



## THE POSTCRANIAL ANATOMY OF *COLORADISAURUS BREVIS* (DINOSAURIA: SAUROPODOMORPHA) FROM THE LATE TRIASSIC OF ARGENTINA AND ITS PHYLOGENETIC IMPLICATIONS

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**Abstract:** Basal sauropodomorphs from the Upper Triassic Los Colorados Formation of north-western Argentina have been known for several decades but most of them are only briefly described. New postcranial remains of *Coloradisaurus brevis*, the most gracile sauropodomorph from this unit, are described here and evaluated within a phylogenetic context. These materials belong to a single individual and include elements of the vertebral column, pectoral girdle, incomplete forelimb, pelvis and hindlimb. These elements share an autapomorphic feature with the type specimen of *Coloradisaurus brevis* and provide novel and unique features that diagnose this taxon, such as pubic apron with semicircular cross-section and with a depression on its anterior surface, distal

surface of the tibia deflected and facing posterodistally and well-developed pyramidal dorsal process of the posteromedial corner of the astragalus. Several postcranial characters of *Coloradisaurus* are exclusively shared with *Lufengosaurus*, from the Lower Jurassic of China. The inclusion of this information in two recent phylogenetic data sets depicts *Coloradisaurus* as closely related to *Lufengosaurus* and well nested within Plateosauria. Both data sets used indicate strong character support for the inclusion of *Coloradisaurus* and *Lufengosaurus* within Massospondylidae.

**Key words:** Triassic, Los Colorados, Sauropodomorpha, Massospondylidae, Plateosauria, phylogeny.

BASAL sauropodomorphs were globally widespread dinosaurs and dominated the large herbivorous fauna from the Late Triassic until Early Jurassic (Serenó 1997, 1999; Galton and Upchurch 2004). In South America, this group includes both basal forms (e.g. *Saturnalia*, *Panphagia* and *Chromogisaurus*) and more derived taxa near to the origin of Sauropoda (e.g. *Mussaurus*, *Leoneosaurus*; Langer *et al.* 1999; Martínez and Alcober 2009; Pol and Powell 2007a; Ezcurra 2010; Pol *et al.* 2011). The highest diversity and abundance of basal sauropodomorphs in the Late Triassic of South America is present in the Ischigualasto-Villa Union Basin in north-western Argentina. Sauropodomorphs of this basin include the oldest basal sauropodomorphs *Panphagia protos* (Martínez and Alcober 2009) and *Chromogisaurus novasi* (Ezcurra 2010) from the Carnian levels of the Ischigualasto Formation (Rogers *et al.* 1993; Martínez *et al.* 2011). The overlying Los Colorados Formation (Norian–Rhaetian; Bonaparte 1972)

includes remains of four sauropodomorph taxa: *Riojasaurus incertus* (Bonaparte 1972; Bonaparte and Pumares 1995), *Lessemsaurus sauropoides* (Bonaparte 1999; Pol and Powell 2007b), *Coloradisaurus brevis* (Bonaparte 1978) and a partially preserved unnamed form (PULR 136, Ezcurra and Apaldetti 2011).

*Coloradisaurus brevis* was originally named *Coloradia brevis* (Bonaparte 1978) and later renamed *Coloradisaurus brevis* by Lambert (1983) given the genus *Coloradia* was preoccupied. The original description of *Coloradisaurus* was mainly based on the skull anatomy of the holotype specimen (PVL 3967), and the presence of isolated postcranial remains was only briefly mentioned (Bonaparte 1978). *Coloradisaurus* was originally referred to Plateosauridae (*sensu* Galton and Cluver 1976) and more specifically as closely related to *Plateosaurus* and *Lufengosaurus*. The affinities of *Coloradisaurus* and *Lufengosaurus* were supported by subsequent studies, although the phylogenetic position

of these two taxa have been regarded as more closely related to *Plateosaurus* than to *Massospondylus* by some authors (Serenio 1999; Galton and Upchurch 2004; Barrett *et al.* 2005; Upchurch *et al.* 2007; Martinez 2009), whereas others authors retrieved *Coloradisaurus* and *Lufengosaurus* as more closely related to *Massospondylus* than to *Plateosaurus* (Yates 2003a, 2004, 2007a, b; Smith and Pol 2007; Sertich and Loewen 2010; Ezcurra 2010).

An articulated postcranial skeleton (PVL 5904, previously reported as field # 6, Yates 2004, 2007a) discovered in the upper section of Los Colorados Formation by José Bonaparte in 1973 is here described and referred as the second known specimen of *Coloradisaurus brevis*. The new information increases our knowledge on the anatomy of *Coloradisaurus brevis* and contributes to understanding the relationships of *Coloradisaurus* within basal sauro-podomorphs.

*Institutional abbreviations.* LV, Museum of Lufeng Dinosaurs, Jingshan, Yunnan Province, China; PVL, Instituto Miguel Lillo, Tucumán, Argentina; PVSJ, Museo de Ciencias Naturales, San Juan, Argentina; UFSM, Universidade Federal de Santa Maria, Santa Maria, Rio Grande do Sul, Brazil.

*Comparative data.* The comparisons with other sauro-podomorphs made in the description were based on the previous publications and on personal observation of specific taxa detailed in Table 1. Except in those cases where the source is

**TABLE 1.** Source of comparative data used in this study.

Taxon and source
<i>Adeopapposaurus mognai</i> , Martinez 2009
<i>Anchisaurus polyzelus</i> , Yates 2004
<i>Antetonitrus ingenipes</i> , Yates and Kitching 2003
<i>Blikanasaurus cromptoni</i> , Galton and Van Heerden, 1998
<i>Glacialisaurus antartica</i> , Smith and Pol 2007
<i>Jingshanosaurus xinwaensis</i> , Zhang and Yang 1994
<i>Lessemsaurus sauropoides</i> , Bonaparte 1999; Pol and Powell 2007b
<i>Leyesaurus marayensis</i> , Apaldetti <i>et al.</i> 2011
<i>Lufengosaurus huenei</i> , Young 1941
<i>Massospondylus carinatus</i> , Cooper 1981
<i>Melanorosaurus readi</i> , Heerden and Galton 1997; Bonnan and Yates 2007
<i>Panphagia protos</i> , PVSJ 874, Martinez and Alcober 2009
<i>Pantydraco caducus</i> , Yates 2003a; Galton <i>et al.</i> 2007
<i>Plateosaurus engelhardti</i> , Galton 2000, 2001; Moser 2003; Yates 2003b
<i>Riojasaurus incertus</i> , PVL 3808; Bonaparte, 1972
<i>Sarahsaurus aurifontanalisis</i> , Rowe <i>et al.</i> 2010
<i>Saturnalia tupiniquim</i> , Langer <i>et al.</i> 1999, 2007; Langer 2003
<i>Seitaad ruessi</i> , Sertich and Loewen 2010
<i>Thecodontosaurus antiquus</i> , Benton <i>et al.</i> 2000
<i>Unaysaurus tolentinoi</i> , Leal <i>et al.</i> 2004
<i>Vulcanodon karibaensis</i> , Cooper 1984
<i>Yunnanosaurus huangi</i> , Young 1942

specified, all the other references are based on the literature listed in this table.

*Anatomical abbreviations.* acf, acromial fossa; acp, acromion process; alp, anterolateral process; apr, pubic apron; ars, articular surface of metacarpal III; asp, ascending process; cas, concavity of the posterior surface of the ascending process; cdf, centrodiapophyseal fossa; cf, cuboid fossa; cof, coracoid foramen; cot, coracoid tubercle; cn, cnemial crest; D11–D12, dorsal vertebra 11 and 12; dep, lateral depression of dorsal centrum; di, diapophysis; dpc, deltopectoral crest; dsp, distal surface of the pubic blade; epi, epipophysis; eps, entepicondylar surface; exf, extensor fossa; fas, fossa of the base of ascending process; fdp, facet for descending process of the tibia; fhe, femoral head; gl, glenoid; ias, iliac articular surface; ibl, iliac blade; ilp, iliac peduncle; isp, ischial peduncle; it, internal tuberosity; lc, lateral condyle; lco, lateral concavity; lt, lesser trochanter; mc, medial condyle; mt, metatarsal; nc, neural canal; nis, notch of the ischial acetabular margin; ns, neural spine; of, obturator foramen; opp, proximal opening of the pubic apron; pa, parapophysis; pap, base of the preacetabular process; pas, pubic articular surface; pcld, posterior centrodiapophyseal lamina; pdp, proximal depression of the pubic apron; pip, proximal ischial plate; plp, posterolateral process; pnc, posteromedial corner; pocdf, postzygodiapophyseal fossa; podl, postzygodiapophyseal lamina; pof, popliteal fossa; pop, base of the postacetabular process; poz, postzygapophysis; ppl, pubic plate; prcdf, prezygodiapophyseal fossa; prdl, prezygodiapophyseal lamina; prz, prezygapophysis; ptb, pubic tuberosity; pup, pubic peduncle; sac, supracetabular crest; rc, radial condyle; spol, spinopostzygapophyseal lamina; sprl, spinoprezygapophyseal lamina; sul, sulcus; tfc, tibiofibular crest; tub, rugose tuberosities of the dorsal end of the scapula; uc, ulnar condyle; 4t, fourth trochanter; I–V, pedal digits I to V.

## SYSTEMATIC PALAEOLOGY

SAURISCHIA Seeley, 1887

SAUROPODOMORPHA von Huene, 1932

Genus COLORADISAURUS Lambert, 1983

*Type species.* *Coloradisaurus brevis* (Bonaparte, 1978).

*Diagnosis.* As for the type and only species.

*Coloradisaurus brevis* (Bonaparte, 1978)

Figures 1–16

- 1978 *Coloradia brevis* Bonaparte, p. 327, figs 1–3.  
 1983 *Coloradisaurus brevis* Lambert, p. 102.  
 1990 *Coloradisaurus brevis* Galton, p. 336, figs 15.3G–H, 15.4C.  
 2004 *Coloradisaurus brevis* Galton and Upchurch, p. 234, figs 12.3G–H, 12.5C.  
 2007a *Coloradisaurus brevis* Yates, p. 33.

*Holotype.* PVL 3967. Skull and mandible found in articulation with the atlas-axis and C3, 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 manual nonterminal and ungual phalanges, right astragalus and calcaneum, distal tarsal and pedal unguals.

*Referred material.* PVL 5904 (field number #6), a partially articulated postcranial skeleton including a single anterior cervical vertebra (C3 or C4), an almost complete dorsal series (D2–D13), an isolated anterior caudal, and two fused midcaudals, complete left scapula and coracoid, isolated right coracoid, right humerus, left metacarpal III, partial left ilium, articulated pubes, right ischium, both femora, both tibiae, proximal third of the left fibula, left astragalus, a medial left distal tarsal and complete left pes.

*Locality and horizon.* Both specimens were found by Bonaparte in the upper section of Los Colorados Formation (Groeber and Stipanovic 1953), commonly regarded as Norian–Rhaetian age (Bonaparte 1972) or tetrapod-based biochron late Coloradian (Bonaparte 1973). The holotype and the specimen described here were found in La Esquina locality, located south of Pagancillo village, La Rioja Province, Argentina.

*Revised diagnosis.* A medium-sized basal sauropodomorph diagnosed by the following unique combination of characters (autapomorphies indicated with an asterisk): preorbital region shorter than in *Lufengosaurus-Plateosaurus*, with the frontal proportionately long; posteroventral corner of antorbital fossa projecting underneath the orbit; broad ascending process of the maxilla; circular upper temporal fenestrae\*; tall, thin bony laminae forming the ventrolateral margins of a deep, ventrally opening fossa on the basisphenoid\*; triangular bony laminae extend from the basiptyergoid processes to the ventrolateral margins of the parasphenoid rostrum\*; dorsoventrally low mandibular ramus; tab-like medial process at the posterior tip 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\* (a similar, although proximodistally more elongate anterior fossa is present on the pubic apron of *Jingshanosaurus* (LV03; AY, pers. obs.), but the fossa of *Jingshanosaurus* differs as it gradually merges with the lamina of the distal pubic apron); semi-circular cross-section of pubic apron, creating a deep trough along posterior surface of pubic apron\*; postero-medial region of the distal surface of the tibia deflected and facing posterodistally\*; pyramidal dorsal process of the posteromedial corner of astragalus almost as high as ascending process\*.

*Remarks.* Two other named species of basal sauropodomorphs are known from the upper section of the Los Colorados Formation, *Riojasaurus incertus* and *Lessemsaurus*

*sauropoides*, as well as a fragmentary material that represents a different sauropodomorph (Ezcurra and Apaldetti 2011). The former is known from several specimens described by Bonaparte (1972), and the latter is known from an assemblage of postcranial remains described by Bonaparte (1999) and Pol and Powell (2007b). The postcranial remains of PVL 5904 share derived and autapomorphic features with the fragmentary postcranium of the type specimen of *Coloradisaurus brevis* (e.g. pyramidal dorsal process of the postero-medial corner of astragalus almost as high as ascending process). These shared characters are used as the basis for referring PVL 5904 to *C. brevis*. The morphology of the material described here (PVL 5904) is also congruent in its morphology with other fragmentary postcranial material of the holotype of *C. brevis* (cervical and dorsal vertebrae, distal humerus and proximal region of the scapula), although these are similarities in generalized characters of basal sauropodomorphs. The only difference observed between PVL 5904 and the type specimen of *C. brevis* is the absence of a ventral keel in the cervical vertebra in the former specimen, which is interpreted as an individual variation but could also be caused by the delamination present on the outer surface of the bones of PVL 5904.

