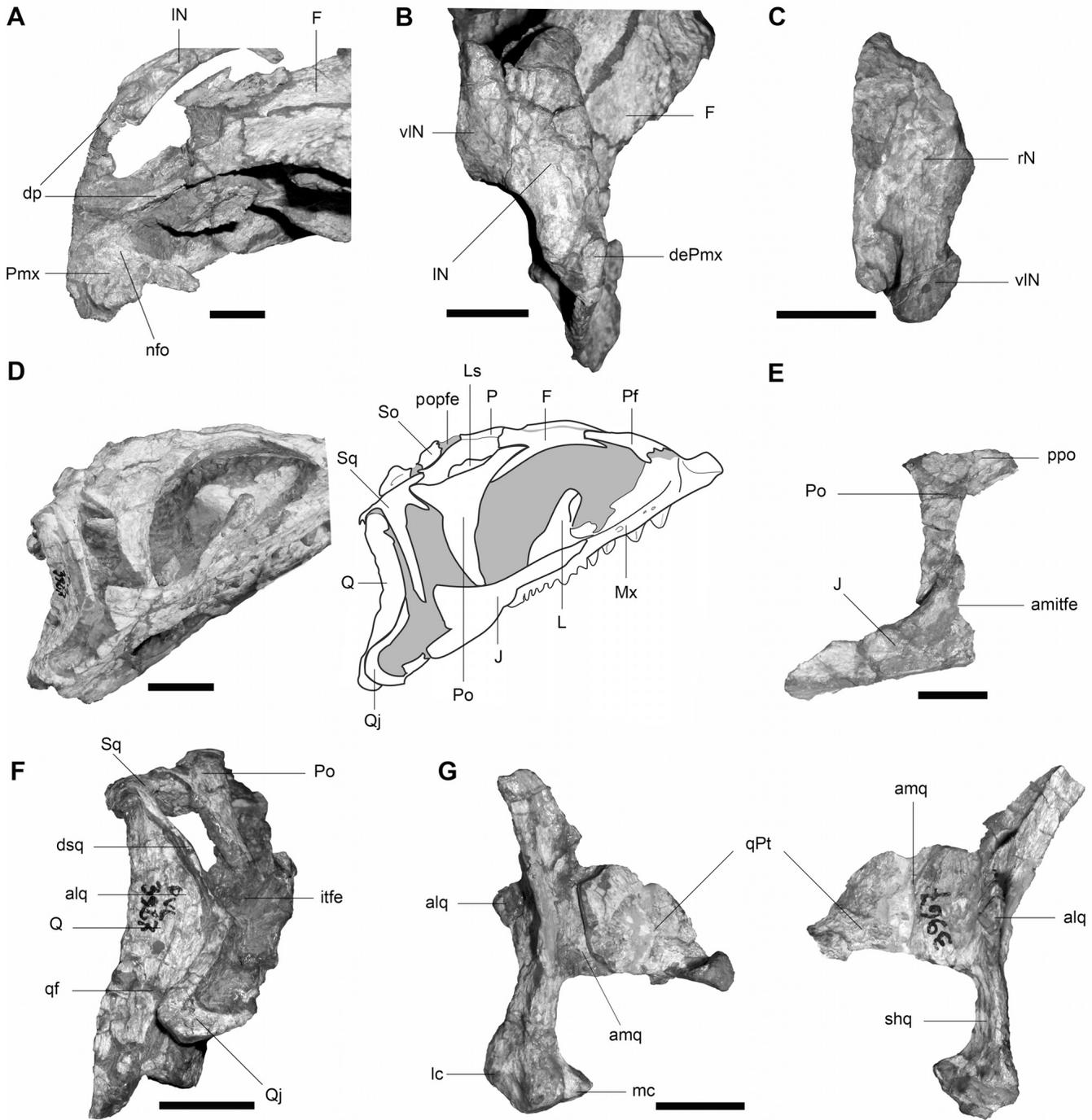


FIGURE 3. Skull elements of *Coloradisaurus brevis* (PVL 3967). **A**, left premaxilla in lateral view; **B**, right premaxilla and nasal in dorsal view; **C**, left nasal in dorsal view; **D**, postorbital region in right lateral view; **E**, left postorbital and jugal in lateral view; **F**, right quadrate and quadratojugal in lateral view; **G**, left quadrate in posteromedial and lateral view. See the text for abbreviations. Scale bars equal 20 mm.

DESCRIPTION

The following description is based on the holotype skull of *Coloradisaurus brevis* (PVL 3967) originally described by Bonaparte (1978). The postcranial elements of the holotype were recently described and compared with the referred material (PVL 5904) of *Coloradisaurus brevis* (Apaldetti et al., 2013). As in PVL 5904, the elements of the holotype have lost the periosteal surface of the preserved bones, which precludes a detailed

observation of some anatomical features. All specimens used in the comparisons are listed in Table 1.

Skull

The skull of *Coloradisaurus* is almost complete, but the dorsal elements are displaced from their original positions (Figs. 1–4; Supplementary Data). The maximum transverse width of the skull is located anterior to the supratemporal fenestrae at the

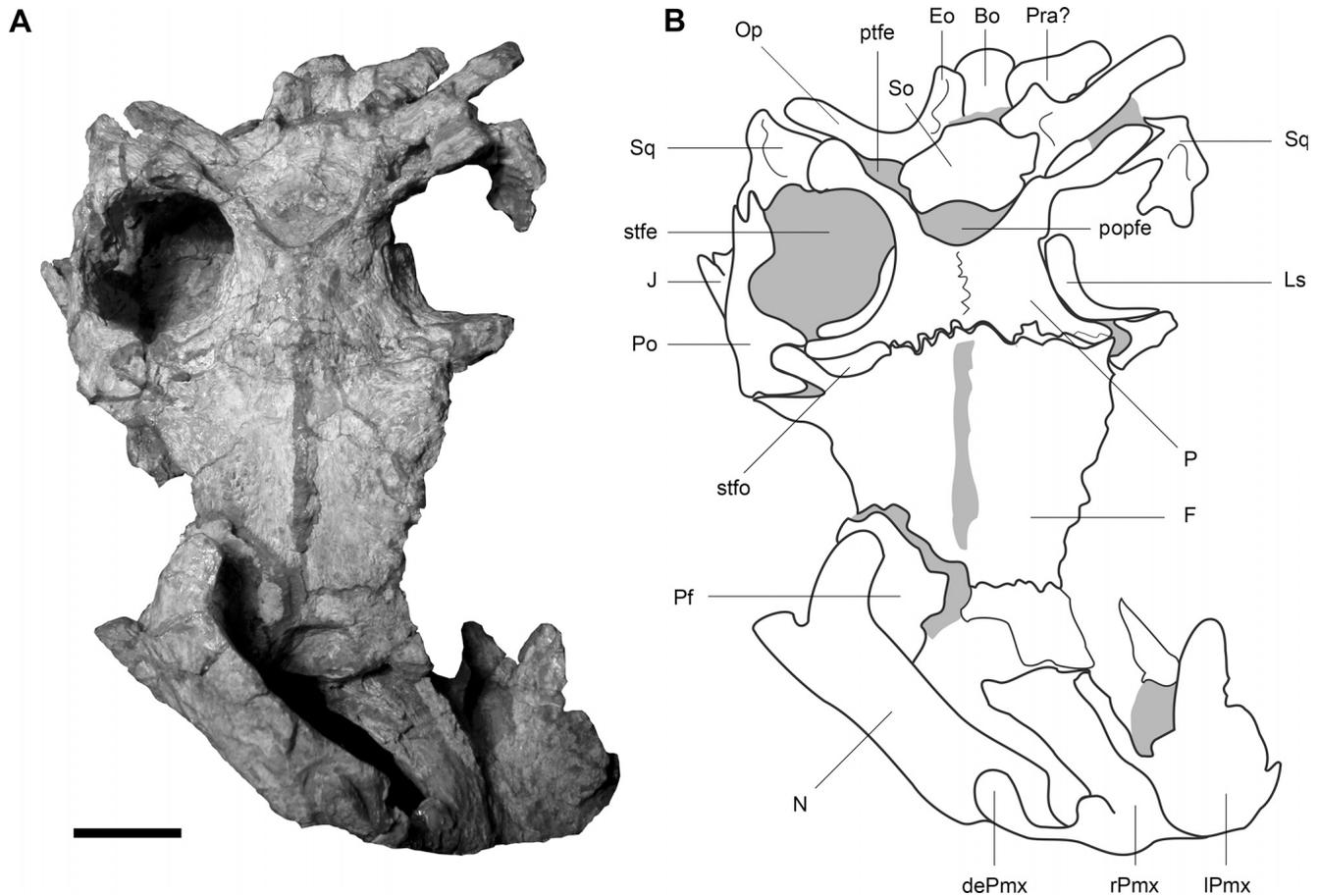


FIGURE 4. Skull of *Coloradisaurus brevis* (PVL 3967) in dorsal view. **A**, photograph; **B**, schematic drawing. See the text for abbreviations. Scale bar equals 20 mm.

level of the sutural contact of the frontals and parietals (Fig. 4), as in most basal sauropodomorphs (e.g., *Plateosaurus*, AMNH 6810; *Massospondylus*, BP/1/5241; *Lufengosaurus*; *Adeopapposaurus*; *Leyesaurus*; *Mussaurus*).

The external naris is subtriangular and occupies approximately 15% of the total anteroposterior length of the skull. The

TABLE 1. List of specimens used in comparisons.

Taxon	Source
<i>Aardonyx celestae</i>	Yates et al., 2010
<i>Adeopapposaurus mognai</i>	Martinez, 2009
<i>Anchisaurus polyzelus</i>	Yates, 2004
<i>Efraasia minor</i>	Yates, 2003b
<i>Leyesaurus marayensis</i>	Apaldetti et al., 2011
<i>Lufengosaurus huenei</i>	Barrett et al., 2005
<i>Massospondylus carinatus</i>	Sues et al., 2004
<i>Melanorosaurus readi</i>	Yates, 2007
<i>Mussaurus patagonicus</i>	Pol and Powell, 2007b
<i>Pantyraco caducus</i>	Yates, 2003a; Galton and Kermack, 2010
<i>Plateosaurus</i> spp.	Galton, 1984, 1985
<i>Riojasaurus incertus</i>	Bonaparte and Pumares, 1995
<i>Sarhsaurus aurifontanalis</i>	Rowe et al., 2010
<i>Thecodontosaurus antiquus</i>	Benton et al., 2000
<i>Unaysaurus tolentinoi</i>	Leal et al., 2004
<i>Yimenosaurus youngi</i>	Bai et al., 1990
<i>Yunnanosaurus huangi</i>	Barrett et al., 2007

The comparisons made by the authors firsthand are noted with their respective collection numbers in the text.

posterior margin of this opening is located posterior to the premaxilla-maxilla suture. The lacrimal is not fully preserved, but the overall shape and size of the antorbital fenestra and the orbit can be estimated. The antorbital fenestra is subtriangular and is set within a wide triangular antorbital fossa (Figs. 1, 8A), similar to that of *Plateosaurus* (AMNH 6810) and *Unaysaurus* (UFMS 11069). The orbit is circular and occupies approximately 30% of the total length of the skull. Although the bones surrounding the infratemporal fenestra are displaced from their natural position, it is possible to observe that the dorsal region of this fenestra is anteroposteriorly narrower than the ventral region (Figs. 1, 3D, 8A). Thus, the anteroventral region of the infratemporal fenestra does not extend underneath the orbit, as also occurs in *Plateosaurus* (AMNH 6810) and *Melanorosaurus*. In most other basal sauropodomorphs, the anteroventral region of the infratemporal fenestra projects anteriorly below the orbit (e.g., *Riojasaurus*, PULR 56, PVSJ 849; *Massospondylus*, BP/1/5241; *Lufengosaurus*, IVPP V15; *Unaysaurus*, UFMS 11069; *Adeopapposaurus*, PVSJ 610; *Sarhsaurus*; *Leyesaurus*).