Furthermore, PVL 5904 can be distinguished from the two other named sauropodomorph taxa from the Los Colorados Formation based on the following postcranial characters. All material of *Lessemsaurus sauropoides* differs from PVL 5904 in having relatively shorter cervical vertebrae and dorsoventrally higher dorsal neural arches, remarkably broad ventral and dorsal expansions of the scapula, a short and robust scapular shaft, a low angle of the acromion, reduced proximal expansion of the humerus with a poorly developed internal tuberosity, a deltopectoral crest extending <0.4 times the humeral length, a less-developed supracetabular crest, lack of a posterior heel on the ischiadic peduncle of the ilium, a relatively shorter and broader pubic apron, the absence of a proximal tuberosity on the anterior margin of the pubic plate, an obturator foramen of the pubis that is completely visible in anterior view, an astragalus lacking an anteroposteriorly expanded medial region and a pyramidal process, and an articular surface of the ascending process of the astragalus that is not anteriorly deflected. *Riojasaurus incertus* differs from the postcranial remains of PVL 5904 in having relatively shorter cervical centra, a more developed dorsal expansion of the scapula and a lower angle of the acromion process, a straight dorsal margin of the humerus, a much broader pubic apron with straight lateral margins, the absence of a proximal tuberosity in the anterior margin of the pubic plate, an obturator foramen of the pubis that is completely visible in anterior view, a poorly expanded distal end of the pubis, a much broader lesser trochanter in the femur and the absence of a dorsal pyramidal process in the postero-

medial corner of the astragalus. The available remains of the recently described sauropodomorph from this unit (PULR 136; Ezcurra and Apaldetti 2011) are distinguished from the material of *C. brevis* described here by the presence of a remarkably robust tibia which has a relatively lower ratio of the proximodistal length to the anteroposterior depth of the proximal end, a more proximally projected lateral condyle lacking ventral deflection, the medial condyle projects further posteriorly than the lateral one, lateral surface of the proximal tibia lacks an elongated concavity, the distal end of the tibia anteroposteriorly wider and more transversely expanded than the proximal end, the posterolateral process of the distal end of the tibia less laterally expanded, and the presence of a shallower notch for the articulation of the astragalus ascending process on the lateral margin of the distal end of the tibia.

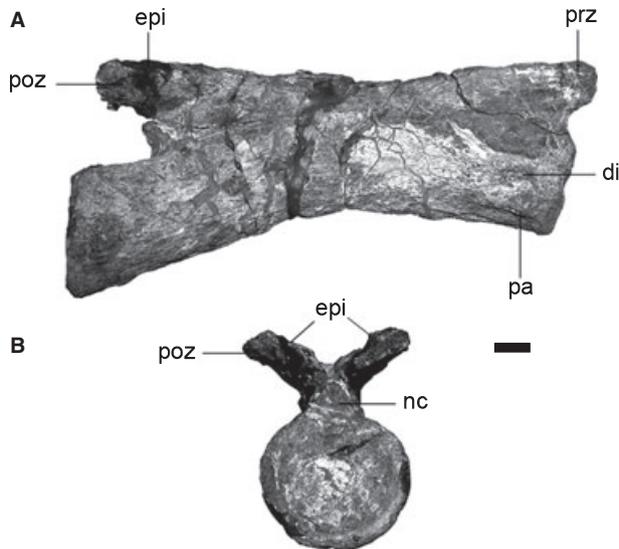
#### Description

The following description is primarily based on the articulated skeleton PVL 5904 but specific comments and comparisons are made with the fragmentary postcranial material of the holotype (PVL 3967) that allows the identification of PVL 5904 as *Coloradisaurus brevis*.

#### Vertebral column

The holotype (PVL 3967) includes the atlas-axis which is articulated with the third cervical vertebra, plus other three disarticulated cervical vertebrae (probably C4–C6) and two disarticulated anterior dorsal vertebrae. PVL 5904 has only a single anterior cervical vertebra that lacks part of the neural arch. This element can be identified as either a C3 or a C4 based on the position of the parapophysis and diapophysis and the length/height ratio of the centrum. PVL 5904 also has an almost complete and articulated dorsal series (D2–D13), an isolated anterior caudal, and two midcaudal vertebrae that are fused to each other along their articular surfaces forming a pathologic callus. In their general proportions, the vertebrae of *Coloradisaurus* are more gracile and slender than those of the other sauropodomorphs known from the Los Colorados Formation (i.e. *Riojasaurus* and *Lessem-saurus*).

**Cervical vertebrae.** The only cervical preserved in PVL 5904 is an anterior cervical vertebra identified here as a third or fourth element. This cervical vertebra has a low and remarkably elongated centrum, with a length/height ratio of 4.5 (Fig. 1). The cervical centrum of PVL 5904 is slightly larger than in massospondylids (e.g. *Massospondylus*, *Lufengosaurus* and *Adeopapposaurus*), which have a length/height ratio close to 4. In other sauropodomorphs, this ratio is usually close to 3 (e.g. *Plateosaurus* and *Riojasaurus*), but *Leyesaurus* has an extremely elongated cervical vertebrae with a length/height ratio of 5 (Apaldetti *et al.*



**FIG. 1.** Cervical vertebra of *Coloradisaurus brevis* (PVL 5904). A, right lateral view. B, posterior view. Scale bar represents 1 cm.

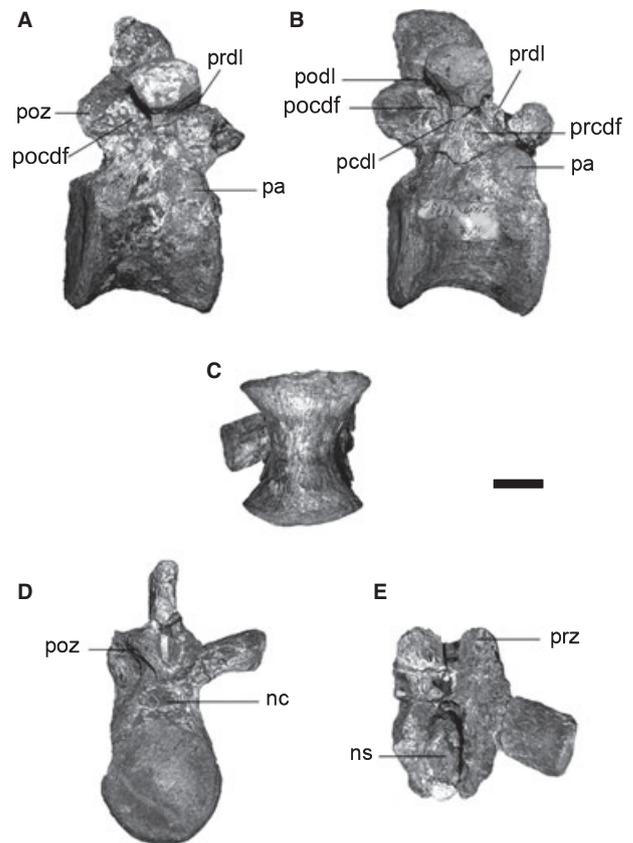
2011). The type specimen of *Coloradisaurus brevis* (PVL 3967) has a proportionately shorter C3, with a length/height ratio of 3.8. This specimen, however, is smaller than PVL 5904, and therefore, we interpret this difference as ontogenetic because of the positive allometry recognized for basal sauropodomorphs (Reisz *et al.* 2005). The articular surfaces of the cervical vertebra of PVL 5904 are amphicoelous and subcircular (Fig. 1B), being approximately as high as wide. The anterior articular surface of the centrum is dorsoventrally lower than the posterior one, being approximately 0.81 times the height of the posterior surface. The ventral surface of the anterior cervical centrum in PVL 5904 is rounded and lacks a sagittal ventral keel. All cervical vertebrae of the holotype of *C. brevis* (PVL 3967) have a slightly developed ventral keel, which is present at least along the anterior half of the centrum in C3. The absence of a ventral keel in PVL 5904 is the only anatomical difference with the holotype. The parapophyses are a low, elongated and located close to the anterior margin of the centrum, bearing a short ridge running posteriorly from it. The diapophyses are small and located right above the parapophyses (Fig. 1A), as in the C3 and C4 of other basal sauropodomorphs (e.g. *Plateosaurus*, *Riojasaurus*). The zygapophyses of the anterior cervical extend parallel to the anteroposterior axis of the centra. The prezygapophyses extend slightly beyond the anterior margin of the centrum, but the postzygapophyses do not extend posterior to the posterior margin of the centrum. The articular facets of the pre- and postzygapophyses face dorsomedially and lateroventrally, respectively, forming an angle of approximately 40 degrees with the longitudinal plane. The epiphysis of this vertebra is a low ridge that extends along the dorsal surface of the postzygapophyses. Although the posterior end of the postzygapophyses is damaged, the posterior end of the right epiphysis decreases in height and does not seem to extend beyond the rear margin of the postzygapophyses, as occurs in some basal sauropodomorphs (e.g. *Panphagia*, *Plateosaurus*, *Massospondylus*, *Adeopapposaurus*, *Yunnanosaurus*

and *Sarhsaurus*). The neural spine of the anterior cervical is broken at its base.

**Dorsal vertebrae.** Twelve dorsal vertebrae are preserved in PVL 5904, including two disarticulated anterior dorsals, a series of five articulated anterior to middle dorsal vertebrae and a series of five articulated middle to posterior dorsals. The two anterior vertebrae are interpreted as D2 and D3, the first series of articulated elements is interpreted as D4–D8, and the second set of dorsals is interpreted as D9–D13 based on comparisons of the position of the parapophysis relative to the neurocentral suture and the diapophysis with articulated dorsal series of other basal sauropodomorphs (e.g. *Adeopapposaurus* and *Plateosaurus*).

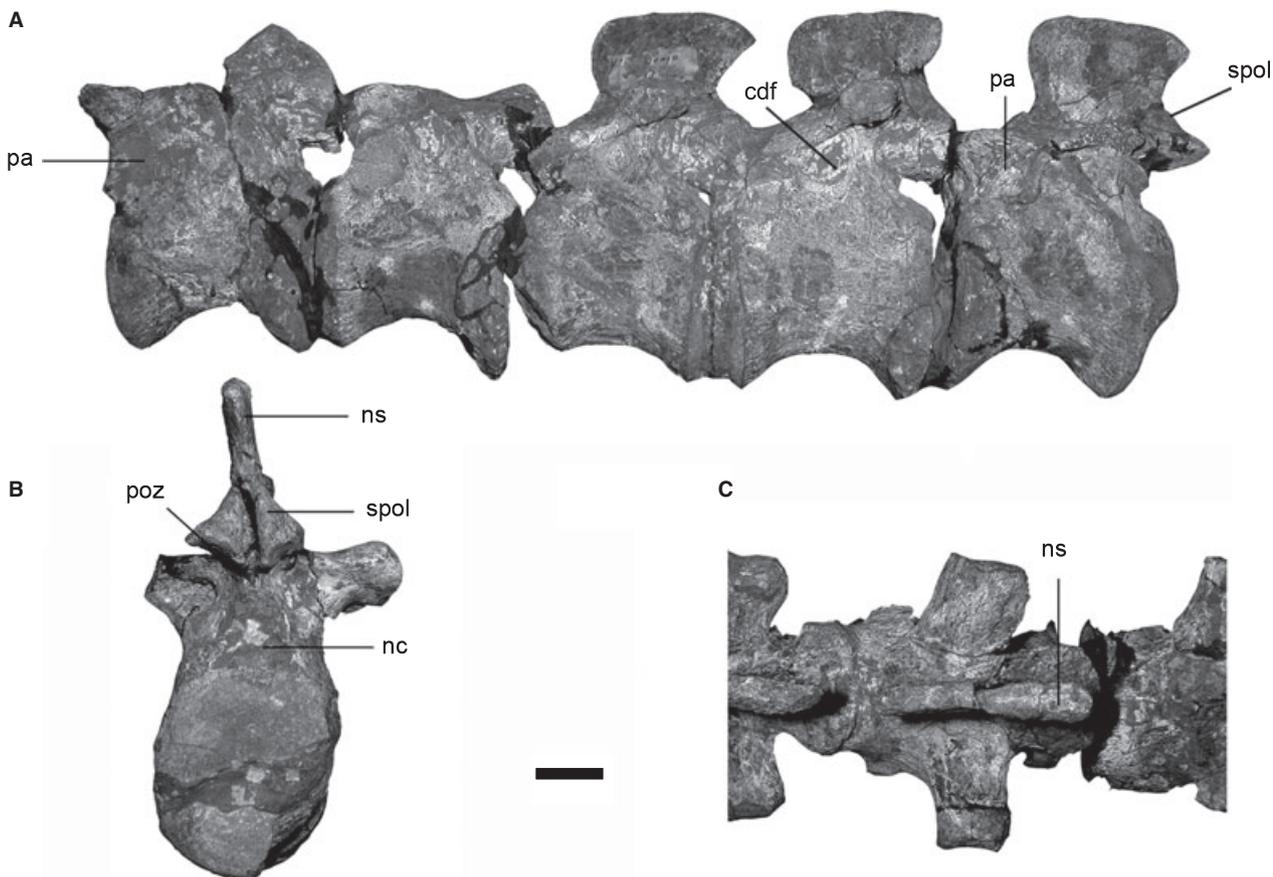
All dorsal centra are amphicoelous and have a markedly constricted ventral surface. The constriction of the dorsal centra becomes more pronounced posteriorly (Figs 3A and 4A), as in most non-sauropod sauropodomorphs. The lateral surfaces of the dorsal centra are slightly concave and lack a distinct depression or pleurocoel, except for the posteriormost dorsal (D13). This vertebra has a distinct and deep depression on the lateral surface of the centrum, below the neurocentral suture (Fig. 4A). This deep depression is imperforate and therefore lacks a true pleurocoel. The anteroposterior length and transversal width of the dorsal centra slightly increase along the dorsal series, and the height of the anterior articular surface is only slightly larger than that of the posterior articular surface (Figs 2A–B, 3A and 4A), as in other basal sauropodomorphs (e.g. *Adeopapposaurus*, *Yunnanosaurus* and *Lessemsaurus*). This contrasts with the condition in *Massospondylus* in which the anterior articular surface is much higher dorsoventrally than the posterior surface (Cooper 1981). The anteroposterior length of the dorsal centra is subequal to the dorsoventral height (measured at the posterior articular surface), being 1.05 on anterior vertebrae and 0.96 on posterior dorsal vertebrae. These proportions are similar to those of other basal sauropodomorphs (e.g. *Riojasaurus*, *Plateosaurus*, *Lufengosaurus* and *Lessemsaurus*), but differ from the elongated dorsal vertebrae of massospondylids with a length/height ratio of approximately 1.5 (e.g. *Massospondylus* and *Adeopapposaurus*). The ventral surface of the dorsal centra of PVL 5904 lacks a sagittal keel (Fig. 2C), a feature also present in the anterior dorsal of the holotype (PVL 3967) of *C. brevis*. In contrast, the anterior dorsal vertebrae of all other basal sauropodomorphs are ventrally keeled (Yates 2007a). The parapophyses of D2 and D3 are teardrop shaped with a ventral acute end (Fig. 2A–B). The parapophysis of D2 is bisected by the neurocentral suture, whereas in D3 approximately 75 per cent of the articular surface of the parapophysis is located on the neural arch. The parapophyses of D4 are located at the anteroventral corner of the neural arch and are the first that are completely placed on the neural arch (Fig. 3A). Posteriorly along the dorsal series of PVL 5904, the parapophyses are ovoid to circular and gradually migrate posterodorsally to the neural arch. The parapophysis and diapophysis are almost in contact in D12, and in D13, they are connected to each other (Fig. 4A), as in other basal sauropodomorphs (e.g. *Massospondylus*).

The neural arches of the dorsal series of PVL 5904 are dorsoventrally lower than their corresponding centrum, as in most non-sauropod sauropodomorphs, but different from some taxa in



**FIG. 2.** Anterior dorsal vertebrae of *Coloradisaurus brevis* (PVL 5904). A, D2 in right lateral view. B, D3 in right lateral view. C, D2 in ventral view. D, D2 in posterior view. E, D2 in dorsal view. Scale bar represents 2 cm.

which the neural arches are higher than the centra (e.g. *Adeopapposaurus* (PVSJ 610) and *Unaysaurus* (UFSM 11069)). *Lessemsaurus*, *Antetonitrus* and more derived forms have an extremely high neural arch that exceeds the centrum height (Yates 2007a). The neural spines are transversely thin and laminar and lack the dorsal spinal table present in other basal sauropodomorphs (e.g. *Plateosaurus*, *Massospondylus* and *Sarhsaurus*). The posteriormost preserved vertebrae have neural spines with a slightly broadened dorsal end, but even these spines lack the markedly broad spinal table present in *Plateosaurus* (Bonaparte 1999). The transverse width of the neural spines varies along the dorsal series, being lateromedially broader in D2–D3 than in the middle dorsals. Additionally, the two posteriormost preserved dorsals have relatively broader neural spines, as in D2–D3 (Figs 2–4). The anteroposterior length of the neural spine progressively increases from the D2 to the D10 and decreases posteriorly from this point (Figs 3 and 4). The neural spine of D2 is anteroposteriorly shorter at its base than its dorsoventral height, whereas the rest of the dorsal vertebrae have neural spines that are longer than high (Figs 2–4). A similar combination of characters in the neural spines of dorsal vertebrae is found in other basal sauropodomorphs, such as *Riojasaurus*, *Unaysaurus* (UFSM 11069)



**FIG. 3.** Anterior-mid dorsal vertebrae of *Coloradisaurus brevis* (PVL 5904). A, D4–D8 in lateral view. B, D8 in posterior view. C, D7 in dorsal view. Scale bar represents 2 cm.

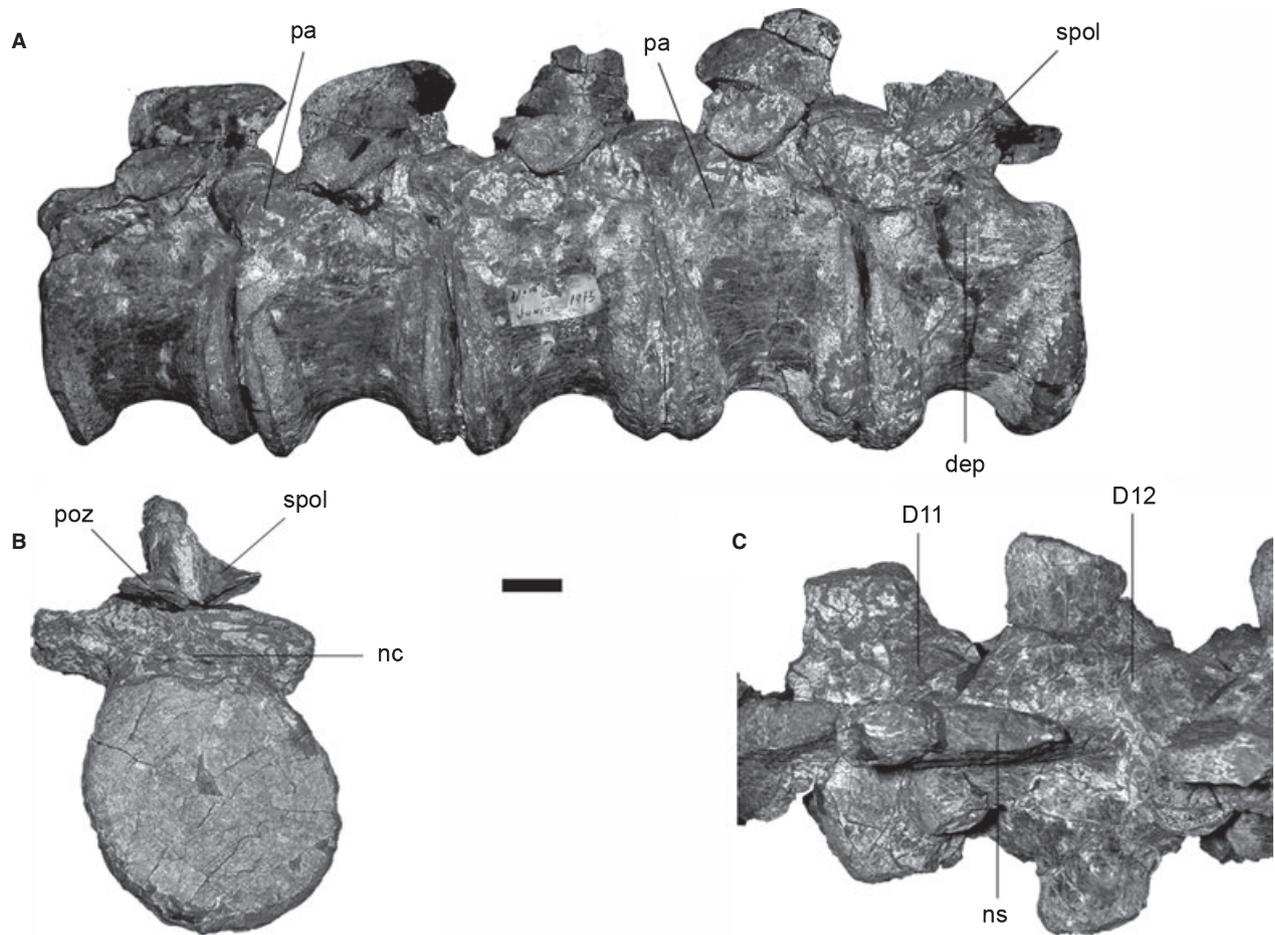
or *Adeopapposaurus* (PVSJ 610), but differs from the condition of most basal sauropodomorphs in which all dorsal vertebrae have longer than high neural spines (e.g. *Plateosaurus*, *Massospondylus*, *Lufengosaurus* and *Sarhsaurus*). In lateral view, the posterior margin of the neural spine of D2 and D3 are straight (Fig. 2A–B), whereas in D6 (and more posterior vertebrae), the posterior margin of the neural spine is markedly concave with the dorsal half of the posterior margin directed posterodorsally and ending in a pointed posterodorsal corner (Figs 3A and 4A). A similar condition has been noted for massospondylids and *Plateosaurus* by Yates (2007a).

The dorsal zygapophyses are short and stout. The prezygapophyses of D2 and D3 are directed anterodorsally with their articular facets facing dorsomedially and forming an angle of 45 degrees with the longitudinal plane. Posteriorly along the dorsal series, the prezygapophyses gradually change their orientation, facing horizontally in the middle to posterior dorsals. A corresponding change in orientation is present in the postzygapophyses. The articular surfaces of the zygapophyses also increase their curvature along the dorsal series. In D2, the articular facets are flat (Fig. 2D), whereas in D8 the articular facets of the postzygapophyses are concave (Fig. 3B). The posteriormost dorsals preserved in PVL 5904, however, have flat postzygapophyseal facets (Fig. 4B). The pre- and postzygapophyses extend beyond the anterior and posterior articular margins of the centra,

respectively. The zygapophyses of D2 extend anteriorly beyond the centrum for approximately 0.2 times the total centrum length, whereas in the last dorsal vertebrae this extension is slightly greater (approximately 0.33 times the total centrum length).

The transverse processes are located at the level of the antero-posterior midpoint of the centrum. They are slightly dorsolaterally directed in the anterior vertebrae (Fig. 2D) and horizontally oriented in posterior dorsal vertebrae (Fig. 4B). In dorsal view, the transverse processes are posteriorly directed in the anterior and middle vertebrae (Figs 2E and 3C) and laterally oriented on the posterior vertebrae (Fig. 4C). The transverse processes increase their anteroposterior length along the dorsal series, reaching their maximum development in the two posteriormost elements (Figs 3 and 4). These two vertebrae (D12 and D13) have robust transverse processes that are as long anteroposteriorly as they are broad lateromedially and have straight anterior and posterior margins (Fig. 4C).

The lamination of the dorsal vertebrae of PVL 5904 resembles that of most nonsauropod sauropodomorphs. The anterior dorsals (D2 through D5) have slightly developed prezygodiapophyseal, postzygodiapophyseal, paradiapophyseal and spinopostzygapophyseal laminae (Figs 2A–B and 3A–B). The posterior centrodiapophyseal lamina is well developed, and the spinoprezygapophyseal lamina is absent. The anterior middle dorsals

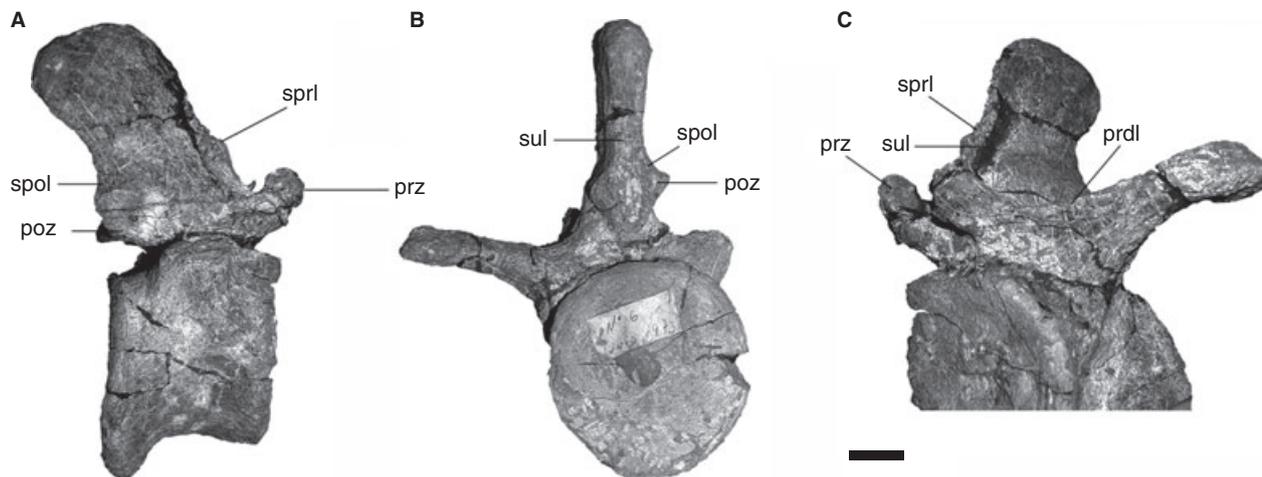


**FIG. 4.** Mid to posterior dorsal vertebrae of *Coloradisaurus brevis* (PVL 5904). A, D9–D13 in lateral view. B, D13 in posterior view. C, D12 in dorsal view. Scale bar represents 2 cm.

(D6 through D8) lack the prezygodiapophyseal lamina (Fig. 3A), and consequently, the prezygodiapophyseal fossa (sensu Wilson *et al.* 2011) is also absent in these vertebrae. Another change in these vertebrae is the reduction in the postzygodiapophyseal laminae (and the postzygodiapophyseal fossa) and the progressive development of the spinopostzygapophyseal laminae (Fig. 3A–B). The laminae of the posterior middle dorsals (D9 through D11) are further reduced, with a low and robust posterior centrodiapophyseal lamina and an extremely short paradiapophyseal lamina. The postzygodiapophyseal lamina is also markedly reduced in these vertebrae (Fig. 4A). These vertebrae have a slightly developed spinoprezygapophyseal lamina, which was absent in previous dorsals. In comparison with D9 to D11, the two posteriormost dorsals (D12 and D13) have remarkably reduced diapophyseal lamination (Fig. 4). The paradiapophyseal lamina is absent owing to the connection of the parapophysis and diapophysis, and the posterior centrodiapophyseal lamina and the postzygodiapophyseal lamina are barely developed. Given the reduction in the diapophyseal lamination, the centrodiapophyseal and postzygodiapophyseal fossae of these posterior dorsals are also significantly reduced in comparison with those of previous vertebrae. The spinopostzygapophyseal laminae are well developed in D12 and D13 and enclose a narrow spin-

opostzygapophyseal fossa (Fig. 4B). The presence or development of the spinoprezygapophyseal lamina, however, cannot be corroborated in these two vertebrae.

**Caudal vertebrae.** Only an anterior caudal vertebra (Fig. 5A–C) and two fused midcaudal vertebrae have been preserved in PVL 5904. The centrum of the anterior caudal is amphicoelous with strongly concave lateral and ventral surfaces. The dorsoventral height of the posterior articular surface is 1.13 times the depth of the anterior one, and both faces are subcircular (Fig. 5A–B). However, the dorsoventral height of the anterior articular surface is subequal to its lateromedial width, whereas the posterior surface is slightly higher than wide (height/width ratio = 1.07). The anteroposterior length of the centrum is slightly shorter than the height of the posterior and anterior articular surfaces (length/height ratio of 0.75 and 0.87, respectively). The ventral edge of the posterior articular surface is ventrally expanded, but lacks a well-developed facet for the articulation a chevron (Fig. 5A–B). The ventral surface of the centrum lacks a longitudinal furrow. The transverse processes are dorsolaterally directed and located at the anteroposterior midpoint of the centrum. They arise close to the dorsal surface of the centrum but are entirely placed on the neural arch (Fig. 5C). The proximal



**FIG. 5.** Caudal vertebra of *Coloradisaurus brevis* (PVL 5904). A, anterior caudal in lateral view. B, anterior caudal in posterior view. C, anterior caudal in anterolateral view. Scale bar represents 2 cm.