As Bonaparte (1978) noted, the supratemporal fenestra of *Coloradisaurus* has a circular shape (Figs. 4, 8B). The distinctive feature of the temporal region that creates the circular shape is the anteriorly concave margin of the posterolateral process of the parietal. This feature is unique among basal sauropodomorphs and is interpreted as an autapomorphy of *Coloradisaurus brevis*. In all basal sauropodomorphs, the posterolateral process of the parietal diverges from the longitudinal axis of the skull at an angle of approximately 45°, which gives to supratemporal

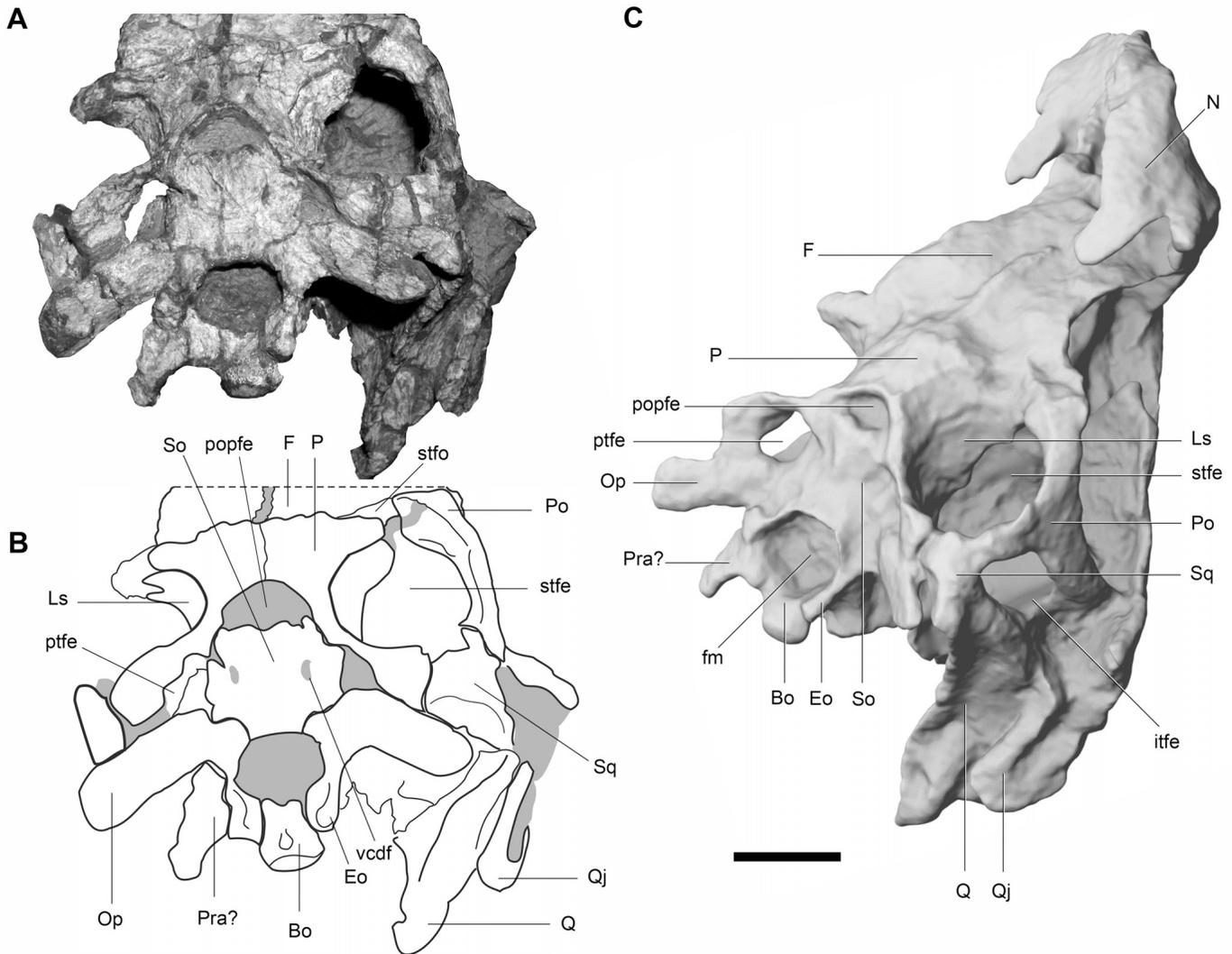


FIGURE 5. Skull of *Coloradisaurus brevis* (PVL 3967) in occipital view. **A**, photograph; **B**, schematic drawing; **C**, image derived from reconstructed photogrammetric model scan of the skull in posterolaterodorsal view. See the text for abbreviations. Scale bar equals 20 mm.

fenestra a typically subtriangular shape in dorsal view (e.g., *Plateosaurus*, AMNH 6810, SMNS 13200; *Massospondylus*, BP/1/5241; *Adeopapposaurus*, PVSJ 610; *Leyesaurus*; *Mussaurus*). The supratemporal fenestra of *Coloradisaurus* is partially exposed in lateral view, because the posterior process of the postorbital is set below the level of the dorsal border of the orbit (Figs. 2, 3D, 8A).

The supratemporal fossa of *Coloradisaurus* is small, in contrast to the large fossae present in *Plateosaurus* (AMNH 6810) or *Unaysaurus*. The external mandibular fenestra occupies approximately 20% of the total anteroposterior mandibular length (Fig. 1). As described by Bonaparte (1978), the position of the mandibular articulation is set below the level of the dentary tooth row, although it is not as ventrally positioned as in *Plateosaurus* (Galton, 1990). The mandibular articulation of most other basal sauropodomorphs is set at the same level as the dentary tooth row (e.g., massospondylids).

Premaxilla—The left premaxilla of *Coloradisaurus* is better preserved than the right one, which is fragmentary and mainly represented by the dorsal process (Supplementary Data). The main body of the premaxilla is rectangular in lateral view and anteroposteriorly longer than dorsoventrally high (Fig. 3A).

This morphology is similar to that of most basal sauropodomorphs (e.g., *Pantydraco*; *Plateosaurus*, AMNH 6810; *Riojasaurus*, PULR 56, PVSJ 849; *Unaysaurus*, UFSM 11069; *Melanorosaurus*), but differs from the subquadrangular premaxillae of massospondylids (e.g., *Massospondylus*, BP/1/5241; *Adeopapposaurus*; *Leyesaurus*) and the anteroposteriorly short premaxilla of *Mussaurus* and *Yimemosaurus*. On the left side, the dorsal part of the lateral surface of the main premaxillary body and the posterior surface of the base of dorsal process bears an almost 'D'-shaped and medially inclined recess, forming the narial fossa (Fig. 3A). No nutrient foramina can be identified on the lateral surface of the premaxilla. The subnarial foramen region is damaged, so it is not possible to determine the morphology of this foramen. On the left side, the anterior margin of the premaxilla is curved and posterodorsally oriented throughout its entire length (Fig. 3A), as in *Plateosaurus* (AMNH 6810) and *Yunnanosaurus*, but differing from massospondylids in which the anterior margin of the premaxilla is straight along its ventral half and posterodorsally oriented along its dorsal region (e.g., *Massospondylus*; *Adeopapposaurus*, PVSJ 568; *Leyesaurus*).

The dorsal process of the premaxilla forms most of the anterior margins of the external narial (Figs. 1, 3A). In lateral view,

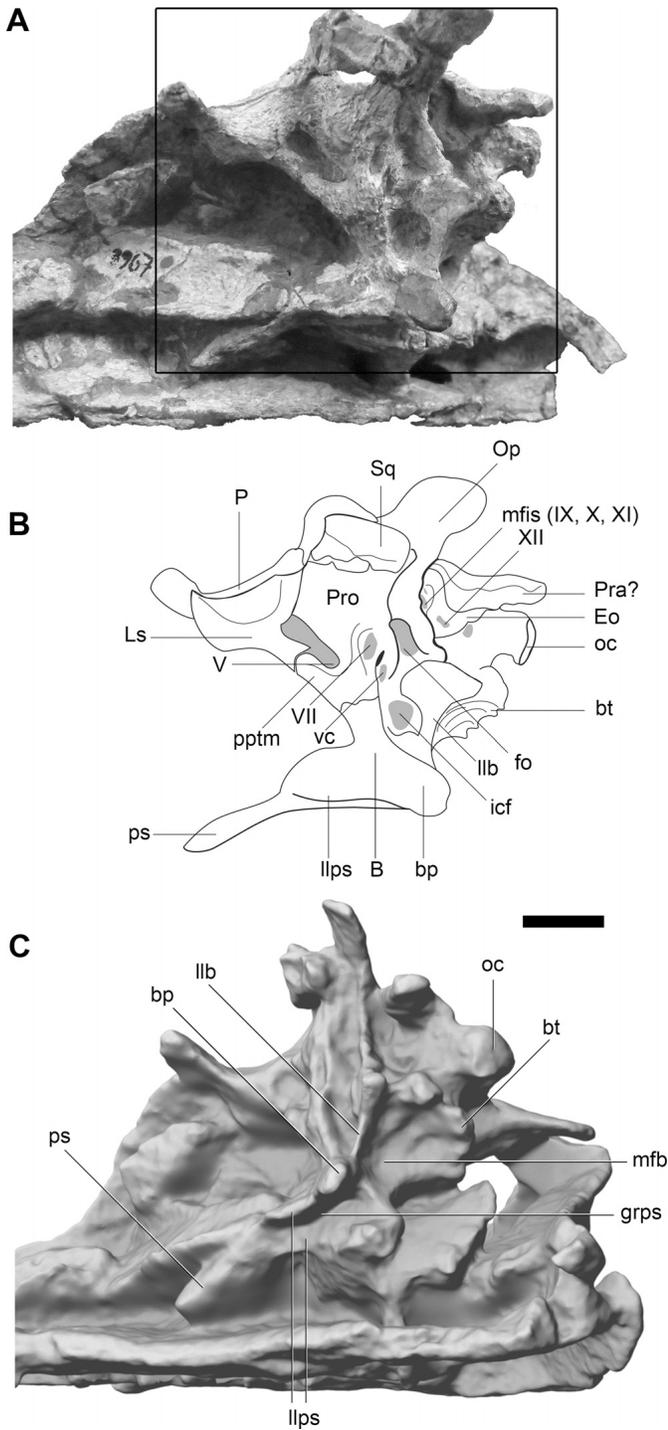


FIGURE 6. Brainscase of *Coloradisaurus brevis* (PVL 3967). **A**, photograph in lateral view; **B**, schematic drawing; **C**, image derived from reconstructed photogrammetric model scan of the skull in posterolateroventral view. Box in **A** shows the region schematics in **B**. See the text for abbreviations. Scale bar equals 20 mm.

the base of the dorsal process is anteroposteriorly broad and tapers dorsally (Figs. 1, 3A). The length of the dorsal process exceeds the total dorsoventral height of the main body of the premaxilla. In dorsal view, the distal end of the premaxillary dorsal process is transversely widened (Fig. 3B), as in several other basal sauropodomorphs (e.g., *Riojasaurus*, PVSJ 849;

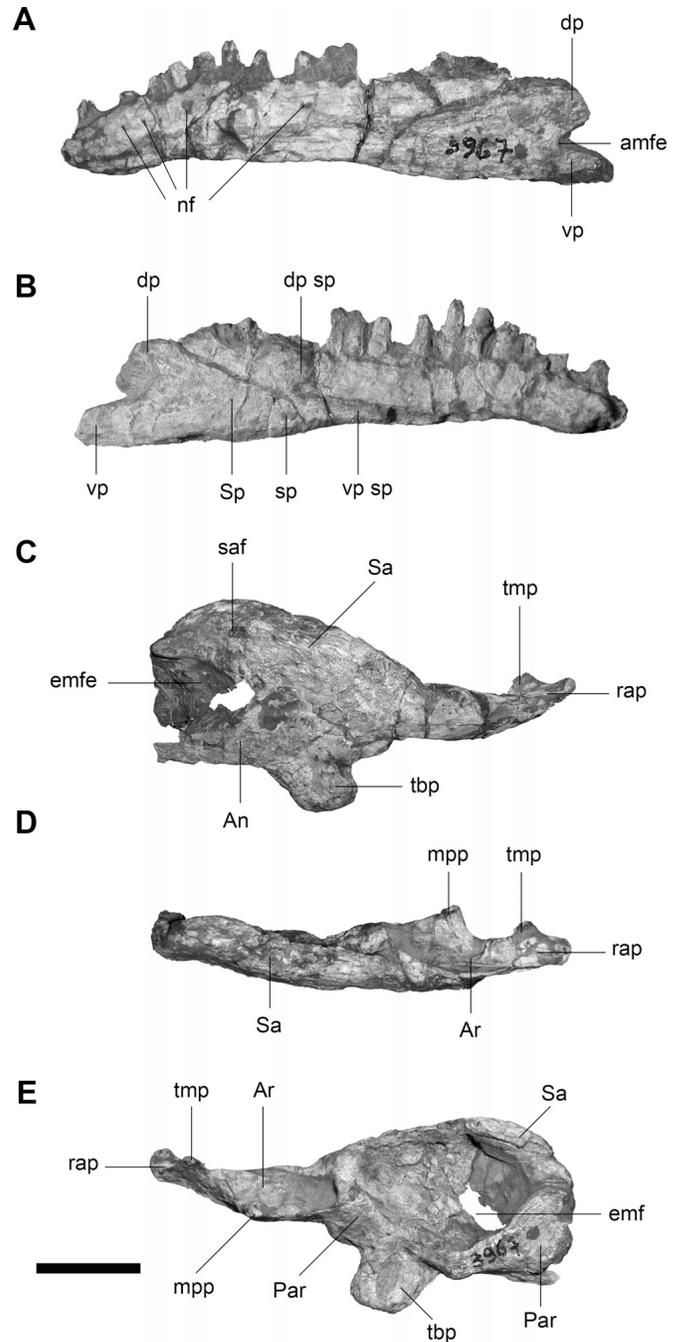


FIGURE 7. Left mandibular elements of *Coloradisaurus brevis* (PVL 3967). Dentary in **A**, lateral and **B**, medial views; **C–E**, surangular, angular, and articular in articulation in **C**, lateral, **D**, dorsal and **E**, medial views. See the text for abbreviations. Scale bar equals 20 mm.

Plateosaurus [Prieto-Márquez and Norell, 2011]; *Yunnanosaurus*). This differs from the condition of some massospondylids, in which the dorsal process of the premaxilla lacks a distal expansion (e.g., *Massospondylus*; *Adeopapposaurus*, PVSJ 610). The posterolateral process of the premaxilla is elongate, forms the ventral border of the external naris, and articulates with the dorsal region of the anterior process of the maxilla (Fig. 1). In lateral view, the dorsoventral height of the posterolateral process of the premaxilla occupies almost half of the total height of the

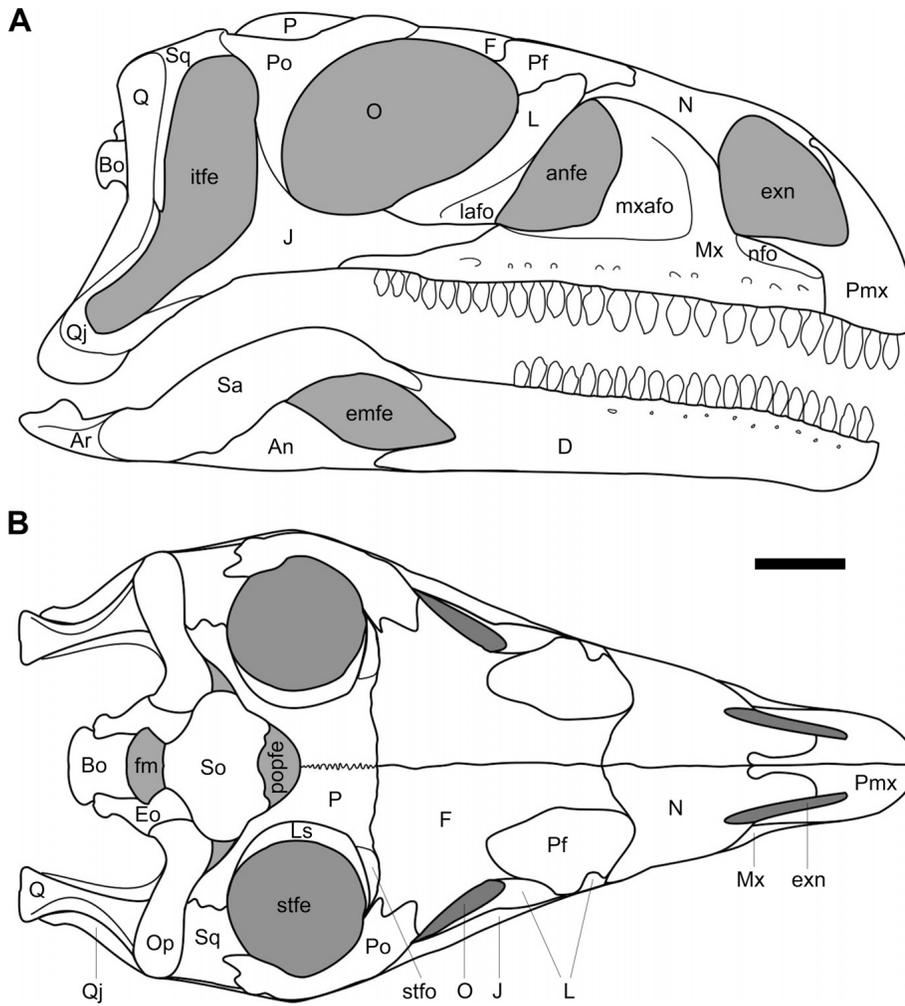


FIGURE 8. Reconstruction of skull of *Coloradisaurus brevis* based on PVL 3967. **A**, lateral and **B**, dorsal views. Gray colors represent openings. See the text for abbreviations. Scale bar equals 20 mm.

main body of the premaxilla (Figs. 1, 3A), similar to that of *Riojasaurus* (PULR 56, PVSJ 849), *Unaysaurus*, and *Yunnanosaurus*. In other basal sauropodomorphs, the height of the posterolateral process occupies approximately 30% of the total length of the main body of the premaxilla (e.g., *Plateosaurus*, AMNH 6810; *Massospondylus*, BP/1/5241; *Adeopapposaurus*; *Leyesaurus*, PVSJ 706; *Melanorosaurus*), or less than 30% (e.g., *Mussaurus*). The posterolateral process and the posterior margin of the premaxillary main body form a right-angled junction that creates an 'L'-shaped suture between the premaxilla and maxilla in lateral view (Figs. 1, 3A).

The premaxillary teeth are not preserved. Bonaparte (1978) inferred the presence of three or four premaxillary teeth, which represents the generalized premaxillary tooth count among basal sauropodomorphs (except *Plateosaurus* and *Aardonyx*). However, based on the holotype, it is not possible to infer the premaxillary tooth count of *Coloradisaurus*.

Maxilla—The right maxilla of *Coloradisaurus* is only exposed in lateral view (Fig. 1; Supplementary Data). As in other basal sauropodomorphs, it has a triradiate lateral profile (Galton and Upchurch, 2004). The anterior process of the maxilla is rectangular and anteroposteriorly longer than dorsoventrally high, as in *Plateosaurus* (AMNH 6810) and *Unaysaurus* (UFSM 11069). The laterodorsal surface of the anterior process of the maxilla is medially inclined and bears an excavated surface that forms the maxillary portion of the narial fossa, similar to that of *Riojasaurus* (PULR 56, PVSJ 849). The dorsal region of the maxillary

narial fossa is overlapped by the posterolateral process of the premaxilla (Fig. 1).

The ascending process is robust and forms a right angle with the longitudinal axis of the maxilla (Fig. 1). The anteroposterior length of the base of the ascending process extends for approximately 30% of the total length of the maxilla. This proportion is similar to that in *Plateosaurus* (35%; Prieto-Márquez and Norell, 2011), *Unaysaurus* (35%; UFSM 11069), and *Melanorosaurus* (30%; NM QR 3314). However, in most other basal sauropodomorphs, this proportion is much smaller (e.g., *Riojasaurus*, PVSJ 849, approximately 22%; *Massospondylus*, BP/1/5241, approximately 20%; *Lufengosaurus*, IVPP V15, approximately 20% [Barrett et al., 2005]; *Adeopapposaurus*, PVSJ 610, 19%). As in *Plateosaurus*, most of the surface of the ascending process is excavated to form the medial lamina of the antorbital fossa (Fig. 1). This condition is different from that of most basal sauropodomorphs, in which the medial wall of the maxilla is anteroposteriorly short (e.g., *Massospondylus*, *Lufengosaurus*, *Adeopapposaurus*, *Leyesaurus*). The medial lamina in *Coloradisaurus* is subtriangular in outline, and its posterior margin is slightly concave as in *Plateosaurus* (AMNH 6810), although in the latter the concavity is more pronounced. The medial lamina extends posteriorly along the ventral region of the antorbital fenestra and forms the floor of the antorbital fossa. In lateral view, the ventral half of the ascending process projects almost vertically, but its dorsal region curves posterodorsally as in other basal sauropodomorphs (e.g., *Plateosaurus*, AMNH 6810;

Lufengosaurus; *Anchisaurus*, YPM 209 [Fedak and Galton, 2007]). The anteroventral margin of the ascending process forms the posteroventral edge of the external naris, and its anterodorsal region is overlapped by the nasal (although these are slightly displaced from their natural positions; Fig. 1).

The main process of the maxilla is long, straight, and extends along the ventral margin of the antorbital region. In lateral view, the dorsal and ventral borders of the main process are parallel to each other along most of their length but converge posteriorly along the maxilla-jugal suture (Fig. 1). The dorsal margin of this process forms the ventral limit of the antorbital fossa. The posterior and posterodorsal regions of the main process of the maxilla are contacted by the jugal; however, given the poor preservation of these regions, further details about these contacts cannot be determined. The lateral surface of the main process is poorly preserved but bears a row of ventrally oriented neurovascular foramina that are set along the entire length of the maxilla. Some of these openings are unusually large due to damage along the lateral surface (Fig. 1). The size of the posterior-most opening may have been enlarged by damage, but it is nonetheless larger than the others and is posteriorly directed, as in other basal sauropodomorphs (Serenó, 1999).

In the original description of *Coloradisaurus*, Bonaparte (1978) mentioned the presence of 23–24 maxillary teeth, but only 22 alveoli are present in the maxilla of PVSJ 3967, and 14 maxillary teeth are exposed in lateral view. In lateral view, the posterior-most maxillary teeth of *Coloradisaurus* reach the anteroposterior midlength of the orbit.

Nasal—Both nasals are partially preserved in PVL 3967. The right nasal is articulated with the premaxilla and maxilla, and the left is disarticulated from the skull (Figs. 1, 2, 3B, C, 4; Supplementary Data). Both elements are incomplete, distorted, and preserve mostly their dorsal surface, which is anteroposteriorly and transversely convex and anteroposteriorly longer than wide. The ventrolateral process of the nasal contacts the lateral surface of the ascending process of the maxilla, and its anterior margin forms the posterodorsal and dorsal margins of the external naris. In lateral view, this process is triangular and extends ventrally down to the dorsoventral half of the ascending process of the maxilla, but fails to contact the posterolateral process of the premaxilla (Fig. 1). This condition is similar to that of *Massospondylus*, *Lufengosaurus*, and *Yunnanosaurus*. In other sauropodomorphs (e.g., *Efraasia*; *Plateosaurus*, AMNH 6810; *Unaysaurus*, UFSM 11069), the nasal extends along the entire anterior region of the ascending process of the maxilla to form the entire posterior margin of the external naris. The medial margin of each nasal is straight, and there is no evidence of a longitudinal depression along their sutural contact (Fig. 3B, C), in contrast to that present in other sauropodomorphs (e.g., *Plateosaurus*, *Massospondylus*, *Lufengosaurus*, *Adeopapposaurus*). Unfortunately, the posterior regions of both nasal elements are poorly preserved, and no details of the nasal-frontal and nasal-lacrimal contacts, as well as the nasal contribution to the antorbital fossa, can be determined.

Lacrimal—Only the ventral third of the right lacrimal has been preserved (Fig. 1; Supplementary Data). This portion of the lacrimal is anterodorsally oriented, as in most basal sauropodomorphs. Its ventral region contacts the dorsal and medial regions of the anterior process of the jugal. The lateral surface of the lacrimal is anteroposteriorly narrow and occupies approximately 30% of the preserved anteroposterior length of this bone, whereas the anterior region is inset, forming a posterior medial wall of the antorbital fossa (Fig. 1). The medial wall of the fossa is a lateromedially thin lamina similar to that in other basal sauropodomorphs (e.g., *Plateosaurus*, AMNH 6810; *Massospondylus*; *Lufengosaurus*; *Adeopapposaurus*). This condition differs from anchisaurian sauropodomorphs, which lack a medial wall of the antorbital fossa at the ventral end of the lacrimal (e.g., *Yunnanosaurus*, *Mussaurus*, *Anchisaurus*).

Prefrontal—The prefrontal is represented by a thin, subrectangular portion of its dorsal surface that is exposed on the right side of the skull (Figs. 3D, 4). The preserved region of the prefrontal is slightly longer anteroposteriorly than transversely wide and almost occupies the entire dorsal surface of this region of the skull, although this may be exaggerated by deformation (Fig. 4). However, a similar condition is present in *Melanorosaurus*, in which the prefrontal occupies 60% of the lateromedial width of the dorsal surface of the skull (Yates, 2007). In most other basal sauropodomorphs, the prefrontal is narrower, occupying between 25% and 50% of the total width of the skull (e.g., *Riojasaurus*, PULR 56, PVSJ 849; *Plateosaurus*, AMNH 6810; *Lufengosaurus*), or less than 25% (e.g., *Massospondylus*, BP/1/5241; *Adeopapposaurus*, PVSJ 610; *Leyesaurus*, PVL 706; *Yunnanosaurus*; *Mussaurus*, PVL 4587). The lateral border of the prefrontal contributes to the anterodorsal region of the orbit, forming the anterior third of the orbital margin (Fig. 3D), as in most basal sauropodomorphs. The sutural contact of the prefrontal with the frontal and other elements cannot be determined.

Frontal—Both frontals are preserved. Each element is subtrapezoidal and anteroposteriorly longer than wide (Fig. 4; Supplementary Data). The anterior region of the frontal is transversely narrow and broadens posteriorly. The interfrontal suture is straight, and both elements have been slightly displaced from each other (Fig. 4). The anterior margin of the left frontal is sutured to the nasals along a transversely oriented suture, whereas the anterior end of the right frontal is broken and partially overlapped by the displaced prefrontal (Fig. 4). At their posterolateral ends, the frontal has a slot-shaped articular facet for the reception of the anteromedial process of the postorbital. Thus, the frontal excludes the postorbital from the dorsal margin of the orbit, as in other basal sauropodomorphs (see Postorbital, below). In lateral view, the lateral margin of the frontal provides a moderate contribution to the orbital margin (Fig. 3D), as in *Riojasaurus* (PULR 56, PVSJ 849) or *Massospondylus* (BP/1/5241). This contribution represents an intermediate condition between the markedly reduced contribution of the frontal in some basal sauropodomorphs taxa (e.g., *Plateosaurus*, AMNH 6810; *Lufengosaurus*; *Melanorosaurus*) and the condition in other sauropodomorphs in which the frontal forms the entire dorsal border of the orbit (e.g., *Pantydraco*, *Adeopapposaurus*, *Leyesaurus*, *Sarahasaurus*, *Yunnanosaurus*).