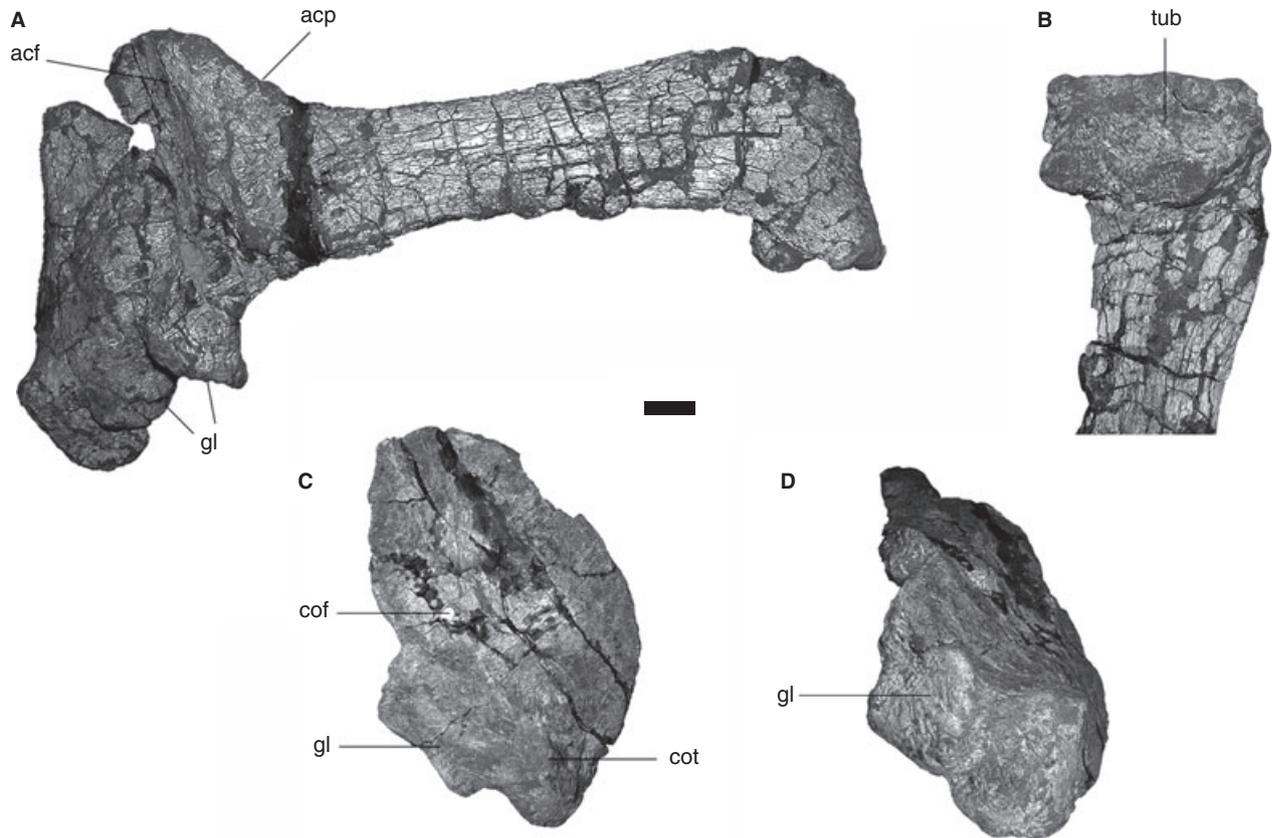
region of the transverse processes is dorsoventrally compressed with an oval cross-section. The anteroposterior length of the transverse process is 0.45 times the total length of the centrum. The prezygapophyses overhang the anterior margin of the centrum by 22 per cent of the total length of the centrum (Fig. 5A). The articular facets face dorsomedially at an angle of 60 degrees with the longitudinal plane. The prezygapophyses project anteriorly so that in lateral view they form an angle of approximately 30 degrees with the longitudinal axis of the centrum (Fig. 5A). The anterior caudal has well-developed spinoprezygapophyseal laminae that meet each other in the dorsal half of the anterior margin of the neural spine (Fig. 5A, C). These laminae enclose a narrow and deep sulcus that extends along the ventral half of the anterior margin of the neural spine (Fig. 5C). The prezygapophyses are connected to the transverse process by a well-developed prezygodiapophyseal lamina that overhangs a deep triangular fossa that faces anterolaterally on the neural arch (Fig. 5C). The postzygapophyses are short and located at the base of the neural spine (Fig. 5B). Their articular facets are sub-oval to subtriangular in shape and face lateroventrally forming an angle of 55 degrees with the longitudinal plane. In lateral view, the postzygapophyses do not overhang the posterior margin of the centrum. The spinopostzygapophyseal laminae are well developed in this vertebra and extend dorsally and parallel to each other along the entire posterior margin of the neural spine. These laminae slightly broaden at the tip of the spine and enclose a narrow sulcus that extends along the entire posterior margin of the neural spine (Fig. 5B). The neural spine is posterodorsally directed and lateromedially thin with straight anterior margin and concave posterior margin. In lateral view, the posterodorsal corner of the neural spine overhangs the posterior margin of the centrum (Fig. 5A). The anteroposterior length of the base of the neural spine is slightly longer than the half of the length of the neural arch. The lateromedial width of the neural spine thickens dorsally.

The two midcaudal vertebrae preserved in PVL 5904 are fused to each other by their articular facets. This contact has an extremely large pathological callus that forms an extensive bony rim

along the lateral and ventral margins of the articular facets. This rim has an irregular shape and extends laterally and ventrally beyond the level of the posterior articular surface of the second vertebra. The neural spine is anteroposteriorly short and directed posterodorsally and the transverse processes are anteroposteriorly narrow and lateromedially short.

#### Pectoral girdle

**Scapula.** The left scapula has been preserved in articulation with the coracoid in PVL 5904 (Fig. 6A). The scapula is slender and gently curved laterally. The posterior blade of the scapula is poorly expanded but the anterior end is much broader (Fig. 6A), as in most basal sauropodomorphs (e.g. *Plateosaurus*, *Massospondylus*, *Lufengosaurus*, *Yunnanosaurus* and *Adeopapposaurus*). The dorsoventrally expansion of the anterior end of the scapula is 0.45 times the anteroposterior scapular length, similar to other basal sauropodomorphs (e.g. *Riojasaurus* (PVL 3663), *Plateosaurus*, *Massospondylus*, *Lufengosaurus*, *Jingshanosaurus* and *Adeopapposaurus*) but differing from the greatly enlarged anterior end of the scapula in *Lessemsaurus*. The acromion process is well developed and has a curved anterodorsal border, forming an angle of approximately 60 degrees with the anteroposterior axis of the scapula (Fig. 6A), similar to *Unaysaurus*. This angle is only slightly smaller than those of massospondylids (e.g. *Massospondylus*, *Lufengosaurus* and *Adeopapposaurus*) and some other sauropodomorphs (*Saturnalia* and *Jingshanosaurus*). Most non-eusauropod sauropodomorphs have acromion processes forming angles of 40–50 degrees, including the two other sauropodomorphs known from Los Colorados Formation (i.e. *Riojasaurus* (PVL 3663), *Lessemsaurus*). The dorsal half of the lateral surface of the anterior end of the scapula bears a broad and shallow acromial fossa, as in most sauropodomorphs (Fig. 6A). The glenoid region occupies the ventral half of the anterior end of the scapula and is the lateromedially thickest portion of the bone. The glenoid facet of the scapula is suboval, faces anteroventrally and is lateromedially broader than the glenoid facet of



**FIG. 6.** Pectoral girdle of *Coloradisaurus brevis* (PVL 5904). A, left scapulocoracoid in lateral view. B, pathological medial surface of scapular blade. C, right coracoid in lateral view. D, right coracoid in anterolateral view. Scale bar represents 2 cm.

the coracoid. The scapular shaft is strap-shaped with slightly concave dorsal and ventral margins (Fig. 6A). The minimum dorsoventral width of the scapular shaft is approximately 0.16 times the anteroposterior scapular length, as in other basal sauropodomorphs (e.g. *Riojasaurus* (PVL 3663), *Plateosaurus*, *Massospondylus*, *Lufengosaurus* and *Adeopapposaurus*). This ratio is, however, smaller than in derived forms such as *Lessemsaurus*, *Antetonitrus* and *Melanorosaurus*, in which this ratio exceeds 0.24.

The posterior expansion of the scapula is approximately 0.3 times the scapular anteroposterior length, as in other noneusauropod sauropodomorphs (e.g. *Plateosaurus*, *Massospondylus*, *Lufengosaurus* and *Adeopapposaurus*). The posterior expansion of the scapula of PVL 5904 is less developed than in *Riojasaurus* (ratio = 0.41; PVL 3663) and *Lessemsaurus* (ratio = 0.59; PVL 4822). The posterior margin of the scapula of PVL 5904 is straight (forming right angles with the dorsal and ventral margins) and has an acute posteroventral process (Fig. 6A–B). By contrast, most basal sauropodomorphs have a convex posterior margin and a poorly developed posteroventral corner of the scapula (e.g. *Riojasaurus* (PVL 3663), *Plateosaurus*, *Massospondylus*, *Lufengosaurus*, *Yunnanosaurus*, *Jingshanosaurus* and *Adeopapposaurus*). The condition in PVL 5904 also differs from the strongly developed posteroventral process present in *Panphagia* and the basal sauropods *Lessemsaurus* and *Antetonitrus*. The posterior end of the scapula of PVL 5904 is squared-off with the

lateral smooth surface but the medial surface has the unusual rugose tuberosities that make this region markedly thickened transversely. This condition differs from the thin and rounded posterior blade of all other sauropodomorphs. The unusual medial surface is likely a pathological feature and certainly affects the shape of the scapula, so we prefer not to include this feature as an autapomorphy of *Coloradisaurus*. New remains of this taxon will certainly help determining if this is an autapomorphy or if it is a pathological feature of PVL 5904. The tuberosities create an irregular posterodorsal margin of the scapular blade in medial view and a sinuous posteroventral margin (Fig. 6B). The ventral margin of the posterior end of the scapula extends ventrally, but this expansion does not extend beyond the level of the ventral margin of the anterior expansion (Fig. 6A).

**Coracoid.** The right coracoid is completely preserved and the left element is slightly damaged anterodorsally but was found in articulation with the scapula (Fig. 6). The coracoid of PVL 5904 is similar in overall morphology to those of other basal sauropodomorphs. It is an elongated oval plate with a laterally convex surface. The long axis of the coracoid is oriented subparallel to the scapulocoracoid suture. The posterior margin of the coracoid is straight along the scapular suture and bears a shallow embayment that forms the glenoid facet. The glenoid region is lateromedially thicker than the rest of the coracoid (Fig. 6C–D).

The glenoid facet is subrectangular and faces posteroventrally. The coracoid tubercle is a well-developed ridge located on the lateral surface that extends from the anteroventrally corner of the coracoid to a point level with the dorsal end of the glenoid facet (Fig. 6C–D), resembling the condition in the fragmentary coracoid of the holotype of *C. brevis* (PVL 3967). The ventral extension of the coracoid tubercle forms a rounded ventral process that is separated from the glenoid facet by a shallow notch. Dorsal to the coracoid tubercle, the lateral surface of the coracoid is pierced by the coracoid foramen, which is located 20 mm from the scapulocoracoid suture. This foramen opens on the medial surface, but is smaller medially than laterally and is located just anterior the posterior margin of the bone.

#### Forelimb

**Humerus.** The right humerus is completely preserved in PVL 5904 (Fig. 7A–C). The humerus is slightly longer than the scapula (1.1 times the scapular length) but shorter than the femur (0.6 times the femoral length). The humerus is more expanded proximally than distally and the shaft is constricted at midlength with markedly concave lateral and medial borders (Fig. 7). As in other sauropodomorphs, the humerus is rotated along the shaft so that the proximal end forms an angle of approximately 25 degrees relative to the transverse axis of the distal end. The width of the proximal expansion of the humerus with respect to humeral length is 0.48, resembling the condition in some basal

sauropodomorphs (e.g. *Riojasaurus*, *Yunnanosaurus*, *Massospondylus*, *Lufengosaurus* and *Adeopapposaurus*) but differing from other taxa that have this ratio ranging between 0.32 and 0.40 (e.g. *Plateosaurus*, *Lessemsaurus*, *Melanorosaurus* and *Antetonitrus*). The proximal margin of the humerus is markedly convex, as in massospondylids (e.g. *Massospondylus* and *Adeopapposaurus*) and more derived sauropodomorphs (e.g. *Lessemsaurus*, *Melanorosaurus* and *Antetonitrus*). This morphology differs from the straight proximal border of the humerus of other sauropodomorphs (e.g. *Saturnalia*, *Pantyraco*, *Riojasaurus*, *Plateosaurus* and *Yunnanosaurus*). The proximal end of the humerus of PVL 5904 has a well-developed internal tuberosity (Fig. 7A–C) as in massospondylids (e.g. *Massospondylus*, *Lufengosaurus* and *Adeopapposaurus*), *Riojasaurus* and *Yunnanosaurus*. Other basal sauropodomorphs have a less-developed humeral internal tuberosity (e.g. *Saturnalia*, *Plateosaurus*, *Lessemsaurus* and *Melanorosaurus*).