Posteriorly, the frontals contact the parietals along a transversely oriented and interdigitated suture, resembling the frontoparietal suture of other basal sauropodomorphs taxa (e.g., *Plateosaurus*, SMNS 13200, AMNH 6810; *Unaysaurus*, UFSM 11069; *Adeopapposaurus*; *Mussaurus*). The posterior end of the frontal is excluded from the supratemporal fenestra by the parietal and postorbital, but enters into the supratemporal fossa as in some other basal sauropodomorphs (e.g., *Plateosaurus*, AMNH 6810; *Unaysaurus*, UFSM 11069; *Lufengosaurus*; *Sarahasaurus*).

Parietal—Both parietals are almost completely preserved and seem to be unfused (Fig. 4; Supplementary Data). The anterolateral process of the parietal contacts the frontal anteriorly, the postorbital laterally, and the laterosphenoid ventrally. This process is laterally curved, is shorter than the posterolateral process, and forms part of the floor of the supratemporal fossa and the anterior wall of the supratemporal fenestra.

The posterolateral process of the parietal is a thin lamina that is anteroposteriorly short and dorsoventrally high (Figs. 4, 5). This process forms the posteromedial floor of the supratemporal fossa and contacts the medial process of the squamosal distally. In posterior view, the medial region of the posterolateral process contacts the dorsolateral margin of the supraoccipital (Fig. 5). The ventral margin of the lateral end of the posterolateral process contacts the dorsal border of the paraoccipital process (Fig. 4). The midsection of the posterolateral process contributes to the posttemporal fenestra, together with the supraoccipital

and the paraoccipital process (Fig. 4). A similar fenestra is also present in *Adeopapposaurus* (PVSJ 610) and in *Yunnanosaurus*, although in the latter taxon it is much smaller. The dorsal edge of the posterolateral process has a sharp ridge that continues anteriorly on to the dorsal surface of the parietal, forming the medial margin of the supratemporal fossa. In dorsal view, the posterolateral process is curved towards its distal end, creating a concave anterior surface, which results in the unusual circular shape of the supratemporal fenestrae (Fig. 4). This feature is unknown in other basal sauropodomorphs and is regarded as an autapomorphy of *Coloradisaurus brevis*. In all other basal sauropodomorphs, the posterolateral processes of the parietal project posterolaterally and usually diverges from the sagittal plane of the skull at an angle of approximately 45°, giving the supratemporal openings a subtriangular shape (e.g., *Riojasaurus*, PULR 56, PVSJ 849; *Plateosaurus*, AMNH 6810; *Unaysaurus*, UFSM 11069; *Massospondylus*, BP/1/5241; *Lufengosaurus*, IVPP V15; *Adeopapposaurus*, PVSJ 610; *Leyesaurus*, PVSJ 706).

Postorbital—The right postorbital is almost complete and articulated with the skull (Fig. 3D), whereas most of the left element is preserved disarticulated from the skull table but articulated with the jugal (Fig. 3E; Supplementary Data). The postorbital is robust and triradiate, with anteromedial and descending processes that are subequal in length and longer than the posterior process (Fig. 3D, E). The anteromedial process articulates with the frontal anteriorly and the parietal medially, the descending process is almost straight and articulates with the ascending process of the jugal, and the posterior process overlaps the anterodorsal process of the squamosal (Fig. 3D, E). The distal end of the anteromedial process is broader at its medial contact with the frontal (Fig. 4). In dorsal view, the anterior-most end of this process is pointed and medially recurved, similar to that of *Riojasaurus* (PULR 56, PVSJ 849), *Massospondylus* (BP/1/5241), *Adeopapposaurus* (PVSJ 610), and *Sarhsaurus*. The anteromedial process fits into the articular notch of the frontal; consequently, the anterior margin of this process does not contribute to the dorsal orbital margin (Fig. 3D). This resembles the condition in massospondylids (e.g., *Massospondylus*, *Adeopapposaurus*, PVSJ 610; *Leyesaurus*, PVSJ 706), but contrasts with the larger contribution of the postorbital to the posterodorsal orbital margin in other sauropodomorphs (e.g., *Plateosaurus*, AMNH 6810; *Sarhsaurus* [Rowe et al., 2010:fig. 4]). Because the distal end of the postorbital anteromedial process is displaced from its natural position, it is not possible to determine its contribution to the anterolateral region of the supratemporal fossa.

The anterior border of the main body of the postorbital and the descending process form most of the posterior margin of the orbit. In lateral view, the descending process of the postorbital of *Coloradisaurus* is robust, almost straight, and tapers distally (Fig. 3D, E), similar to that of *Plateosaurus* (AMNH 6810) and *Mussaurus*. Other basal sauropodomorphs have an anteriorly curved descending process of the postorbital (e.g., *Riojasaurus*, PULR 56; *Massospondylus*, BP/1/5241; *Lufengosaurus*; *Adeopapposaurus*).

The posterior process of the postorbital is subtriangular and short in comparison with the other processes, but is anteroposteriorly longer than high (Fig. 3D). As in other basal sauropodomorphs, this process fits into a 'V'-shaped facet on the lateral surface of the anterior process of the squamosal. This process is horizontal and posteromedially oriented and forms the lateral margin of the supratemporal fenestra and the anterodorsal margin of the infratemporal fenestra. The dorsal border of the posterior process is set well below the dorsal surface of the parietal, so the supratemporal fenestra is visible in lateral view, as in other basal sauropodomorphs (e.g., *Riojasaurus*, PULR 56, PVSJ 849; *Plateosaurus*, AMNH 6810; *Massospondylus*, BP/1/5241; *Adeopapposaurus*, PVSJ 610; *Leyesaurus*).

Jugal—The right jugal is almost complete and has been preserved in articulation with the skull, whereas the left element is incomplete and has been preserved articulated to the postorbital but isolated from the other skull elements (Fig. 3D, E; Supplementary Data). As in other basal sauropodomorphs, the jugal of *Coloradisaurus* is a triradiate, flattened bone that is 'Y'-shaped in lateral view. The anterior process of the jugal is the most robust, forms the main body of the bone, and tapers anteriorly to articulate with the maxilla ventrally and the lacrimal dorsally (Fig. 1). The anterior end of the jugal is pointed and, judging by the preserved articular facets, reached the posteroventral margin of the antorbital fenestra (Fig. 1). This differs from the interpretation of Bonaparte (1978:fig. 1), who regarded the jugal as reaching only to the posterior end of the base of the lacrimal. The minimum dorsoventral height of the suborbital region of the jugal is approximately 20% of its total anteroposterior length (measured from the anterior end of the jugal to the anteroventral corner of the infratemporal fenestra), as in massospondylids (e.g., *Riojasaurus*, PULR 56; *Massospondylus*, BP/1/5241; *Lufengosaurus* [Barrett et al., 2005:fig. 1]; *Adeopapposaurus*, PVSJ 610; *Leyesaurus*, PVSJ 706).

The ascending process of the jugal is slender, pointed, and contacts the descending process of the postorbital along the ventral third of its posterior margin (Fig. 3E). Fragments of the posterior (= quadratojugal) process are preserved attached to the anterior process of the quadratojugal (Fig. 3D). These fragments indicate that the jugal extended, at least, along the anterior half of the ventral margin of the infratemporal fenestra. The left jugal preserves both the posterior and ascending processes, which diverge at an angle of approximately 90°. This condition is similar to *Pantydraco*, *Riojasaurus* (PULR 56, PVSJ 849), and *Plateosaurus* (AMNH 6810), but differs from all other basal sauropodomorphs in which this angle is lower. In both jugals, the anteroventral corners of the infratemporal fenestrae do not extend underneath the orbit (Figs. 1, 3E), a feature shared with *Plateosaurus* but differing from the condition in most other basal sauropodomorphs in which the anteroventral corner of the infratemporal fenestra extends beneath the orbit (see above).

Quadratojugal—The quadratojugal is only known from a fragment on the right side of the skull (Fig. 3D; Supplementary Data). This shows that the posteroventral corner of the quadratojugal is rounded and lacks the expanded process present in *Plateosaurus* (AMNH 6810) and *Lufengosaurus*. The anterior process of the quadratojugal is poorly preserved, and it can only be determined that it formed the posterior half of the ventral margin of the infratemporal fenestra (Fig. 3D). The ascending process of the quadratojugal is slender and tapers dorsally, where it contacted the descending process of the squamosal. The ascending process of the quadratojugal forms the ventral half of the posterior margin of the infratemporal fenestra (Fig. 3D). In lateral view, both processes of the quadratojugal diverge from each other at an angle of approximately 80° and form an acute posteroventral corner of the infratemporal fenestra (Fig. 3D, F). In contrast, in most other basal sauropodomorphs, these two processes are almost perpendicular to each other (e.g., *Massospondylus*, BP/1/5241; *Yunnanosaurus*; *Unaysaurus* [Leal et al., 2004:fig. 2]; *Adeopapposaurus*, PVSJ 610; *Leyesaurus*; *Melanorosaurus*). However, the quadratojugal processes of *Plateosaurus* (AMNH 6810) and *Lufengosaurus* diverge almost parallel to each other.

Quadrate—Both quadrates are preserved. The right quadrate is articulated with the skull and preserves most of both processes, although it is slightly distorted (Fig. 3F; Supplementary Data). The left quadrate lacks most of the anterolateral process, but has the entire anteromedial process in articulation with the quadrate wing of the pterygoid (Fig. 3G).

The anterolateral process of the quadrate diverges from the anteromedial process at an angle of approximately 90°. Both

processes are separated from each other by a wide and shallow concave anterior surface that extends along the entire length of the quadrate shaft. The anterolateral process extends along the dorsal half of the shaft and contacts the descending process of the squamosal on its dorsal half and the ascending process of the quadratojugal on its ventral half (Fig. 3F). The anteromedial process of the quadrate is triangular and articulates medially with the quadrate wing of the pterygoid (Fig. 3G). This process extends for less than 70% (approximately 65%) of the total dorsoventral height of the quadrate. This condition is also present in some basal sauropodomorphs (e.g., *Riojasaurus*, PULR 56; *Masospondylus*; *Melanorosaurus*; *Mussaurus*), but differs from the condition in most taxa in which the anteromedial process extends along more than 70% of total quadrate length (e.g., *Efraasia*; *Pantydraco*; *Plateosaurus*, AMNH 6810; *Adeopapposaurus*; *Leyesaurus*).

The quadrate foramen is circular and opens at the base of the anterolateral process close to the middle of the main shaft (Fig. 3F). The right quadrate head is not exposed because it is covered by the squamosal and matrix, whereas in the left quadrate the dorsal region is slightly eroded, so it has a squared dorsal end (Fig. 3F, G). The main shaft of the quadrate is lateromedially compressed and gently sinuous in lateral and posterior views, although the latter feature may have been accentuated by deformation. The ventral end of the main shaft is mediolaterally expanded to form the condyles that articulate with the mandible (Fig. 3G). The articular condyles of both quadrates are strongly deformed, resulting in a blunt end on the right quadrate and in two flat surfaces on the left element (Fig. 3F, G). Despite the poor preservation of the condyles, the ventral surface of the medial condyle in the left quadrate is more ventrally positioned than the lateral condyle (Fig. 3G), as in other basal sauropodomorphs (e.g., *Riojasaurus*; right quadrate of *Plateosaurus* [Prieto-Márquez and Norell, 2011]; *Lufengosaurus*; *Adeopapposaurus*, PVSJ 568; *Yunnanosaurus*).

Squamosal—Partial squamosals of PVL 3967 are preserved articulated with the skull (Figs. 2, 3D, 4; Supplementary Data). Most of the information on the descending process comes from the left squamosal (Fig. 2), whereas the right squamosal is more complete and includes at least parts of its four processes (Figs. 3D, 4, 5). The anterolateral process of the squamosal is anteroposteriorly short, and its lateral surface has a triangular slot for the articulation of the posterior process of the postorbital (Fig. 2). This process, together with the anteromedial process of the squamosal, forms the posterolateral margin of the supratemporal fenestra (Figs. 4, 5). The anteromedial process of the squamosal is laminar and slightly curved and meets the posterolateral process of the parietal at its medial end (Fig. 4).

In lateral view, the descending process of the squamosal is long, slender, and tapers distally (Figs. 2, 3D). The strap-like morphology of this process is similar to that of all other basal sauropodomorphs, except for *Melanorosaurus* in which this process is broad and triangular in lateral view. The descending process articulates with the anterior margin of the anterolateral process of the quadrate and extends ventrally along the dorsal half of the posterior margin of the infratemporal fenestra, as in most basal sauropodomorphs (Fig. 3D, F). As noted above, the ventral end of the descending process contacts the ascending process of the quadratojugal (Fig. 3F).

The posteroventral process of the squamosal of *Coloradisaurus* is anteroposteriorly short and articulates with the paraoccipital process on its posteromedial surface, but these elements are disarticulated from the natural position in PVL 3967 (Fig. 5). The ventral surface of the posteroventral process is concave for the reception of the quadrate head. In lateral view, the posteroventral process of the squamosal diverges from the descending process at an angle of approximately 90° (Fig. 3D), as in other

basal sauropodomorphs (e.g., *Plateosaurus*, AMNH 6810; *Masospondylus*, BP/1/5241; *Adeopapposaurus*, PVSJ 610).

Braincase

Most of the braincase elements are well preserved and articulated. The braincase is displaced from its natural position, so most of its elements are almost completely visible in lateral and occipital views (Figs. 5, 6; Supplementary Data).

In lateral view, the occipital plate is strongly inclined forward and oriented at approximately 45° with respect to the horizontal plane (Fig. 5C), although this orientation may have been affected by the dorsoventral crushing of the skull. A similar condition is also present in *Lufengosaurus*, whereas other basal sauropodomorphs have a more slightly vertically inclined occipital plate (e.g., *Plateosaurus*, AMNH 6810; *Masospondylus*; *Adeopapposaurus*).

The posttemporal fenestra opens in posterior view (Fig. 5). This fenestra is delimited by the parietal, supraoccipital, and opisthotic. On the left side, the posttemporal fenestra has been enlarged by damage. Some other basal sauropodomorphs have a similar-sized posttemporal fenestra (e.g., *Adeopapposaurus* [Martínez, 2009:fig. 3]), but most taxa have much smaller posttemporal fenestrae (e.g., *Masospondylus* [Sues et al., 2004:fig.6], *Yunnanosaurus* [Barrett et al., 2007:fig. 6], *Melanorosaurus* [Yates, 2007:fig. 8]).

Supraoccipital—The supraoccipital of *Coloradisaurus* is almost complete, missing its dorsal-most portion. The preserved region is subrectangular and transversely wider than dorsoventrally high (Fig. 5). Similar proportions of the supraoccipital are present in several basal sauropodomorphs (e.g., *Efraasia*; *Thecodontosaurus*; *Pantydraco*; *Panphagia*, PVSJ 874; *Masospondylus*; *Adeopapposaurus*, PVSJ 610; *Mussaurus*), whereas most other taxa have a subtriangular supraoccipital that is dorsoventrally higher than transversely wide.

The anterolateral contact with the prootic cannot be observed. In posterior view, the supraoccipital contacts the parietals dorsolaterally, and its lateral edges form the medial borders of the posttemporal fenestra (Fig. 5). The lateroventral margins of the supraoccipital are concave, slightly sinuous, and contact the opisthotic. Hence, the supraoccipital-opisthotic contact forms a sinuous or irregular suture, similar to that of *Plateosaurus* (SMNS 13200; Galton, 1984:fig. 2C), *Masospondylus* (BP/1/4779), and *Adeopapposaurus* (PVSJ 568), but different from the straight suture of other basal sauropodomorphs, such as *Melanorosaurus* (Yates, 2007:fig. 8). Dorsally, the supraoccipital forms the posterior margin of the postparietal fenestra or fontanelle (Figs. 4, 5). The postparietal fenestra opens dorsally, has a semicircular shape, and is lateromedially wider than longitudinally long. This fenestra is also visible in posterior view due to the displacement of the occipital plate. Although other basal sauropodomorphs also have a postparietal fenestra, they usually have a smaller opening than in *Coloradisaurus* (e.g., *Riojasaurus*, PULR 56, PVSJ 849; *Plateosaurus*, SMNS 12949, 13200; *Masospondylus*, BP/1/5241; *Adeopapposaurus*, PVSJ 568; *Sarahasaurus*; *Anchisaurus*, YPM 1883; *Melanorosaurus*; *Mussaurus*). The ventral margin of the supraoccipital is straight to slightly concave and forms the dorsal border of the foramen magnum (Fig. 5).

The posterior surface of the supraoccipital lacks a sagittal ridge or nuchal crest, which is a feature found commonly in other basal sauropodomorphs, such as *Plateosaurus* (Galton, 1984), *Lufengosaurus*, *Melanorosaurus*, and *Mussaurus*. In each lateral region, the dorsal half of the posterior surface of the supraoccipital has paired shallow concavities in which the foramen for the vena capitis dorsalis is located (Fig. 5). These foramina are dorsoventrally elongated, crescent-shaped, and open dorsolaterally.

Exoccipital-Opisthotic—The suture between the exoccipital and opisthotic is not distinguishable (Figs. 5, 6). Each exoccipital contacts the dorsolateral region of the basioccipital and the ventral region of the supraoccipital. The exoccipital forms the lateral margin of the foramen magnum and the posterolateral region of the braincase (Figs. 5, 6). In posterior view, the right exoccipital is mostly complete, whereas the left element is poorly preserved and hidden by an articulated fragment of bone that may be the left proatlas (Fig. 5). In this view, the exoccipital is dorsoventrally elongated, with a rounded posteroventral process that extends over the basioccipital. In lateral view, the exoccipital is curved and its straight ventral border contacts the basioccipital along its entire length.

The exoccipital bears two foramina for the branches of the hypoglossal nerve (cranial nerve XII) that are visible in posterolateral view (Fig. 6A, B), located posteroventral to the edge of the metotic fissure and almost at the same level as the base of the foramen magnum. Bonaparte (1978:fig. 3) originally identified a foramen for nerve XI on the lateral surface of the exoccipital just anterior to the openings for cranial nerve XII. Based on comparisons with other sauropodomorphs (e.g., *Plateosaurus* [Prieto-Márquez and Norell, 2011:fig. 27B], *Massospondylus* [Gow, 1990:fig. 7], *Melanorosaurus* [Yates, 2007:fig. 10B]), however, we regard this foramen as part of the metotic fissure. In PVL 3967, the metotic fissure is located anterodorsal to the foramina for cranial nerve XII and posteriorly to the crista tuberalis, close to the suture with the opisthotic. The metotic fissure is an elliptical slot in which are exposed the foramina for the cranial nerves IX, X, XI (Fig. 6A, B).

The exoccipital and opisthotic form the paraoccipital process. The opisthotic is a rectangular process with a constant dorsoventral depth along its entire length that is posterolaterally directed in dorsal view (Figs. 4, 5C). The posterior surface of the opisthotic is slightly concave. The dorsomedial region of the opisthotic contacts the supraoccipital and articulates with the prootic anterolaterally (Figs. 5, 6).

Basioccipital—The posterior surface of the basioccipital contacts the exoccipitals laterally and forms the ventral margin of the foramen magnum (Fig. 5). Anteriorly, the basioccipital contacts the basisphenoid along its lateroventral margins. The posterior end of the basioccipital expands to form the occipital condyle, which is circular with convex dorsal and ventral margins, as in all other basal sauropodomorphs.

In lateral view, the ventral margin of the occipital condyle is located dorsal to the level of the basal tubera and parasphenoid rostrum (Fig. 6), resembling the ‘stepped’ condition of *Plateosaurus* and *Lufengosaurus*. In several other basal sauropodomorphs, the ventral margin of the occipital condyle is approximately in line with the base of the basiptyergoid processes and the longitudinal axis of the parasphenoid rostrum (e.g., *Efraasia*; *Thecodontosaurus*, YPM 2192 [Galton, 1990]; *Massospondylus*, BP/1/4934 [Sues et al., 2004]; *Adeopapposaurus*). In more derived sauropodomorphs, the bases of the basiptyergoid process are set below the level of the basioccipital and parasphenoid rostrum (e.g., eusauropods [Galton, 1990; Yates, 2010]). The basioccipital extends ventrally from the condylar region to form part of the basal tubera. The basioccipital component of the basal tubera is located posteromedial to the basisphenoid component, as in *Massospondylus carinatus* (SAM-PK-K1314), *M. kaalae* (Barrett, 2009), and *Jingshanosaurus* (LV 3; Yates, 2007).

Basisphenoid—The basisphenoid forms the anterior region of the braincase floor, from the level of the basal tubera to the anterior region of the basiptyergoid processes. The basisphenoid is well exposed in lateral and ventral views (Fig. 6). The anterodorsal region of the basisphenoid is overlapped by the prootic laterally (Fig. 6A, B). In lateral view, the posterodorsal region of the basisphenoid has a wide circular depression

located dorsal to the base of the basiptyergoid process. This depression may represent the passage for the internal carotid artery, but this region is poorly preserved and its large size has probably been exaggerated by damage (Fig. 6B). Dorsal to this depression and just at the limit with the prootic, the basisphenoid forms part of the margin of the Vidian canal (Fig. 6B). Posterodorsal to the Vidian canal is the concave surface of the fenestra ovalis (Fig. 6B).

On the ventral surface, the posterior region of the basisphenoid extends laterally to contact the basioccipital at the slender basal tubera (Fig. 6C). Anterior to the tubera, between the basal tubera and basiptyergoid processes, the basisphenoid has a deep and wide median fossa that faces posteroventrally (Fig. 6C). Other basal sauropodomorphs also have a deep recess on the ventral surface of the basisphenoid (e.g., *Riojasaurus*, PVSJ 849; *Massospondylus*, SAM-PK-K1314; *Adeopapposaurus*, PVSJ 568), but the fossa in *Coloradisaurus* is different in being bounded laterally by a thin, tall lamina that extends from the basal tuberae to the basiptyergoid processes (Fig. 6C). This lamina forms the lateral margins of the ventral fossa and is interpreted as an autapomorphy of *Coloradisaurus*.

The basiptyergoid processes are lateromedially flattened and not distally expanded (Fig. 6C), as in *Massospondylus kaalae* (Barrett, 2009) and *Leyesaurus*. Other basal sauropodomorphs have distally expanded basiptyergoid process (e.g., *Riojasaurus*, PVSJ 849, [Bonaparte and Pumares, 1995]; *Massospondylus carinatus*; *Adeopapposaurus*, PVSJ 568; *Mussaurus*). The basiptyergoid processes of *Coloradisaurus* are directed ventrolaterally and slightly posteriorly. The posterior orientation of the basiptyergoid processes of *Coloradisaurus* differs from the condition of other basal sauropodomorphs, in which the processes are either slightly anteriorly oriented (e.g., *Efraasia* [Fedak and Galton, 2007]; *Pantyraco*; *Riojasaurus*, PULR 56; *Leyesaurus*, PVSJ 706) or vertically oriented in lateral view (e.g., *Thecodontosaurus*, YPM 2192 [Benton et al., 2000]; *Plateosaurus*, AMNH 6810; *Massospondylus*, BP/1/4779, SAM-PK-K1314; *Lufengosaurus*; *Adeopapposaurus*; *Mussaurus*). As in most basal sauropodomorphs, the basiptyergoid processes of *Coloradisaurus* diverge from each other, forming an angle of approximately 90° in posterior view, and lack the transverse lamina that connects the left and right processes in *Plateosaurus* (Galton, 2001; Yates, 2003a).

Parasphenoid—The parasphenoid of PVL 3967 is exposed in lateral and ventral views (Fig. 6). The parasphenoid projects anteriorly from the base of the basiptyergoid processes and is an elongated, anteriorly pointed, and transversely compressed process with a subtriangular cross-section. The ventral surface of the parasphenoid bears a deep longitudinal groove that extends from the base of basiptyergoid processes up to the midlength of the parasphenoid (Fig. 6C). This depression is laterally bounded on each side by a thin and triangular lamina. This lamina extends along the entire lateral length of the parasphenoidal groove, from the base of basiptyergoid processes to the anteroposterior midpoint of the parasphenoid (Fig. 6C). In lateral view, this lamina is observed as a triangular wall of the proximal half of the ventral surface of the parasphenoid (Fig. 6A, B). The highly developed triangular bony laminae are therefore recognized here as an autapomorphy of *Coloradisaurus*. Other basal sauropodomorphs such as *Plateosaurus* (AMNH 6810) and *Adeopapposaurus* (PVSJ 568; Martínez, 2009) also have a similar groove limited laterally by a thin lamina, but in these forms the lamina is not well as developed, both ventrally and anteriorly, as in *Coloradisaurus*. In lateral view, the parasphenoid rostrum and the base of the basiptyergoid process are both set well below the level of the occipital condyle and basal tuberae.

Laterosphenoid—Both laterosphenoids are preserved in their natural positions (Figs. 4, 5). The laterosphenoid is concave and subtriangular in lateral view and forms the anterior region of the lateral wall of the braincase (Figs. 5, 6). The laterosphenoid

contacts the frontal anteriorly and the distal end of the anteromedial process of the postorbital laterally, but the poor preservation of the specimen obscures details of these contacts. Dorsally, the laterosphenoid is attached to the anterolateral process of the parietal and forms the ventral region of the anteromedial wall of the supratemporal fenestra. The ventral end of the laterosphenoid tapers towards its contact with the anterodorsal region of the prootic. In this region, the laterosphenoid bears a deep notch that defines the anterior margin of the trigeminal nerve foramen (Fig. 6).

Prootic—The prootic forms most of the lateral wall of the braincase, but is only visible in left lateral view (Fig. 6). The prootic contacts the laterosphenoid along its anterodorsal surface and is posteriorly fused to the anterior region of the opisthotic. The latter contact is denoted by a rough convex surface. The dorsal contacts with the parietal and supraoccipital are not clearly preserved. The prootic has a relatively straight contact with the basisphenoid along its ventral margin, which is located dorsal to the base of the basispterygoid processes (Fig. 6A, B).