The deltopectoral crest of the humerus is prominent and extends for approximately 45 per cent of the humeral length, as in most basal sauropodomorphs. The deltopectoral crest rises gradually from the proximal margin of the humerus and is directed slightly distomedially along this region (Fig. 7A). At its proximal region, the anterior surface of the deltopectoral crest is lateromedially broadened and bears a slightly developed lateral rim. The distal half of the crest is straight and extends parallel to the longitudinal axis of the humerus, as in most nonsauropod sauropodomorphs. The distal margin of the deltopectoral crest is abrupt and concave in lateral view (Fig. 7B). The lateral surface

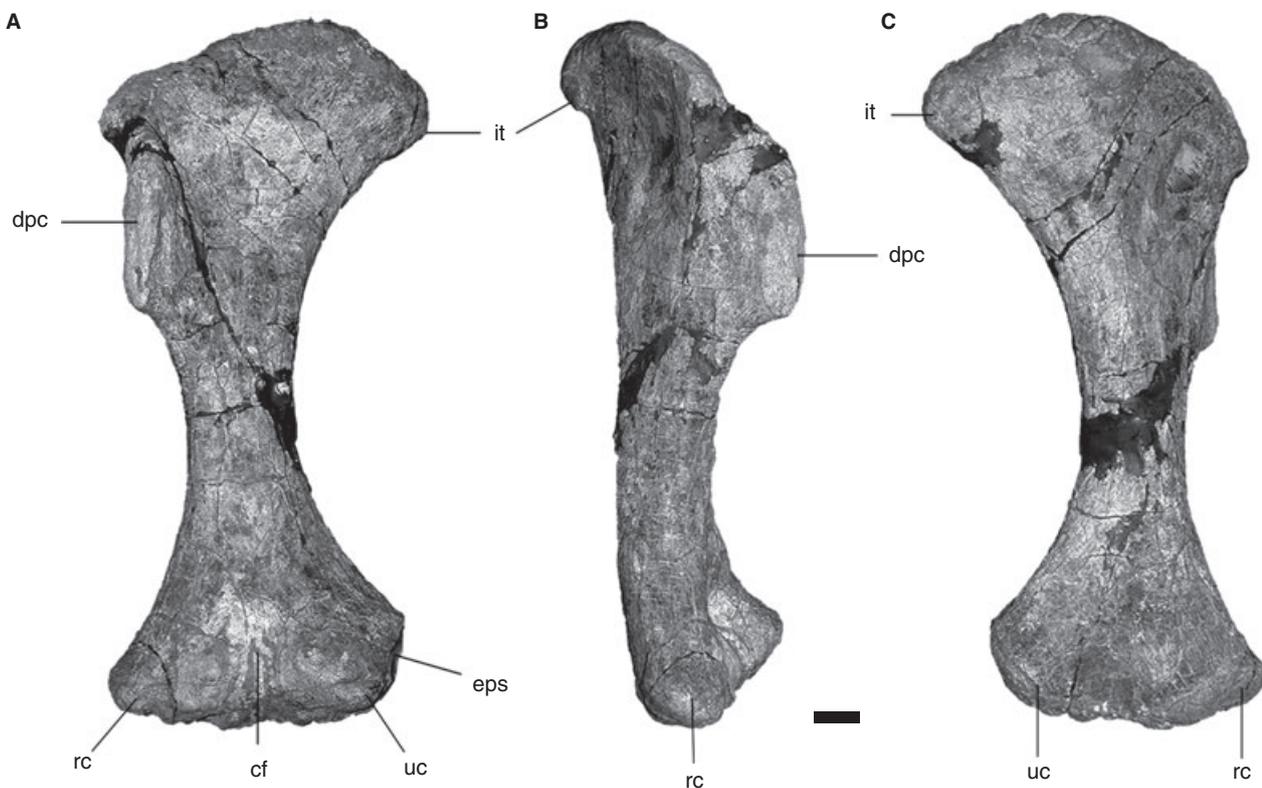


FIG. 7. Right humerus of *Coloradisaurus brevis* (PVL 5904). A, anterior view. B, lateral view. C, posterior view. Scale bar represents 2 cm.

of the deltopectoral crest of PVL 5904 bears a poorly defined sulcus that runs parallel to the lateral margin of the anterior surface. This, however, differs from the distinct rugose pit located centrally on the lateral surface noted for *Massospondylus* and *Lufengosaurus* (Yates 2007a).

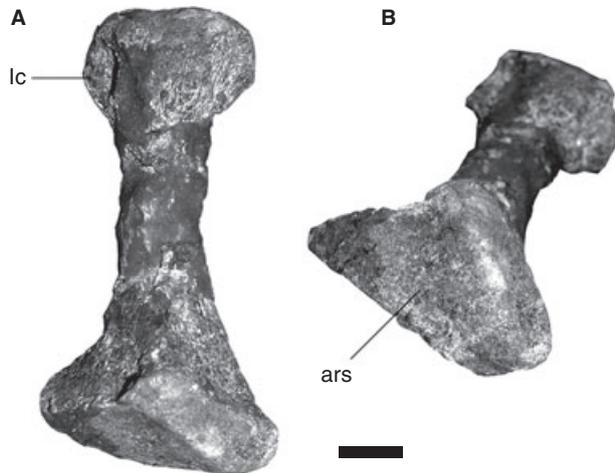
The distal condyles are rounded and well developed, with the ulnar condyle larger than the radial one. Medial to the ulnar condyle, there is a flat entepicondylar surface that faces ventromedially (Fig. 7A), as in most basal sauropodomorphs. The anterior surface of the distal region of the humerus has a deep

and well-defined semicircular cuboid fossa (Fig. 7A). This fossa is lateromedially broad and is also present in the fragmentary distal end of the humerus in the type specimen of *C. brevis* (PVL 3967).

**Metacarpal III.** An isolated left metacarpal III is preserved in PVL 5904 (Fig. 8). The proximal articular surface of the metacarpal is slightly concave and subtriangular, with its longest axis transversely oriented (Fig. 8A–B). The proximal region has a slightly concave dorsomedial surface that would be overlapped by metacarpal II, whereas the flat ventral surface would overlap metacarpal IV. The shaft of metacarpal III is elliptical in cross-section. The distal end is transversely narrower than the proximal end and lacks an intercondylar groove (Fig. 8A), as in the metacarpal III of *Massospondylus* and *Adeopapposaurus*. The transverse width of the distal articular surface is larger than its dorsoventral height (width/height ratio = 1.75). The distal condyles are wider ventrally than dorsally, and the lateral surface has a deeper collateral pit than the medial surface of the distal region.

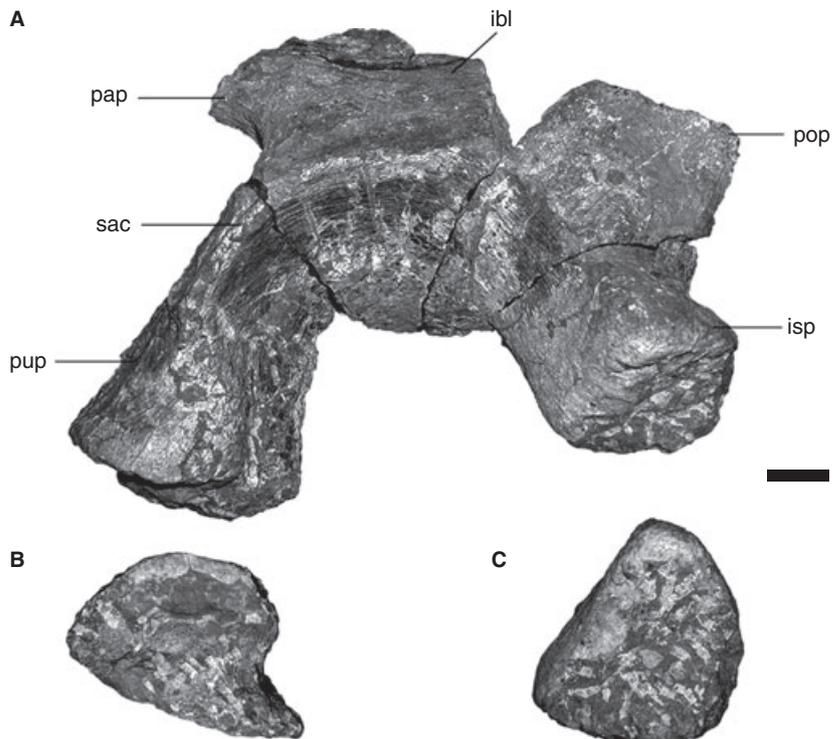
#### Pelvic Girdle

**Ilium.** An incomplete left ilium is preserved in PVL 5904 (Fig. 9). The preserved region of the ilium includes the pubic and ischial peduncles, the anteroventral region of the iliac blade and the base of preacetabular and postacetabular processes (Fig. 9A–C). The overall shape of the ilium is similar to the condition present in most noneusauropod sauropodomorphs. A small portion of the iliac blade is preserved dorsal to the sup-



**FIG. 8.** Left metacarpal III of *Coloradisaurus brevis* (PVL 5904). A, dorsal view. B, proximal view. Scale bar represents 1 cm.

**FIG. 9.** Left ilium of *Coloradisaurus brevis* (PVL 5904). A, lateral view. B, pubic peduncle in distal view. C, ischial peduncle in distal view. Scale bar represents 2 cm.



racetabular crest. This region is laterally concave and probably corresponds to the area for attachment of the *m. iliofemoralis*. This region includes the base of the preacetabular process, which judging from the preserved region, was likely to have been dorsoventrally low (Fig. 9A). The ventral margin of this process arises at an almost right angle with respect to the anterior margin of the pubic peduncle.

The acetabulum is dorsoventrally high, anteroposteriorly long and completely open as in all sauropodomorphs except for the basal taxa *Panphagia* and *Saturnalia*. The supracetabular crest is well developed, sharp and with a curved lateral margin. This crest extends from the dorsal region of the anterior acetabular margin up to the anteroposterior midpoint of the acetabulum (Fig. 9A). This morphology is similar to that of most nonsauropod sauropodomorphs (e.g. *Adeopapposaurus*, *Massospondylus*, *Plateosaurus* and *Riojasaurus*). The internal surface of the acetabulum is lateromedially broad and slightly concave along the pubic peduncle and the acetabular roof. The posterior region of the internal articular surface is flat or even slightly convex towards the distal end of the ischial peduncle.

The pubic peduncle is longer than the ischial peduncle, extending anteroventrally and gradually curving ventrally along its length (Fig. 9A). The distal end of the pubic peduncle is slightly expanded anteroposteriorly (Fig. 9A–B), a condition also present in *Lessemsaurus* but absent in other noneusauropod sauropodomorphs. The distal articular facet for the pubis is subrectangular in shape (Fig. 9B), with its anteroposterior length 80 per cent of the lateromedial width. The anterior surface of the pubic peduncle is broad and convex and the medial surface is flat and extends further posteriorly than the lateral surface. This posterior extension of the medial surface of the pubic peduncle creates a thin and narrow medial wall of the acetabulum (Fig. 9A–B), which contributes to the concave articular anterior surface of the acetabulum described earlier.

The ischial peduncle is shorter than the pubic peduncle, as in all basal sauropodomorphs (Fig. 9A). The articular facet for the ischium is subtriangular, with the long axis lateromedially oriented, a flat anterior surface, a broad medial surface and a slightly convex posterior surface (Fig. 9C). The ischial peduncle of PVL 5904 has the distinctive heel at its posteroventral edge, as in some noneusauropod sauropodomorphs (e.g. *Plateosaurus*, *Riojasaurus* and *Adeopapposaurus*). Other taxa, including *Lessemsaurus*, lack the posterior heel of the ischial peduncle. The posterior margin of the ischial peduncle is lateromedially broad and rounded, lacking the distinct brevis crest that is present in the posterior margin of the ischial peduncle of *Lessemsaurus* (Pol and Powell 2007b).

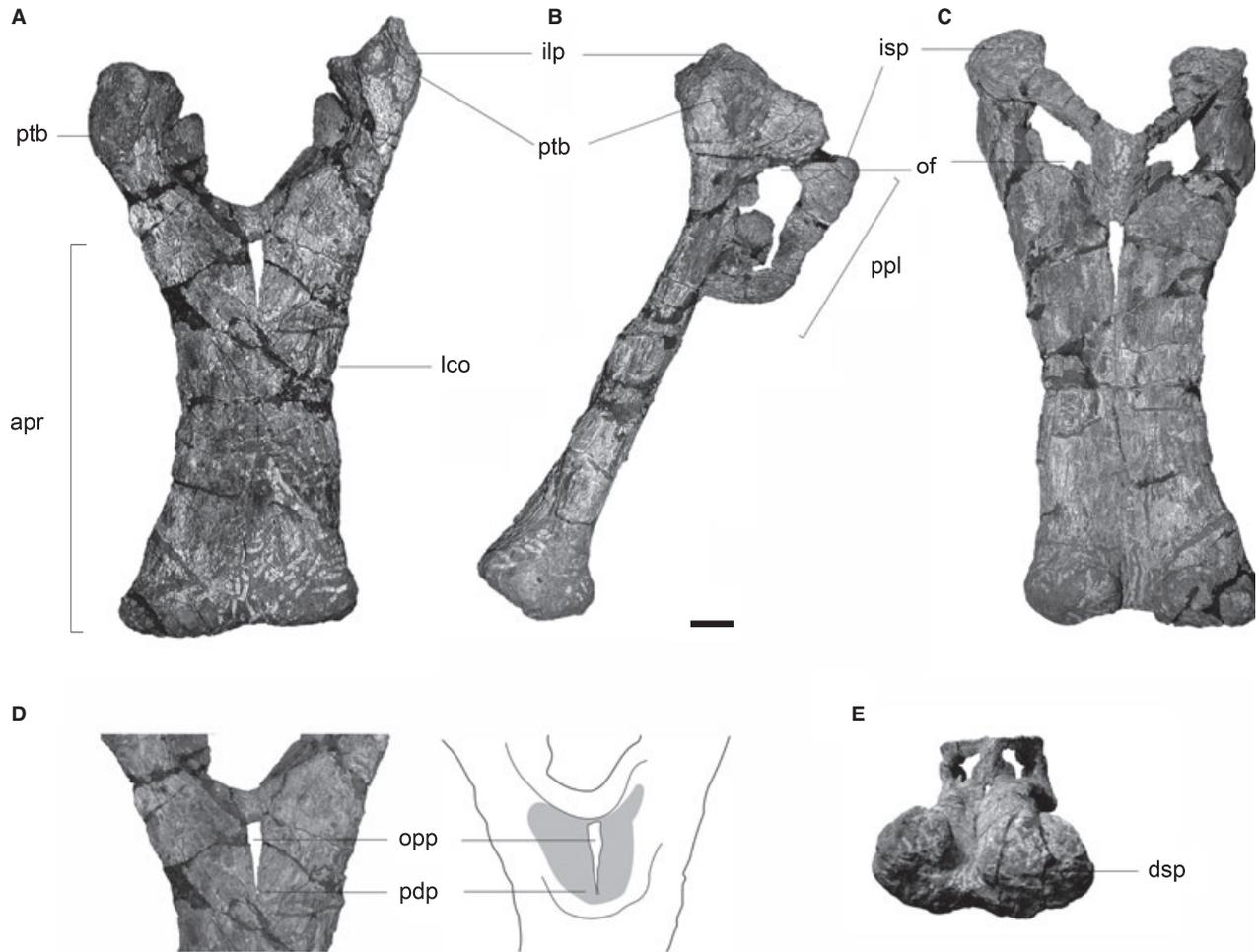
*Pubis*. Both pubes are preserved in articulation in PVL 5904 (Fig. 10). The proximodistal length of the pubis is approximately 0.75 times the femoral length, as in other basal sauropodomorphs (e.g. *Saturnalia*, *Massospondylus* and *Melanorosaurus*). The pubes of PVL 5904 are narrow and elongated (Fig. 10A–C). The maximum lateromedial width of the pubes (measured at the level of the iliac processes) is approximately 0.5 times of the pubic proximodistal length, being narrower than in most basal sauropodomorphs (e.g. *Plateosaurus*, *Massospondylus*, *Yunnanosaurus*, *Anchisaurus* and *Lessemsaurus*) in which this

ratio varies between 0.65 and 0.71. The only exception seems to be *Adeopapposaurus* that has a similarly narrow and elongated pubes.

The pubic plate occupies approximately one-quarter of the total pubic length (Fig. 10B), resembling the condition in other basal sauropodomorphs (e.g. *Plateosaurus*, *Massospondylus*, *Adeopapposaurus*, *Lufengosaurus* and *Yunnanosaurus*) but differing from the more extensive pubic plate of basal sauropods (e.g. *Lessemsaurus* and *Vulcanodon*). The obturator foramen is a large, elliptical opening, which seems to be relatively larger than in other sauropodomorphs. The margins of this opening, however, are damaged so that the natural size of the obturator foramen was likely smaller than preserved in PVL 5904. The obturator foramen faces lateromedially, as in most basal sauropodomorphs (e.g. *Massospondylus*, *Adeopapposaurus*, *Lufengosaurus* and *Seitaad*). Despite the size of the obturator foramen, this aperture is poorly exposed in anterior view (Fig. 10A), as in *Saturnalia*. This contrasts with the obturator foramen of most sauropodomorphs that are completely exposed in anterior view (Yates 2007a). The anteroproximal corner of the pubic plate bears a moderately developed tuberosity (Fig. 10A–B). This tuberosity is located below the articular facet for the ilium and well above the origin of the pubic apron. *Plateosaurus* and more basal sauropodomorphs have a more strongly developed pubic tubercle at the proximal end of the pubic apron (Yates 2003b), positioned much more ventrally than the tuberosity of PVL 5904. The difference in the position of this protuberance suggests these structures are not homologous. Furthermore, the pubis of *Saturnalia* (Langer 2003) bears a proximally located tuberosity (similar to that of PVL 5904) in addition to a more distally located and well-developed pubic tubercle. The proximal tuberosity also distinguishes the pubis of PVL 5904 from the pubes of both *Riojasaurus* and *Lessemsaurus*.

The pubic apron is proximodistally elongated and occupies approximately three-quarters of the entire pubic length. The apron is lateromedially narrow and has concave lateral margins (Fig. 10A), as in massospondylids (e.g. *Massospondylus*, *Lufengosaurus* and *Adeopapposaurus*), *Lessemsaurus* and *Sarhsaurus*. Other sauropodomorphs, including *Riojasaurus*, have straight lateral margins of the pubic apron. The central region of the pubic apron has a minimum lateromedial width that is approximately 0.35 times the proximodistal length, resembling the condition of the above-mentioned massospondylids and *Anchisaurus* but differing from the lateromedially broad pubic apron of other basal sauropodomorphs. The medial constriction of the pubic apron, however, is not as reduced in comparison with the proximal width of the pubis as in *Anchisaurus* (Yates 2004).

The pubic apron of PVL 5904 differs from that of all other noneusauropod sauropodomorphs in several features. First, along the proximal third of the pubic apron, each blade has a tear-drop cross-section, with a slightly broad and rounded lateral margin and a thin laminar medial region that is ventromedially directed. The medial margins of the left and right pubes do not contact each other at this region, leaving a elongated slit-like opening that extends along the proximal third of the pubic apron (Fig. 10D). Second, the anterior surface of the pubic apron bears a deep and proximally facing depression, located in the proximal third of the pubic apron (Fig. 10D). This depres-



**FIG. 10.** Conjoined pubes of *Coloradisaurus brevis* (PVL 5904). A, anterior view. B, lateral view. C, posteroventral view. D, anterior view of proximal pubic apron. E, distal view. Scale bar represents 3 cm.

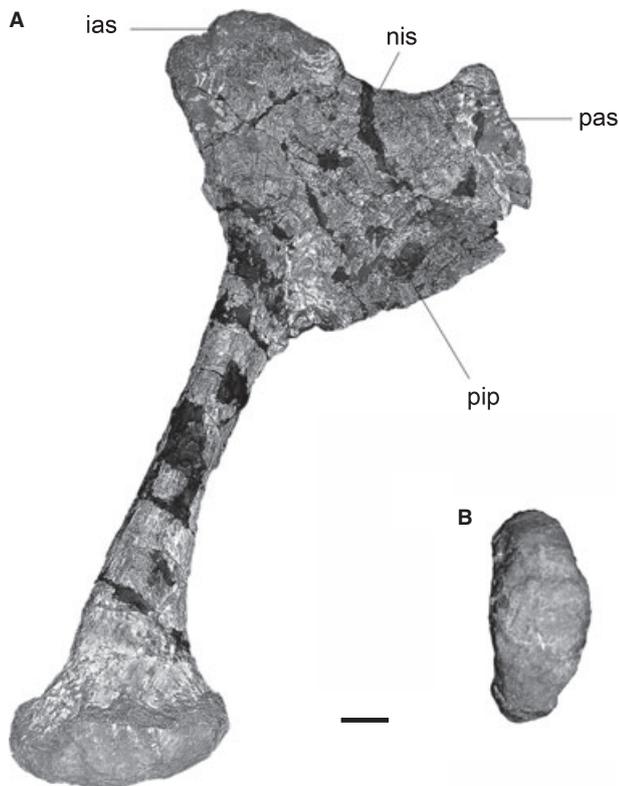
sion is posteriorly covered by the laminar region of the pubic apron, just distal to the medial slit. This depression is 2 cm long anteroposteriorly. Third, each pubis has a semicircular cross-section along the distal two-thirds of the pubic apron. Along this region, the anterior surface is flat or slightly convex (Fig. 10B) and the posterior surface is highly convex (Fig. 10E). The two blades of the pubic apron meet each other along this region and their medial margins are anteroposteriorly thin in comparison with the lateral borders. The peculiar shape of each pubic blade creates a deep trough-shaped depression along the posterior surface of the sutural contact of the pubes (Fig. 10E). This combination of characters is unique among sauropodomorphs, including the two other known taxa from Los Colorados Formation (*Riojasaurus* and *Lessemsaurus*).

The distal end of the pubis is anteroposteriorly expanded, with an anteroposterior length that is 0.17 times the proximodistal length of the pubis. At the distal end, the pubis is approximately twice as expanded in anteroposterior dimension as the pubic apron. This relative expansion is more developed than in massospondylids (except for *Lufengosaurus*) and resembles the proportions of *Plateosaurus* (Yates 2007a). The distal surface of the pubic expansion is subovoid (Fig. 10E), with straight ante-

rior margin and strongly convex posterior margin (resembling the cross-section shape of the pubic apron).

**Ischium.** Only the complete right ischium is preserved in PVL 5904 (Fig. 11A). It is a Y-shaped bone that is lateromedially thin and subequal in proximodistal length to the pubis. The proximal plate is the thinnest region of the ischium and occupies the proximal third of the bone (Fig. 11A). This proximal plate is medially concave and laterally convex. The pubic articular area is subtriangular, and the articular area for the ilium is subovoid and slightly larger than the former. The pubic and iliac articular regions are separated by a concave notch that contributes to the acetabular margin. The posterior margin of the ischial plate is damaged at its distal end so that it cannot be determined if PVL 5904 had a distinct notch separating the pubic region of the ischial plate from the ischial shaft, a condition present in *Plateosaurus* (Yates 2003b) and *Riojasaurus* (Bonaparte 1972).

The ischial shaft is rod-like and subtriangular in cross-section, as in all noneusauropod sauropodomorphs (except *Panphagia*). The dorsoventral depth of the ischial shaft is approximately subequal to its lateromedial width. This is the generalized condition of most basal sauropodomorphs, except for some basal taxa (e.g.



**FIG. 11.** Right ischium of *Coloradisaurus brevis* (PVL 5904). A, lateral view. B, distal view. Scale bar represents 2 cm.

*Saturnalia* and *Thecodontosaurus*), *Anchisaurus* and eusauropods, which have flattened ischial shafts that are much wider than they deep (Yates 2003b). In lateral view, the dorsal margin of the shaft is straight whereas the ventral margin is slightly concave (Fig. 11A). This differs from the straight and parallel margins of the ischial shaft in other sauropodomorphs (e.g. *Plateosaurus*, *Lufengosaurus* and *Adeopapposaurus*). The medial surface of the distal region of the ischial shaft is flat, forming an extensive contact surface for the left ischium.

The distal end of the ischium is subovoid, with the major dorsoventral axis oriented along the sagittal axis (Fig. 11B). This axis is more than twice the lateromedial width of the distal end of the right ischium, as in massospondylids, *Plateosaurus* and *Yunnanosaurus* (Yates 2007a). This morphology differs from the condition of the two other known sauropodomorphs from the Los Colorados Formation (*Riojasaurus* (PVL 3805) and *Lessem-saurus* (PVL 4822/63)), in which the dorsoventral height of the distal end of the ischium is lesser than twice the lateromedial width.

#### Hindlimb

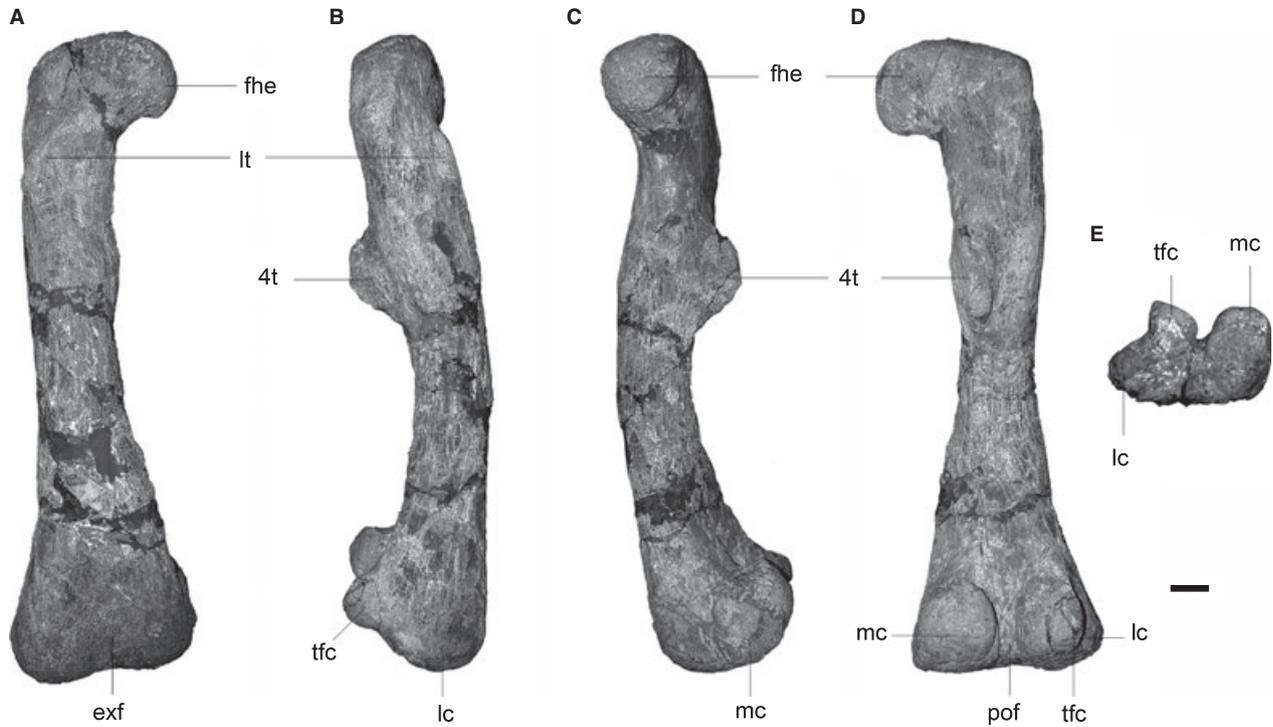
The hindlimb of PVL 5904 includes both femora, both tibiae, the proximal end of the left fibula, the left astragalus, a medial left distal tarsal and an almost complete left pes. The holotype of *C. brevis* (PVL 3967) includes the right astragalus and calcaneum.

*Femur.* Both femora are complete in PVL 5904. The femur is straight in anterior view but sigmoidal in lateral view (Fig. 12), with the distal end posteriorly bent, as in other noneusauropod sauropodomorphs. The femoral head is well developed, and its medial articular surface has an anteroposterior width subequal to its dorsoventral height. The proximal and distal regions of the femur are rotated along its major axis at an angle of approximately 30 degrees, as *Adeopapposaurus*, *Plateosaurus* and more basal sauropodomorphs.