In lateral view, the prootic is higher than long and is divided in two distinct subrectangular regions. The dorsal region is larger, slightly concave, and forms most of the articular region with the opisthotic. This region is separated from a ventral subrectangular surface by a constriction located between the openings for cranial nerves V and VII (Fig. 6B). At the level of the constriction, the anterior margin of the prootic has a deep notch that forms the posteroventral edge of the trigeminal nerve foramen (cranial nerve V). Towards the posterior margin of the constriction, the prootic encloses the facial nerve (cranial nerve VII). In this region, the posterior margin of the prootic forms the anterior rim of the fenestra ovalis (Fig. 6B). The smaller ventrally positioned rectangular region of the prootic is located ventral to the exit of these cranial nerves. This surface is laminar, dorsoventrally expanded towards its anterior end, and forms an area for the attachment of the *M. protractor pterygoideus*.

Palate

Most of the palatal elements are not preserved. Laminar, elongated fragments that probably represent portions of the palatine are preserved on the left side of the holotype (Fig. 2). A fragment of a probable right pterygoid is preserved between the braincase and mandible, but no further details can be obtained.

Mandible

Both mandibular rami are preserved (Figs. 1, 7). The right mandibular ramus is almost complete and is preserved in articulation with the skull, whereas the left ramus includes all its elements but is disarticulated from the skull (Supplementary Data). The mandibular external fenestra is wide, and its length is approximately 20% of the total mandibular length. The coronoid eminence is approximately 1.5 times higher than dentary height. The jaw articulation is low and almost level with the ventral margin of the mandible, as in some other basal sauropodomorphs (e.g., plateosaurids).

Dentary—Both dentaries are preserved (Figs. 1, 7A, B). The dentary is slender and elongate, with an anteroposterior length that is five times its maximum height. The dentary forms more than the half of the total mandibular length (Fig. 1). Its dorsal and ventral margins are almost parallel to each other along most of its length, except for the posterior-most region in which the dentary increases in depth (Fig. 7A). The ventral margin of the dentary is ventrally curved at its symphyseal region, although the degree of curvature may have been influenced by the presence of an almost vertical fracture located at the beginning of the ventrally oriented region (Fig. 7A). The anterior region of the left dentary, which is better preserved than in the right dentary, is blunt and lacks the ventral expansion present in some other basal

sauropodomorphs (e.g., *Melanorosaurus*, *Mussaurus*). The lateral surface of the dentary bears a longitudinal row of neurovascular foramina that is set parallel and just ventral to the alveolar margin. These foramina are subequal in size, although the size of some was likely affected by damage (Figs. 1, 7A).

The first alveolus of the dentary is inset a short distance from the anterior end of the symphyseal region. This edentulous space is equivalent to the width of an alveolus, a condition present in most basal sauropodomorphs. The lower tooth row occupies most of the dorsal margin of the dentary and includes at least 18 alveoli (with 12–13 partially preserved teeth). The posterior end of the dentary is divided into two processes that delimit the anterior margin of the external mandibular fenestra (Fig. 7A, B). The dorsal process is contacted laterally by the surangular and forms the anterodorsal margin of the mandibular fenestra and the anterior region of the coronoid eminence. The ventral process of the posterior end of the dentary extends further posteriorly than the dorsal process, contacts the angular, and forms the anteroventral margin of the external mandibular fenestra.

Splénial—The splénial is a thin, laminar, and trapezoidal bone that covers the posterior half of the medial surface of the dentary (Fig. 7B). This element is poorly preserved and mainly recognized by its anterior margin, which is separated from the dentary by matrix. The anterior end of the splénial is forked, forming two processes that are parallel to the dorsal and ventral borders of the dentary. The dorsal process is short and high, whereas the ventral process is pointed, long, and extends close to the ventral margin (Fig. 7B). This elongated ventral process extends anteriorly as far as in other basal sauropodomorphs, in which the anteroventral tip reaches the anterior half of the medial surface of the dentary (measured on the medial side, from the anterior margin of the internal mandibular fenestra to the anterior margin of the dentary). This condition is present in *Plateosaurus* (Galton, 1984:fig. 3B), *M. kaalae* (Barrett, 2009:fig. 7B), and *Adeopapposaurus* (PVSJ 568). The splénial ventral process of *Coloradisaurus* seems to be narrower and more elongated than in other taxa, but none of the above-mentioned taxa (including also *Massospondylus*, SAM-PK-K1314) has a completely preserved anterior ventral process of the splénial. The anteroventral region of the splénial bears a small splénial foramen (Figs. 2B, 7B). The posterior margin of the splénial is not clearly identifiable.

Surangular—The surangular articulates anteriorly with the dentary, ventrally with the angular, and posteromedially with the articular (Figs. 1, 7C–E). The lateral surface of the surangular is convex, and its ventral margin forms the dorsal and posterodorsal margins of the external mandibular fenestra. The dorsal margin of the surangular is sigmoid, being strongly convex along its anterior two-thirds (forming the coronoid eminence; Figs. 1, 7C). The anterior region of the dorsal surface is pierced by an anteriorly open foramen. The posterior third of the dorsal margin of the surangular is concave, and its height decreases posteriorly where it articulates with the articular (Fig. 7C). The medial surface of the surangular is concave and ventrally contacts the angular anteriorly and the prearticular posteriorly (Fig. 7E).

Angular—Both angulars are preserved, although the left element has better preservation (Figs. 1, 7C–E). The angular is a laminar, anteroposteriorly elongate, strap-like bone (Figs. 1, 7C). The dorsal margin of the angular forms the ventral border of the external mandibular fenestra (Fig. 7C). The anterior end of the angular contacts the ventral process of the posterior end of the dentary. The medial surface of the angular is overlapped by a subtriangular fragment of the prearticular (Fig. 7E).

The ventral border of the left angular has a peculiar tabular bony process that projects ventrally (Fig. 7C–E). This tabular projection has an elongated cavity on its medial surface, which is filled by matrix and is possibly connected with the elongated—although thinner—concavity of the lateral surface (Fig. 7C–E). This projection, which is unique among basal

sauropodomorphs, is absent from the right angular, so we interpret this process as a pathological feature. This pathology may be related to the unnatural sharp bend located at the midsection of the prearticular (Fig. 7E) that could represent the healing mark of a partially fractured jaw (see Prearticular).

Prearticular—The left prearticular has been partly preserved and is only visible in medial view (Fig. 7E). The preserved fragment is flat and irregularly shaped and articulates with the surangular dorsally, the angular ventrally, and the articular posteriorly. Medially, the prearticular surrounds the ventral margin of the medial mandibular fossa (Fig. 7E). The anterior region of the prearticular is represented by a subtriangular fragment, which lies on the anterior region of the medial mandibular fossa. Posteriorly, the prearticular decreases in size and forms a triangular process that extends dorsally, anterior to the glenoid fossa (Fig. 7E). This posterior triangular process articulates posteromedially with the anterolateral surface of the articular and posteriorly ends in a thin laminar projection that underlies the articular. In other basal sauropodomorphs, the prearticular extends anteriorly along the posterior region of the medial surface of the dentary, but in PVL 3967 this portion of the prearticular has not been preserved (Fig. 7). The narrow midsection of the prearticular has a sharp bend, immediately anterior to the ventral tabular projection. In all other dinosaurs, this section of the prearticular is straight with a gently bowed dorsal margin. This appears to be a badly healed fracture, which was probably the cause of the ventral bony outgrowth described in the left angular (Fig. 7E).

Articular—Only the left articular has been preserved (Fig. 7C–E). As in all basal sauropodomorphs, it has an irregular morphology. In dorsal view, the anterior half of the articular forms the glenoid surface and posteriorly it forms the retroarticular process (Fig. 7D). The glenoid facet of the articular is set below the alveolar margin, approximately level with the ventral margin of the mandible, as in some other basal sauropodomorphs (e.g., *Efraasia*; *Plateosaurus*, AMNH 6810; *Lufengosaurus*; *Unaysaurus*). This condition differs from other basal sauropodomorph taxa in which the mandibular articulation is set at approximately the same level as the alveolar margin of the dentary (e.g., *Massospondylus*, BP/1/4934; *Riojasaurus*, PULR 56, PVSJ 849; *Adeopapposaurus*, PVSJ 610; *Leyesaurus*, PVSJ 706). The glenoid region expands medially to form the pyramidal process of the articular (Fig. 7D), which is similar to that of *Plateosaurus* (AMNH 6810; Prieto-Márquez and Norell, 2011). The lateral border of the articular is set into a posterior depression of the medial surface of the surangular. The ventral border of the articular is exposed in lateral view and is slightly convex (Fig. 7C).

The retroarticular process is transversely narrow but has a blunt apex with a rugose surface for the insertion of the M. depressor mandibulae (Fig. 7C, D). On the medial surface of the retroarticular process, the articular has a distinct, small, tab-like process that projects medially. This process is subrectangular in shape and is visible in lateral, dorsal, and medial views (Fig. 7C–E). This feature is not present in any other basal sauropodomorph; therefore, we interpret it as an autapomorphy of *Coloradisaurus brevis*. However, the left articular has not been preserved, so it cannot be determined with certainty if this unusual feature is pathological or not. One of the reasons for suspecting a pathological origin for this small process is that the right mandibular ramus has another distinctive process—a large tabular bony projection located on the ventral margin of the angular—that is considered pathological given its absence on the right angular (see above). The presence of a pathological structure in the same mandibular ramus suggests caution in interpreting the medial process of the right articular as a definitive diagnostic feature of *Coloradisaurus brevis*. For the moment we have listed this feature as a diagnostic character of this taxon,

but we note that further remains are necessary to confirm its status as an autapomorphy.

Dentition

The dentition is not well preserved and none of the exposed teeth are complete (Figs. 1, 7A; Supplementary Data). Moreover, some of the preserved teeth were damaged during preparation. Only the right maxilla and dentaries include some teeth. The right maxilla preserves 14 teeth from the approximately 22–24 alveoli, whereas the right and left dentaries have 13 and 12 partly preserved teeth, respectively (out of the, at least, 18 dentary alveoli). The premaxillary dentition has not been preserved.

All teeth are vertically oriented and lanceolate. The teeth have a basal constriction and are apicobasally higher than mesiodistally wide. The maxillary teeth have their maximum mesiodistal expansion located in the basal third of the crown (Fig. 1). All teeth are labiolingually flattened, with the labial surface slightly convex and the lingual surface almost flat. Most of the crowns have a slightly rugose labial surface with longitudinal striations, similar to those of *Melanorosaurus*, although this feature may have been affected by the poor preservation.

The marginal serrations are rarely preserved but are present in some teeth. In particular, one of the posterior maxillary teeth has broad, rounded denticles, which are oriented at 45° with respect to the apicobasal axis of the crown, resembling the condition of other basal sauropodomorphs (Galton, 1985; Benton et al., 2000). This maxillary crown has denticles restricted to the apical third of the mesial and distal margins, as in *Massospondylus* (BP/1/5241; Sues et al., 2004). The preserved denticles of the lower dentition are also restricted to the apical third of the crowns, which are only observed on the mesial margin of the second preserved dentary tooth of the right mandible. Further information is unavailable.

DISCUSSION

This redescription of PVL 3967 enhances our knowledge of the craniomandibular anatomy of *Coloradisaurus* and has implications for understanding the unique combination of characters present in this taxon. The craniomandibular remains of *Coloradisaurus* have autapomorphic characters that clearly distinguish this taxon from all other known sauropodomorphs (see below).

The phylogenetic affinities of *Coloradisaurus* are debated (see Apaldetti et al., 2013), but a modified version of the phylogenetic analysis of Yates et al. (2010), which is the most extensive data set on basal sauropodomorphs published to date, finds strong character support for placing it close to *Lufengosaurus* and nested within Massospondylidae. Within this context, the craniomandibular anatomy of *Coloradisaurus* provides information for evaluating the phylogenetic signal present in the skull and mandible of this taxon.

Phylogenetic Signal in the Skull of *Coloradisaurus*

As noted above, the affinities of *Coloradisaurus* are debated, and the original interpretation of Bonaparte (1978), followed by several authors (Serenó, 1999; Galton and Upchurch, 2004; Barrett et al., 2005; Upchurch et al., 2007; Martínez, 2009), was that this taxon was closely related to *Plateosaurus* and *Lufengosaurus*. Most of these authors only considered the craniomandibular information published by Bonaparte (1978) sometimes complemented by firsthand examination of the holotype. Several of the similarities between the skull and mandible of *Coloradisaurus* and *Plateosaurus* noted by previous authors are confirmed in this study (see below). However, the postcranial anatomy of *Coloradisaurus*, which is currently known from both the type specimen and more complete referred material (see Apaldetti et al., 2013),

revealed the presence of numerous derived features of the postcranium that are shared exclusively with massospondylids.

Revision of the cranial anatomy of *Coloradisaurus* therefore allows us to evaluate the phylogenetic signal of the cranial characters present in PVL 3967. Here, we review the phylogenetic signal of the cranial and postcranial characters in *Coloradisaurus* based on exploratory analyses of the data matrix published by Apaldetti et al. (2013) that includes the largest taxon and character sampling regimens for basal sauropodomorphs (based on an expansion of Yates et al., 2010).