The lesser trochanter of PVL 5904 is a distinct ridge located near the centre of the anterior surface (Fig. 12A). This ridge runs proximodistally and its proximal end reaches a point approximately level with the distal margin of the femoral head, as in massospondylids (e.g. *Massospondylus*, *Lufengosaurus* and *Adeopapposaurus*) and other basal sauropodomorphs. Distally the lesser trochanter decreases more gradually in height than proximally (Fig. 12C). The lesser trochanter has a concave medial margin and is markedly higher than wide at its base, in contrast to the broad lesser trochanter of *Riojasaurus* (PVL 3808).

The fourth trochanter is a well-developed crest with a mostly straight profile in lateral view (Fig. 12B). The fourth trochanter is located on the proximal half of the femoral shaft, as in most basal sauropodomorphs. More derived taxa have the fourth trochanter located at midlength of the femoral shaft (e.g. *Melanorosaurus*, *Lessem-saurus*, *Antetonitrus*, *Vulcanodon* and eusauropods). Moreover, the fourth trochanter is placed close to the medial margin of the femoral shaft (Fig. 12D), as in some massospondylids (e.g. *Lufengosaurus* and *Adeopapposaurus*), *Riojasaurus* and more derived taxa (e.g. *Anchisaurus*, *Aardonyx*, *Melanorosaurus*, *Lessem-saurus* and *Antetonitrus*). In posterior view, the fourth trochanter has a medially concave profile that creates a medial depression for the insertion of the *m. caudofemoralis longus*. Distally the fourth trochanter ends abruptly forming an almost right-angled distal corner.

The femoral shaft is subcircular, as in most noneusauropod sauropodomorphs, and has a constant width along its length. The distal end of the femur is markedly expanded lateromedially (Fig. 12A, D), being its lateromedial width (at the level of the condyles) more than twice the minimum lateromedial width of the femoral shaft. The distal end of the femur is lateromedially broader than anteroposteriorly long. A shallow extensor fossa occupies the central region of the anterior surface of the distal end. The distolateral corner of the femur is rounded, whereas the distomedial corner forms a right angle between the straight medial and distal margins of the femur. The lateral condyle is subrectangular in shape and is posteriorly limited by the tibiofibular crest (Fig. 12B, D–E). The tibiofibular crest is robust and well developed with its posterior apex pointing posterolaterally (Fig. 12B, D–E). The distal surface of the tibiofibular crest is slightly broader lateromedially than long anteroposteriorly, with a width/length ratio of 1.3 (Fig. 12E). Most basal sauropodomorphs have slightly narrower distal surfaces of the tibiofibular crest, but *Lufengosaurus* and *Glacialisaurus* have lateromedially broader tibiofibular crests (Smith and Pol 2007). The distal surface of the tibiofibular crest in PVL 5904, however, is not as broad as in these taxa. A broad and shallow concave surface separates the tibiofibular crest from the lateral condyle. The medial condyle is much larger than the lateral condyle. The



**FIG. 12.** Femur of *Coloradisaurus brevis* (PVL 5904). A, Right femur in anterior view. B, lateral view. C, medial view. D, posterior view. E, Left femur in distal view. Scale bar represents 3 cm.

distal surface of this condyle is subrectangular, being anteroposteriorly longer than lateromedially wide and having rounded margins (Fig. 12E). Proximally, the medial condyle ends abruptly on the posterior surface of the femur and lacks an adductor ridge (Fig. 12C). The posterior surface of the distal end of the femur has a deep popliteal fossa between the lateral and medial condyles (Fig. 12D).

**Tibia.** The length of the tibia of PVL 5904 is approximately 0.87 times the length of the femur, resembling the proportions of all noneusauropod sauropodomorphs. The proximal end of the tibia is robust and its proximal articular surface is subtriangular, with the long axis anterolateral-posteromedially directed (Fig. 13A–D). The expansion along this axis is approximately 0.39 times the proximodistal length of the tibia, differing from the more robust basal sauropodomorphs (e.g. PULR 136, *Blikanasaurus*) in which this ratio is approximately 0.5. The cnemial crest is robust, anterolaterally oriented and has a concave lateral margin and a slightly convex medial margin (Fig. 13A–B). The lateral (fibular) condyle of the tibia projects almost as far posteriorly as the medial (internal) condyle of the tibia (Fig. 13B, D), resembling the condition in *Plateosaurus* and differing from the tibia of most sauropodomorphs (including PULR 136) in which the medial condyle clearly projects more posteriorly than the lateral one (Serenó 1999). The posterior edges of the condyles merge together to form a straight posterolateral margin on the proximal surface of the tibia (Fig. 13D). The lateral condyle is slightly deflected ventrally so that its flat articular surface faces posterodorsally (Fig. 13B). The medial condyle is horizontally oriented but has a slightly concave proximal

articular surface (Fig. 13C–D). Although the posterior margin of the two condyles is not separated by a notch in proximal view, the posterior surface of the proximal tibia is concave in the central area below the condyles (Fig. 13B–D). The lateral surface of the proximal tibia bears a shallow and proximodistally elongated concavity that extends between the lateral margin of the cnemial crest and a longitudinal ridge that extends distally from the lateral surface of the lateral condyle (Fig. 13B). A similar ridge has been recognized as the fibular articular facet in other sauropodomorphs (e.g. Langer 2003). This ridge disappears at the distal end of the tibial shaft where it forms an elongated bulge.

The shaft of the tibia is straight and subelliptical in cross-section. The distal end of the tibia is slightly expanded and is transversely wider than anteroposteriorly long (Fig. 13A–C, E). The anteroposterior length of the distal end of the tibia is greater medially than laterally, as in other basal sauropodomorphs (*Saturnalia*, *Panphagia*, *Adeopapposaurus* and *Lufengosaurus*), but differing from the robust sauropodomorph from the Los Colorado Formation (PULR 136; Ezcurra and Apaldetti 2011) in which the lateral and medial margina are subequal in width. In distal view, the anterior and posterior margins are straight and transversely oriented (Fig. 13E). The medial margin is straight but obliquely oriented so that the posteromedial corner of the distal tibia forms an acute angle. The lateral margin bears the notch for the articulation of the astragalar ascending process that is bounded by the anterolateral and posterolateral process of the distal tibia (Fig. 13E). The posterolateral process of the tibia (or posterior malleolous) projects as far laterally as the anterolateral process, as in massospondylids, *Plateosaurus*, and more basal sauropodomorphs (Yates 2004), but different from PULR 136



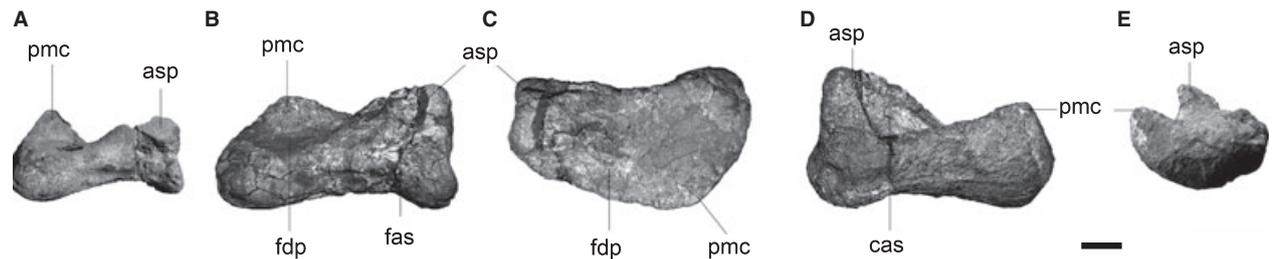
**FIG. 13.** Tibia of *Coloradisaurus brevis* (PVL 5904). A, Left tibia in anterior view. B, lateral view. C, medial view. D, proximal view. E, Right tibia in distal view. Scale bar represents 3 cm.

(Ezcurra and Apaldetti 2011) in which the posterolateral process does not reach the level of the anterolateral process. As in most basal sauropodomorphs the posterolateral process also exceeds distally the limit of the anterolateral process (Fig. 13B). The distal surface of the posterolateral process is oriented horizontally forming a right angle with the proximodistal axis of the tibia. The distal surface of the anterolateral process, instead, is oblique and faces distolaterally for the articulation of the ascending process of the astragalus (Fig. 13B, E). The posteromedial corner of the distal articular end of the tibia is slightly deflected, facing posterodistally (Fig. 13C), similar to PULR 136 (Ezcurra and Apaldetti 2011). All other basal sauropodomorphs (including specimens of *Riojasaurus* and *Lessemsaurus*) have this region oriented horizontally and facing distally.

**Fibula.** Only the proximal third of the left fibula is preserved in PVL 5904. The proximal region of the fibula is anteroposteriorly

expanded with a convex lateral surface and an almost flat medial surface with two smooth concavities. Thus, the proximal end has convex lateral margin and the medial margin is posteriorly straight and anteriorly convex, forming a crescentic profile in proximal view. In lateral view, the anterior border of the proximal region is straight for a short distance below the proximal margin and the posterior border is broken. The preserved portion of the fibular shaft is lateromedially compressed and gradually narrows distally. In lateral view, the margins of the fibular shaft are slightly sinuous, although this could have been accentuated by preservational causes.

**Astragalus.** The left astragalus is preserved in PVL 5904 and resembles in several derived characters the right astragalus known from the holotype of *C. brevis* (PVL 3967) (Fig. 14). The main body of the astragalus is subtrapezoidal in proximal view with its major axis lateromedially oriented (Fig. 14C). The lateral



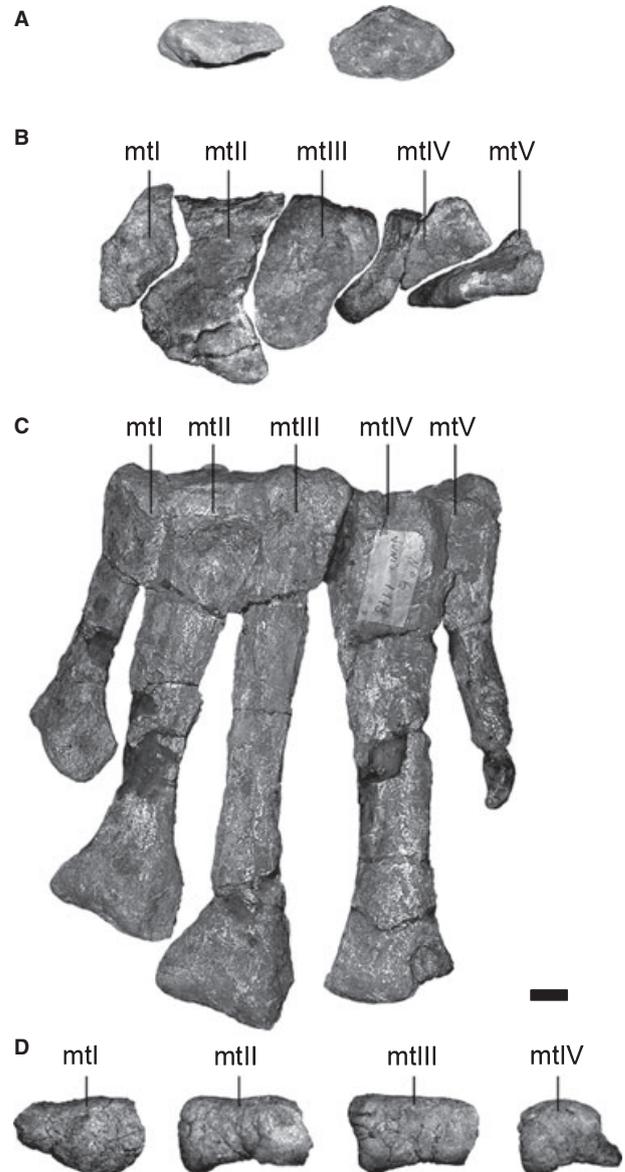
**FIG. 14.** Astragalus of *Coloradisaurus brevis*. A, right astragalus (inverted) of holotype (PVL 3967) in anterior view. B–E, left astragalus of PVL 5904 in B, anterior, C, proximal, D, posterior, E, and medial views. Scale bar represents 2 cm.

margin of the astragalus body is anteroposteriorly shorter than the medial margin, as in most noneusauropod sauropodomorphs (e.g. *Thecodontosaurus*, *Riojasaurus* (PVL 3846), *Plateosaurus*, *Massospondylus*, *Adeopapposaurus*, *Melanorosaurus* and *Lessemsaurus*). The distal surface is slightly anteroposteriorly convex, as in all noneusauropod sauropodomorphs.

The proximal surface of the astragalus bears the ascending process at the anterolateral corner and a flat to slightly concave articular surface for the descending process of the tibia (Fig. 14B–C), a set of features characteristic of basal sauropodomorphs. The posteromedial corner of the astragalus of the holotype and PVL 5904 has an extremely well-developed pyramidal dorsal process (Fig. 14A–B, D–E) that projects proximally and covers the posteromedial corner of the distal articular facet of the tibia. A pyramidal process has been noted as a derived feature also present in two massospondylids (e.g. *Massospondylus*, *Lufengosaurus*; Yates 2007a) and is also present in *Adeopapposaurus*. The pyramidal process, however, is much more developed in *Coloradisaurus* than in these sauropodomorphs, being almost as high as the lateral ascending process of the astragalus (Fig. 14A–B). Thus, the posteromedial corner forms a markedly elevated rim of the proximal articular facet of the astragalus. The anterior margin of the astragalus is straight along lateral half but is markedly convex towards the anteromedial corner, which projects more anteriorly than the anterolateral corner of the astragalus (Fig. 14C).

The ascending process is prominent and subrectangular in proximal view and occupies the anterolateral region of the proximal surface of the astragalus (Fig. 14C). The lateromedial width of the ascending process is approximately 0.43 the astragalus width and its anteroposterior length is 0.45 the astragalus length, resembling the proportions of other basal sauropodomorphs (e.g. *Riojasaurus* (PVL 3846), *Plateosaurus*, *Massospondylus*, *Lufengosaurus*, *Adeopapposaurus* and *Glacialisaurus*), but being more reduced than in *Lessemsaurus*. The proximal articular surface of the ascending process faces anterodorsomedially (Fig. 14E), as in other sauropodomorphs, but also differs from the condition of *Lessemsaurus* in which this surface faces dorsomedially. In anterior view, the base of the ascending process has a well-developed fossa (Fig. 14B), as in most noneusauropod sauropodomorphs. The posterior concave surface of the ascending process of the astragalus bears a distinct ovoid depression located close to the medial end of the ascending process (Fig. 14D). Within this depression, there are two small pits that may represent the vascular foramina recognized in other basal sauropodomorphs (Smith and Pol 2007). The lateral margin of the astragalus is straight and lacks the fibular facet present in other taxa (e.g. *Saturnalia*, *Thecodontosaurus* and *Plateosaurus*).