Two exploratory analyses reveal disparity in the phylogenetic signals revealed by the skull and postcranium of *Coloradisaurus*. The first analysis was performed by modifying the data matrix so that the postcranial character scorings of *Coloradisaurus* were replaced by missing entries (see Supplementary Data). The resultant most parsimonious trees (MPTs) from this analysis (288 MPTs, tree length [TL] = 1245 steps, consistency index [CI] = 0.340, retention index [RI] = 0.659) ally this taxon to plateosaurids rather than massospondylids (Fig. 9A). The second exploratory analysis partitioned the data matrix into craniomandibular and postcranial characters and analyzed them separately (see Supplementary Data). The most parsimonious topologies of the craniomandibular data matrix (89814 MPTs, TL = 348 steps, CI = 0.397, RI = 0.693) place it in a basal position (Fig. 9B), closer to plateosaurids (although not forming a clade with the two species of *Plateosaurus*), but the most parsimonious topologies retrieved in the postcranial data matrix (440 MPTs, TL = 889 steps, CI = 0.321, RI = 0.656) unequivocally places *Coloradisaurus* as part of Massospondylidae (Fig. 9C). These two exploratory analyses reveal that there are conflicting phylogenetic signals obtained from the skull and postcranial characters of *Coloradisaurus* and explain why previous authors have suggested its plateosaurid affinities when only the holotype skull was considered.

It is important to note that the conflict in the phylogenetic signal between the craniomandibular and postcranial data noted for *Coloradisaurus* does not extend to all basal sauropodomorphs. The topologies retrieved in the partitioned analyses are congruent with the general pattern of relationships retrieved in the complete data set (except for the position of some particular taxa, including *Coloradisaurus*; see Fig. 9B–D). This general agreement between the phylogenetic signals obtained from the skull and postcranium of basal sauropodomorphs is revealed by the incongruence length difference (ILD) test (Farris et al., 1995) when applied to the craniomandibular and postcranial partition. The ILD indicates that the two partitions are not significantly incongruent when compared with two randomly chosen partitions of the entire data set ($P = 0.73$).

Given that the craniomandibular characters are providing a different phylogenetic signal, we discuss below the craniomandibular characters that support either plateosaurid or massospondylid affinities.

Massospondylid Characters

Of the characters supporting the inclusion of *Coloradisaurus* within Massospondylidae, one is cranial and 11 are postcranial. Furthermore, two features of the skull that Bonaparte (1978) interpreted as diagnostic of *Coloradisaurus* (short rostrum and frontals longer than nasals) more closely resemble the condition of massospondylids than plateosaurids, although these characters are subject to continuous variation among basal sauropodomorphs and have not been included as characters in phylogenetic analyses. Here, we review these features by comparing the condition in *Coloradisaurus* with those of other basal sauropodomorphs.

Jugal Contribution to the Antorbital Fenestra—The anterior end of the main body of the jugal of *Coloradisaurus* is not well preserved and it has been interpreted in different ways.

Bonaparte (1978:fig. 1) interpreted the anterior extension of the jugal as reaching the posterior end of the base of the lacrimal. Here, we suggest that the anterior end of the jugal of *Coloradisaurus* extends further anteriorly, entering into the antorbital fossa and probably contributing to the posteroventral margin of the antorbital fenestra (Fig. 8A).

Sues et al. (2004) observed that, except in the juvenile specimen BP/1/4376, the jugal of *Massospondylus* contributes to the antorbital fenestra. Other massospondylid taxa (e.g., *Lufengosaurus*, *Adeopapposaurus*, *Leyesaurus*), together with *Jingshanosaurus* and *Saraksaurus*, also have elongated jugals that extend anteriorly to reach the antorbital fenestra. Among plateosaurids this feature is difficult to determine because this region varies among the known specimens of *Plateosaurus*, with some specimens lacking a contribution of the jugal to the antorbital fenestra (e.g., GPIT 1; Galton, 2001: fig.3) and others showing moderate participation of the jugal (e.g., SMNS 13200).

Although it would be necessary to have better preserved specimens of *Coloradisaurus* to confirm without doubt the participation of the jugal in the antorbital fenestra, it seems clear to us that the jugal of PVL 3967 extends much more anteriorly than in the original interpretation of Bonaparte (1978), being similar to (or approaching closely) to the condition of massospondylids.

As noted above, the bulk of the evidence that place *Coloradisaurus* within Massospondylidae is from the postcranial characters. There are 11 postcranial characters that support the inclusion of *Coloradisaurus* within Massospondylidae rather than its inclusion in Plateosauridae, centered in different anatomical regions of the postcranium, which were discussed in Apaldetti et al. (2013).

Massospondylid Skull Characters Originally Proposed by Bonaparte (1978)—Two of the skull characters regarded as diagnostic of *Coloradisaurus brevis* by Bonaparte (1978) are not exclusive to this taxon and resemble the condition found in massospondylids: the short preorbital region of the skull and the frontal length relative to the nasal length.

Bonaparte (1978:328) noted that the preorbital region of the skull—from the anterior margin of the orbit to the anterior tip of the premaxilla—was shorter than in *Plateosaurus* and *Lufengosaurus*. In PVL 3967, this region is proportionally shorter than the orbitotemporal region of the skull (from the anterior margin of the orbit to the posterior-most tip of the skull), with a length ratio of approximately 0.8 (Fig. 8A). A similar proportion is present in the skull of other massospondylids, in which this ratio ranges between 0.7 and 0.85 (e.g., *Massospondylus*, BP/1/5241; *Adeopapposaurus*, PVSJ 610; *Leyesaurus*, PVSJ 706). Nevertheless, this condition is also found in other non-massospondylid basal sauropodomorph, such as *Yunnanosaurus* (Barrett et al., 2007:fig. 2). However, other basal sauropodomorphs have an elongated preorbital region that is longer than the orbitotemporal region of the skull, with length ratios ranging between 1.05 and 1.3, such as in *Efraasia* (Yates, 2003b:fig. 9), *Riojasaurus* (PVSJ 849; Bonaparte and Pumares, 1995:fig. 3), *Melanorosaurus* (Yates, 2007:fig. 6), *Aardonyx* (Yates et al., 2010:fig. 2b), and plateosaurids (species of *Plateosaurus*, SMNS 13200, AMNH 6810; *Unaysaurus* [Leal et al., 2004:fig. 2]).

The ratio of preorbital/orbitotemporal length has a continuous variation among basal sauropodomorphs, and a relatively short preorbital region is not exclusive of massospondylids. However, it is interesting to note that the condition of *Coloradisaurus* resembles that of massospondylids more than that of other basal sauropodomorphs with an elongated preorbital region, notably those present in plateosaurid specimens.

Bonaparte (1978:329) mentioned the presence of long frontals and short nasals in *Coloradisaurus* and related this feature with the previous character, because a shorter rostrum is likely to result from having relatively short nasals. In the original description, Bonaparte (1978:329) also noted that this feature

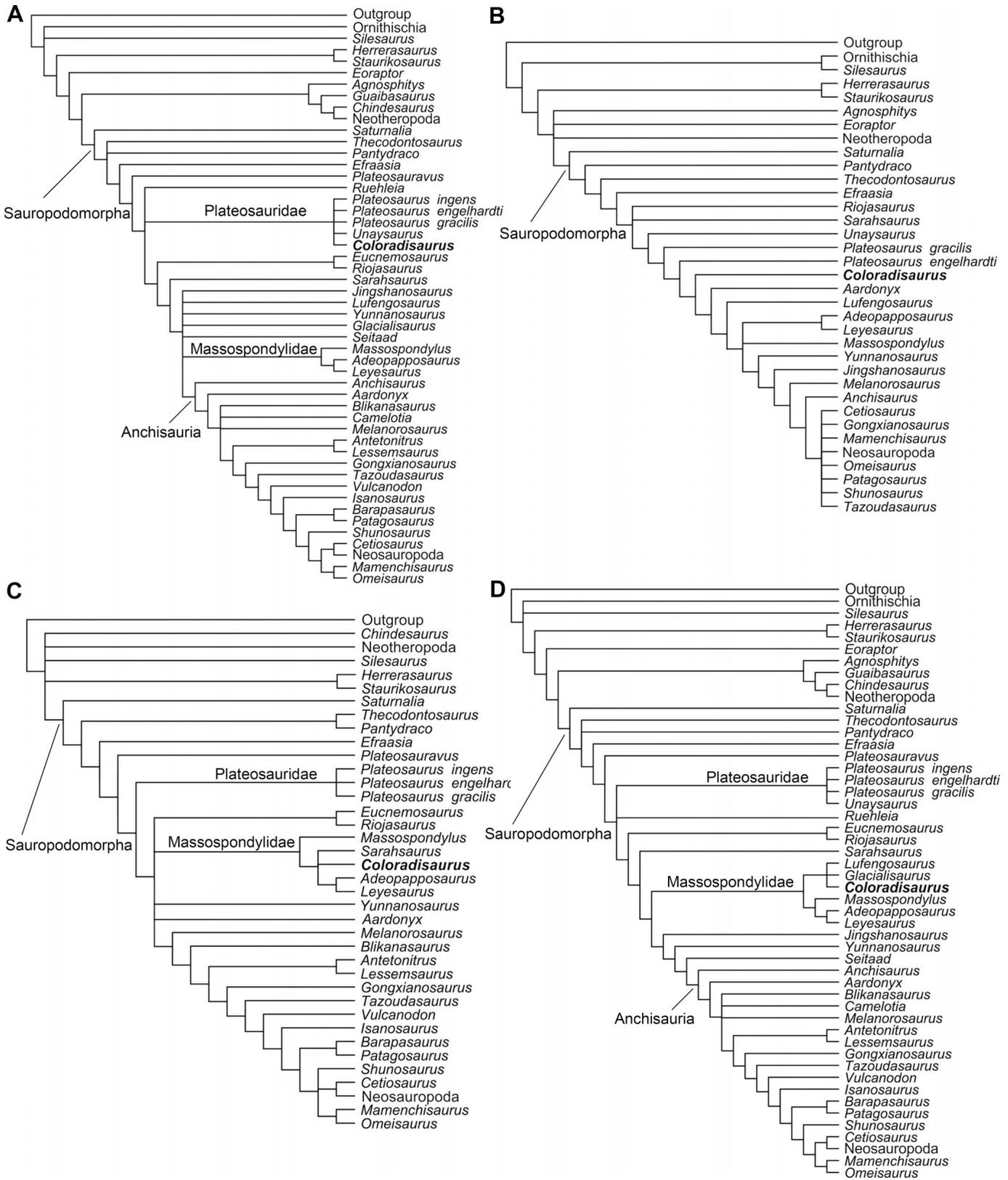


FIGURE 9. Phylogenetic positions of *Coloradisaurus* after different modifications of the original data matrix published by Apaldetti et al. (2013). **A**, strict consensus of most parsimonious trees (MPTs) from a modified matrix with postcranial scorings for *Coloradisaurus* replaced by missing entries; **B**, reduced strict consensus (ignoring the position of *Antetonitrus* and *Seitaad*) of MPTs from the matrix with the cranial partition; **C**, reduced strict consensus (ignoring the position of *Agnosphitys*, *Anchisaurus*, *Camelotia*, *Eoraptor*, *Guaibasaurus*, *Jingshanosaurus*, *Lufengosaurus*, *Ornithischia*, *Rueleia*, *Unaysaurus*, *Glacialisaurus*, and *Seitaad*) of MPTs from the matrix with the postcranial partition; **D**, strict consensus of MPTs from the complete data matrix (Apaldetti et al., 2013; see Supplementary Data).

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constituted the principal difference between *Coloradisaurus* and *Plateosaurus*/*Lufengosaurus*. However, it is not currently possible to establish a direct relationship between having a short preorbital region and the presence of frontals that are longer than the nasals. Most of the basal sauropodomorphs with a short preorbital region lack completely preserved nasals, which precludes a precise comparison with the length of the frontals (e.g., *Pantydraco* [Yates, 2003a]; *Massospondylus carinatus*, BP/1/4779; *Massospondylus kaalae* [Barrett, 2009]; *Adeopapposaurus*, PVSJ 610, 568; *Leyesaurus*, PVSJ 706; *Yunnanosaurus*; *Lufengosaurus*). The only massospondylid with a short preorbital region and complete nasals is *Massospondylus* (BP/1/5241), and this specimen has nasals that are longer than the frontals (Sues et al., 2004:fig. 7). Similarly, basal sauropodomorphs with a preorbital region longer than the orbitotemporal region of the skull also have nasals that are longer than the frontals (e.g., *Efraasia*, *Plateosaurus*, *Melanorosaurus*). In sum, this feature does not seem to be informative in resolving the affinities of *Coloradisaurus* and does not seem to be related to the rostrum length.

Plateosaurid Characters

In the phylogenetic data set used here (modified version of Yates et al., 2010; see also Apaldetti et al., 2013), there are five cranial and two postcranial characters that support an alternative phylogenetic signal: the putative affinities of *Coloradisaurus* with plateosaurids. Bonaparte (1978) originally mentioned some of these features, in addition to the presence of a projection of the antorbital fossa underneath the orbit (a character subject to continuous variation among basal sauropodomorphs that was not included in the phylogenetic data set). The character distribution of these features among basal sauropodomorphs and their phylogenetic implication are discussed here.

Crescentic and Broad Maxillary Antorbital Fossa—This character was originally noted by Bonaparte (1978:328) for *Coloradisaurus* as having a broad ascending process of the maxilla (Fig. 8A), and was one of the characters that led this author to relate *Coloradisaurus* with *Plateosaurus*.

The maxillary contribution to the antorbital fossa is formed by a wide and well-developed triangular medial lamina in plateosaurids (*Plateosaurus*, SMNS 13200, AMNH 6810; *Unaysaurus*), as well as in more derived forms such as *Melanorosaurus* and *Aardonyx*. Most other basal sauropodomorphs, including massospondylids, have an anteriorly reduced antorbital fossa, formed by a narrow medial lamina of the maxilla that has a concave posterior margin that runs almost parallel to the anterior margin of the fossa (e.g., *Massospondylus*, *Lufengosaurus*, *Adeopapposaurus*, *Jingshanosaurus*, *Anchisaurus*). The broad medial lamina of the ascending process of the maxilla that extends within the antorbital fossa in *Coloradisaurus* clearly resembles the condition of *Plateosaurus* and provides evidence favoring the affinities of these taxa. This feature has been included in the phylogenetic data set (Apaldetti et al., 2013:character 32), but is most parsimoniously interpreted as convergently acquired in *Coloradisaurus* and *Plateosaurus*.

Prefrontal Width—In dorsal view, the prefrontal of *Coloradisaurus* is markedly wide and occupies more than half of the dorsal surface of the interorbital region of the skull (Fig. 8B). This condition resembles to that of *Melanorosaurus*, in which the prefrontal occupies 60% of the lateromedial width of the dorsal surface of the skull at its widest point (Yates, 2007). Other basal sauropodomorphs have a relatively wide prefrontal that extends between 25% and 50% of the dorsal width of the skull (e.g., *Plateosaurus*, AMNH 6810; *Lufengosaurus* [Barrett et al., 2005: fig. 3]; *Sarhsaurus* [Rowe et al., 2010:fig. 4]; *Aardonyx* [Yates et al., 2010]). In contrast, massospondylids such as *Massospondylus* (BP/1/5241), *Adeopapposaurus* (PVSJ 610), and *Leyesaurus* (PVSJ 706), have a maximum transverse width of the prefrontal

that is less than 25% of the skull width. This condition is not unique to massospondylids, because it is also found in *Pantydraco* (Yates, 2003a) and *Yunnanosaurus* (Barrett et al., 2007: fig. 4). Although the condition of *Coloradisaurus* is not identical to that of plateosaurids, the presence of a broad prefrontal more closely resembles the plateosaurid condition than that of massospondylids. This feature has been included in the phylogenetic data set (Apaldetti et al., 2013:character 45), and the presence of a broad prefrontal (maximum transverse width more than 0.25 of the skull width at that level) is most parsimoniously interpreted as convergently acquired by *Coloradisaurus*, *Plateosaurus engelhardti*, *Sarhsaurus*, and *Aardonyx* and more derived forms (e.g., *Melanorosaurus*).

Infratemporal Fenestra behind the Orbit—The infratemporal fenestra of basal sauropodomorphs has an hourglass-shaped outline with the dorsal end anteroposteriorly narrower than the ventral end. In most basal sauropodomorphs, the anteroventral margin of this fenestra extends underneath the posterior half of the orbit (e.g., *Riojasaurus*, PULR 56, PVSJ 849; *Massospondylus*, BP/1/4934; *Adeopapposaurus*, PVSJ 610; *Lufengosaurus*; *Leyesaurus*; *Sarhsaurus*; *Yunnanosaurus*; *Aardonyx*). In other basal sauropodomorphs, such as plateosaurids, the anteroventral margin of the infratemporal fenestra does not reach the posterior margin of the orbit (e.g., *Efraasia* and *Plateosaurus* [Yates, 2003b]; *Melanorosaurus*). A further modification of this feature is found in *Anchisaurus* and eusauropods (Yates, 2004), in which the anteroventral region of the infratemporal fenestra extends anteriorly as far as the midlength of the orbit.

In PVL 3967, the anteroventral margin of the infratemporal fenestra is preserved on both jugals where the ascending postorbital process diverge from the posterior process. The morphology of the jugal indicates that the infratemporal fenestra did not extend underneath the orbit in *Coloradisaurus*, resembling the condition of plateosaurids (Fig. 8A). This feature has been included in the phylogenetic data set (Apaldetti et al., 2013:character 57), and the position of the anterior margin of the infratemporal fenestra behind the orbit is most parsimoniously interpreted as a reversal in *Coloradisaurus* to the condition found in non-massopodan sauropodomorphs.

Stepped Braincase—Three major conditions have been recognized in the arrangement of the elements of the braincase in lateral view among sauropodomorphs (Galton, 1985, 1990; Yates and Kitching, 2003). Basal sauropodomorphs (e.g., *Massospondylus carinatus*, BP/1/4376; *Adeopapposaurus*, PVSJ 568; *Leyesaurus*, PVSJ 706; *Sarhsaurus*) have a horizontal ventral margin of the braincase, with the occipital condyle, basal tubera, the base of basiptyergoid processes, and parasphenoid rostrum almost aligned in lateral view. This condition is also present in the most basal sauropodomorphs, such as *Thecodontosaurus* and *Saturnalia* (Yates, 2004), suggesting that it represents the plesiomorphic condition of the group. However, PVL 3967 shares with *Plateosaurus* (AMNH 6810) and *Lufengosaurus* (Galton, 1990; Barrett et al., 2005) the presence of a stepped floor of the braincase, because the bases of the basiptyergoid processes and the parasphenoid rostrum are set below the level of the basal tubera and the ventral margin of the basioccipital condyle (Fig. 6). The third braincase morphology is present in derived sauropodomorphs (eusauropods), in which the parasphenoid rostrum is approximately level with the ventral margin of the occipital condyle and well above the level of the bases of the basiptyergoid processes (Yates, 2010). This feature has been included in the phylogenetic data set (Apaldetti et al., 2013:character 81), and the presence of a stepped floor of the braincase is most parsimoniously interpreted as convergently acquired by plateosaurids (i.e., *Plateosaurus* and *Unaysaurus*), *Sarhsaurus*, and the *Lufengosaurus* + *Coloradisaurus* clade within Massospondylidae.

Septum Spanning the Basipterygoid Space—The ventral surface of the basisphenoid of *Plateosaurus* (e.g., AMNH 6810) has a bony transverse wall that extends between the basipterygoid processes. This median wall is a stout rectangular process that projects ventrally. A well-developed and robust septum is absent in all other basal sauropodomorphs and has been regarded as diagnostic of *Plateosaurus* (Galton, 1990, 2001; Yates 2003b; Prieto-Márquez and Norell, 2011).

However, other basal sauropodomorphs have an interbasipterygoid septum that spans the bases of the basipterygoid processes. This transverse wall is shallow and not as developed as in *Plateosaurus*. This condition is present in *Efraasia*, *Anchisaurus* (YPM 209; Fedak and Galton, 2007), and *Sarahsaurus*. PVL 3967 also has a median septum between the basipterygoid processes that forms the anterior wall of the median fossa of the ventral surface of the basisphenoid. Massospondylids (including *Lufengosaurus*) lack this septum, differing from the condition in the above-mentioned taxa. This feature has been included in the phylogenetic data set (Apaldetti et al., 2013:character 85), and the presence of a septum between the basipterygoid processes is most parsimoniously interpreted as convergently acquired by the previously mentioned taxa and *Coloradisaurus* (Fig. 6C).

Finally, the two postcranial characters related to the plateosaurid condition are discussed in Apaldetti et al. (2013).

Plateosaurid Skull Characters Originally Proposed by Bonaparte (1978)—Among those characters proposed by Bonaparte (1978) as diagnostic of *Coloradisaurus brevis*, three of them are not exclusive of this taxon and resemble the condition found in plateosaurids: broad ascending process of the maxilla (discussed above), the extension of the antorbital fossa underneath the orbit, and the low mandibular articulation.

Bonaparte (1978) noted that the base of the lacrimal of PVL 3967 was posteroventrally directed so that the antorbital fossa extended underneath the orbit (Fig. 8A). This resembles the condition of *Plateosaurus* (AMNH 6810), and possibly *Yunnanosaurus* (Barrett et al., 2007:fig. 2; although this latter skull is eroded), in which there is a posterior projection of the posteroventral corner of the antorbital fossa under the anterior region of the orbit. Other basal sauropodomorphs have the antorbital fenestra completely anterior to the anterior margin of the orbit (e.g., *Pantyraco* [Yates, 2004:fig. 2], *Massospondylus* [Sues et al., 2004:figs. 1, 5, 7], *Lufengosaurus* [Barrett et al., 2005:fig. 1], *Melanorosaurus* [Yates, 2007:fig. 6]).

Several recently discovered basal sauropodomorph taxa have morphologies that create difficulties in the definition of this character for its use in phylogenetic analyses. For instance, there are several basal sauropodomorphs in which the posteroventral corner of the antorbital fenestra has an intermediate position, where it is not possible to define precisely its posterior extension (e.g., *Unaysaurus* [Leal et al., 2004:fig. 2], *Adeopapposaurus*, PVSJ 610; *Leyesaurus* [Apaldetti et al., 2011:fig. 3]). Furthermore, in some of the specimens of *Plateosaurus* (e.g., SMNS 13200), the posteroventral corner of the antorbital fossa also has an intermediate condition, suggesting that this character may be subject to intraspecific variation (either ontogenetic, sexual, or individual). In sum, the posteroventral projection of the antorbital fossa underneath the orbit is an undeniable similarity between *Coloradisaurus* and some specimens of *Plateosaurus*, as originally noted by Bonaparte (1978). However, the presence of multiple taxa with intermediate morphologies, as well as the recognition of intraspecific variation in *Plateosaurus*, led to the exclusion of this feature in recently published phylogenetic data sets (e.g., Upchurch et al., 2007; Yates et al., 2010; Apaldetti et al., 2013).

Bonaparte (1978) observed that the mandibular articulation of *Coloradisaurus* was notably low and even more ventrally offset than in *Plateosaurus*, and proposed this feature as diagnostic for *Coloradisaurus*. Actually, a low mandibular articulation is a generalized feature among basal sauropodomorphs, namely, a jaw

joint set well below to the level of the dorsal margin of the dentary (e.g., *Efraasia*; *Plateosaurus*, SMNS 13200, AMNH 6810; *Unaysaurus*, UFSM 11069; *Lufengosaurus*; *Sarahsaurus*; *Anchisaurus*, YPM 1883; *Melanorosaurus*). Only a few basal sauropodomorphs have a much higher mandibular articulation so that the joint lies above the dorsal margin of the dentary. This condition is present in *Riojasaurus* (PULR 56, PVSJ 849), *Yunnanosaurus*, and the massospondylids *Massospondylus* (BP/1/4934, 4779), *Adeopapposaurus* (PVSJ 610), and *Leyesaurus* (PVSJ 706).

Finally, based on the observations and interpretations herein, the low position of the mandibular articulation in PVL 3967 is not much more depressed than in *Plateosaurus*; therefore, this condition is not diagnostic of *Coloradisaurus* (Fig. 8A). However, the condition present in *Coloradisaurus* resembles that of plateosaurids and differs from those of most massospondylids.

CONCLUSIONS

Coloradisaurus brevis has been known for 35 years, but its craniomandibular anatomy has been only briefly described (Bonaparte, 1978) and its affinities have been controversial. This contribution describes in detail the craniomandibular anatomy of the holotype specimen and complements a recent study on the postcranium of a referred specimen (Apaldetti et al., 2013). Careful comparisons of PVL 3967 with other taxa reveal the presence of autapomorphic skull features, some of which were originally noted by Bonaparte (1978): circular upper temporal fenestrae, lamina on the ventrolateral margins of the ventral fossa of the basisphenoid, triangular lamina on the ventral surface of the parasphenoid, and tab-like medial process at the posterior end of the mandible.

This new information allows a more complete diagnosis of this taxon, providing additional information on its phylogenetic placement among basal sauropodomorphs. As a result of this study, we identified conflicting phylogenetic signals in the cranial anatomy of *Coloradisaurus*, with some characters showing similarities to those of plateosaurids and others resembling the conditions seen in massospondylids. Many postcranial features, however, support the placement of *Coloradisaurus* within Massospondylidae; therefore, this taxon is most parsimoniously interpreted as belonging to this group. Within this context, *Coloradisaurus* is interpreted as having acquired convergently several characters that are otherwise known only in plateosaurids, highlighting the conflicting patterns of character distribution (homoplasy) among basal sauropodomorphs.

ACKNOWLEDGMENTS

We are indebted to J. Powell for allowing the study of PVL 3967. Access to specimens was provided by J. Powell (PVL), E. Vaccari and G. Cisterna (PULR), Á. Da Rosa (UFSM), R. Wild (SMNS), S. Kaal (SAM), M. Norell (AMNH), J. Gauthier (YPM), B. Rubidge and A. Yates (BPI), R. Nuttal and E. Butler (NM QR), and X. Xu (IVPP). Some collection visits were funded by a Jurassic Foundation grant (to C.A.). P. Falkingham is thanked for his help with photogrammetric reconstruction software. We thank J. Carballido for his comments and suggestions on the early stage of the manuscript. The reviewers (P. Galton and A. Yates) and P. Barrett (editor) are thanked for their input that improved the quality of the manuscript.

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Submitted January 22, 2013; revisions received October 16, 2013; accepted October 19, 2013.
Handling editor: Paul Barrett.