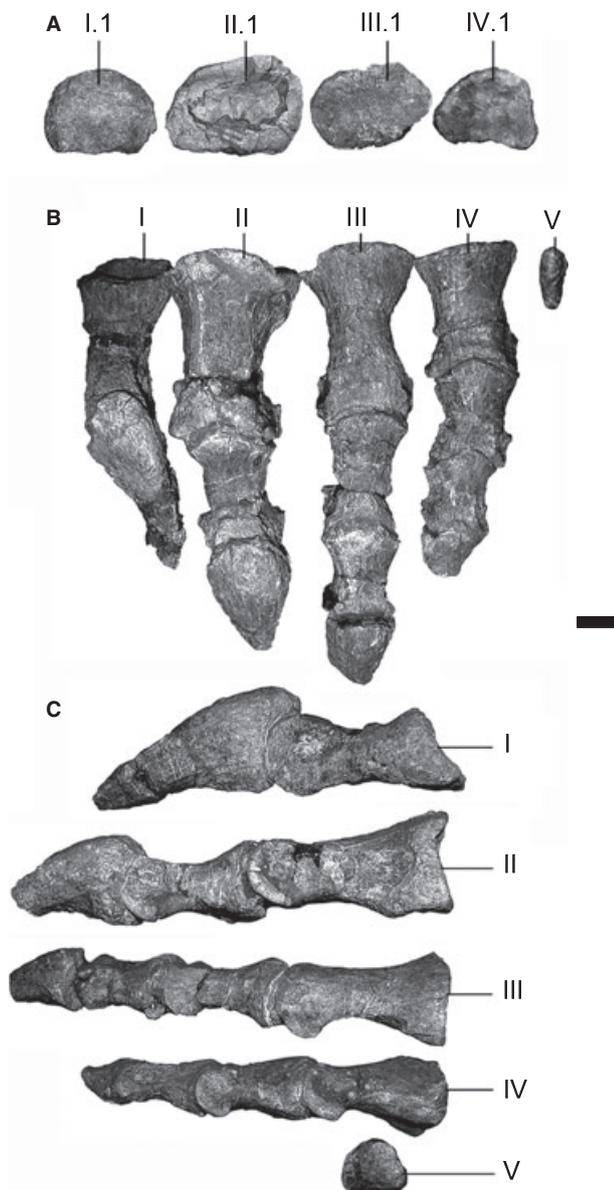
**Distal tarsal.** Only the medial left distal tarsal is preserved in PVL 5904 (Fig. 15A). This element is proximodistally flat and subtriangular in proximal view. All of the corners are rounded except for the anterolateral corner that is pointed. The proximal articular surface of the distal tarsal is slightly convex whereas the distal surface is flat to slightly concave (Fig. 15A). The anterior half is proximodistally low and increases in depth posteriorly, being its posteromedial region the deepest portion of the bone, as in other basal sauropodomorphs (e.g. *Saturnalia*, *Lufengosaurus*, *Glacialisaurus*, *Adeopapposaurus*, and *Leyesaurus*).



**FIG. 15.** Left distal medial tarsal and metatarsus of *Coloradisaurus brevis* (PVL 5904). A, distal medial tarsal in anterior and proximal view. B, metatarsals I–V in proximal view (plantar is to the bottom, inverted view). C, dorsal view. D, metatarsals I–IV in distal view. Scale bar represents 1 cm.

**Pes.** An almost complete left foot is preserved in PVL 5904, lacking the distal end of ungual of digit III, the distal half of phalanx IV.4 and the ungual of digit IV. The metatarsus is completely preserved in articulation (Fig. 15B–C) and the phalanges of each digit are also completely articulated (Fig. 16).

The proximal articular surface of metatarsal I is subovoid with acute plantar and dorsal margins and an elongated dorsoplantar axis (Fig. 15B). The shaft has an elliptical cross-section and is slightly constricted along its length with a lateromedial width similar to that of metatarsal III (Fig. 15C), as in most noneusauropod sauropodomorphs. The proximodistal length of metatarsal I is approximately 0.58 times the length of the metatarsal III.



**FIG. 16.** Left pedal phalanges of *Coloradisaurus brevis* (PVL 5904). A, proximal view (plantar is to the bottom). B, dorsal view. C, lateral view. Scale bar represents 1 cm.

The lateral distal condyle is more developed than the medial condyle. In distal view, the dorsoventral height and lateromedial width of the lateral condyle is more than twice the size of the medial condyle (Fig. 15D). The medial surface of the distal region of metatarsal I has a broad and poorly defined fossa but the lateral surface has a rounded and shallow collateral ligament pit. Metatarsal I lacks a dorsal depression for the extensor ligament.

The proximal articular surface of metatarsal II has an hour-glass shape with markedly concave medial and lateral margins (Fig. 15B), as in all noneusauropod sauropodomorphs. The ventrolateral corner of the proximal surface of metatarsal II is well developed and extends laterally overlapping the ventromedial

region of metatarsal III. An expanded ventrolateral flange of the proximal surface of metatarsal II is also present in massospondylids (Smith and Pol 2007), but is absent or poorly developed in other taxa (e.g. *Plateosaurus*). The shaft of metatarsal II is sub-rectangular with sharply defined ridges along the laterodorsal and mediadorsal edges (Fig. 15C). The distal end of metatarsal II is slightly twisted laterally relative to the proximal end. The lateral condyle is lateromedially broader but dorsoplantarly lower than the medial condyle (Fig. 15D). The distal condyles are separated by a shallow groove that is more pronounced towards the plantar end. The medial and lateral collateral ligament pits are shallow and poorly defined.

Metatarsal III is the longest element of the metatarsus (Fig. 15C). Its proximal articular surface is subtriangular, with a lateromedial straight and broader dorsal margin and slightly narrower but rounded ventral end that is well exposed in plantar view (Fig. 15B). The lateral margin of the proximal surface is concave and the medial margin is convex, fitting in the lateral concavity of metatarsal II. The shaft of the metatarsal III is slender and dorsoventrally flattened. As in other basal sauropodomorph taxa (e.g. *Massospondylus*, *Adeopapposaurus* and *Lessemsaurus*), the distal end of metatarsal III is slightly deflected medially with respect to its proximodistal axis. The condyles are roughly symmetrical in lateromedial width but the medial condyle is slightly higher dorsoplantarly (Fig. 15D). Two shallow grooves are present on the distal surface of the metatarsal III between the lateral and medial condyles. These grooves are closely located to each other at the plantar edge of the distal surface and gradually diverge dorsally. The lateral collateral ligament pit is shallow and rounded, but the medial surface is damaged so that the presence of a pit cannot be confirmed. The dorsal surface of the distal metatarsal III has a shallow depression for the extensor ligament.

Metatarsal IV is proximodistally shorter than the metatarsal III (Fig. 15C). As in all noneusauropod sauropodomorphs, the proximal end of metatarsal IV is broader than the distal end and has subtriangular outline. The proximal articular surface is dorsoventrally low, with its lateromedial axis almost three times its dorsoventral height. The dorsal margin of the proximal articular surface forms an obtuse angle with the medial margin (Fig. 15B), as in other basal sauropodomorphs (e.g. *Saturnalia*, *Massospondylus*, *Lufengosaurus*, *Glacialisaurus*, *Adeopapposaurus*, *Yunmanosaurus* and *Leyesaurus*), but differing from *Plateosaurus* and *Blikanosaurus* in which this angle is almost right. The dorso-medial margin of the proximal articular surface is slightly concave and receives the lateral margin of the proximal metatarsal III. The dorsal apex of the proximal surface of metatarsal IV forms the proximalmost point of a crest that extends proximodistally along the dorsal surface of this bone, as in most noneusauropod sauropodomorphs. The shaft is dorsoventrally compressed with an elliptical cross-section. The transverse width of the distal end of metatarsal IV is narrower than that of metatarsal III. The distal end of metatarsal IV is lateromedially broader than dorsoplantarly high. The medial condyle is lateromedially narrow and vertically oriented (Fig. 15D). The lateral condyle has a well-developed ventrolateral flange, as in most noneusauropod sauropodomorphs. A broad triangular intercondylar groove extends along the plantar half of the distal surface. The medial surface of the distal region is flat and lacks a

collateral ligament pit but the lateral surface bears a broad and ovoid pit. The dorsal fossa for the extensor ligament is absent in metatarsal IV.

As in all basal sauropodomorphs, metatarsal V is short, flat and funnel-shaped. Its proximodistal length is 0.47 times the length of metatarsal III (Fig. 15C). The proximal end of the metatarsal V is dorsoventrally low and lateromedially broad and underlies the ventral end of metatarsal IV (Fig. 15B). In proximal view, the lateral half is dorsoventral deeper than the medial half. The transverse width of its proximal end is approximately 0.54 times its proximodistal length. Metatarsal V tapers distally and ends in a small hemispherical articular distal surface.

The phalangeal formula of the pes of PVL 5904 is 2-3-4-5?-1. The fourth digit has four nonterminal phalanges, so its phalangeal count was probably five, as in other basal sauropodomorphs. All pedal phalanges are in articulation and they have similar morphology to those of most nonsauropod sauropodomorphs (e.g. *Saturnalia*, *Riojasaurus*, *Massospondylus*, *Pantyraco*, *Adeopapposaurus*, *Seitaad* and *Leyesaurus*), which are proximodistally longer than transversely broad and with a lateromedial constriction at midshaft (Fig. 16). Moreover, all phalanges of PVL 5904 have distal ends with expanded plantar surfaces that are wider than the dorsal surface. The proximal ends of the first phalanges of digits I–IV are subovoid (kidney-shaped on digits I and IV) and are lateromedially wider than their distal ends (Fig. 16A). All first phalanges lack a distinct dorsal process. These phalanges have a lateromedial constriction at midlength of their shafts. At the distal end, the collateral ligament pits are deep, especially on the first phalanges of digits II–IV. The second phalanx of digit II, III and IV are less elongated and narrower than the previous phalanges. Their proximal end is as broad as their distal end. The dorsal processes are rounded, instead of being acute as in the second phalanges of other taxa (e.g. *Massospondylus* and *Adeopapposaurus*). In contrast to the first phalanges of PVL 5904, the second phalanges have their minimum lateromedial width in the distal region of the shaft, just before the distal condyles (Fig. 16B). Distally, the second phalanges of digits II and IV have a noticeable development of their lateral and medial condyles. The collateral ligament pits of the second phalanges are well developed and deep. The third phalanges of digit III and IV are proximodistally shorter and less constricted at their distal halves than the second phalanges. These phalanges are dorsoventrally low along their entire length (Fig. 16C). The third phalanx of digit III has the transverse width of its proximal articular surface subequal to its distal end, whereas on digit IV the transverse width of the proximal end is slightly less than its distal articular surface. Distally, the condyles are well developed with deep and rounded collateral ligament pits. Only the proximal half of the fourth phalanx of digit IV has been preserved. Apparently, this would be the smallest of the above-mentioned phalanges. The proximal articular surface of this phalanx is lateromedially narrower than that of the other phalanges. The phalanx of digit V is the smallest of the pes. This phalanx is lateromedially flattened and proximodistally elongated (Fig. 16B–C). The proximodistal length is 0.23 times the length of the fifth metatarsal. The dorsal surface of the phalanx of digit V is markedly convex, whereas its ventral surface is slightly concave and lateromedially narrower than the dorsal surface

(Fig. 16C). Ungual I is the largest and most robust of the pes. It is laterally compressed and has a prominent dorsal process with a pointed proximodorsal apex. The proximal region of the ungual of digit II is globose in dorsal view (Fig. 16B). This ungual is proximodistally longer than lateromedially wide. The distal end of the second ungual is broken. The ungual of digit III is incomplete, lacking its distal end. This ungual is lateromedially narrower and less robust than those of digits I and II. A shallow groove runs proximodistally along the lateral and medial surface of the ungual of digit III. As in the digit II, the dorsal process is weakly developed. The ungual of digit IV is not preserved in PVL 5904.

## DISCUSSION

The partially articulated skeleton PVL 5904 offers new information on the almost unknown postcranial anatomy of *Coloradisaurus brevis*. This not only increases our knowledge of its anatomy but also provides critical information to test the debated phylogenetic affinities of this taxon. Here, we explore the impact of the postcranial information provided by PVL 5904 on two major topics, the previously proposed affinities of *Coloradisaurus* and *Lufengosaurus* and the phylogenetic placement of these taxa among basal sauropodomorphs. These two topics were explored using slightly modified versions of two recent data matrices for basal sauropodomorphs, published by Yates *et al.* (2010) and Upchurch *et al.* (2007). Although the former analysis is more comprehensive in terms of taxon and character sampling, we have explored the impact of the new postcranial information of *C. brevis* in the data matrix of Upchurch *et al.* (2007) because of the highly different phylogenetic position retrieved for this taxon in the latter study. In the following discussion, we first introduce the modifications made to both data sets and then present the results obtained in terms of affinities with *Lufengosaurus* and the phylogenetic position of these taxa relative to other sauropodomorphs, evaluating the relevance of postcranial characters and the degree of character support for competing hypotheses.

Yates *et al.* (2010). Five recently described taxa that have been postulated as possibly related to massospondylids and/or *Coloradisaurus* were added to this data set: *Glacialisaurus* (Smith and Pol 2007), *Adeopapposaurus* (Martinez 2009), *Seitaad* (Sertich and Loewen 2010), *Sarhsaurus* (Attridge *et al.* 1985; Rowe *et al.* 2010) and *Leyesaurus* (Apaldetti *et al.*, 2011). The basal sauropodomorph *Ignavusaurus* (Knoll, 2010) was not considered in the present work because it was recently regarded as a juvenile specimen of *Massospondylus* (Yates *et al.* 2011). The scorings for these taxa were taken from the data sets provided in their original descriptions (Table 1).

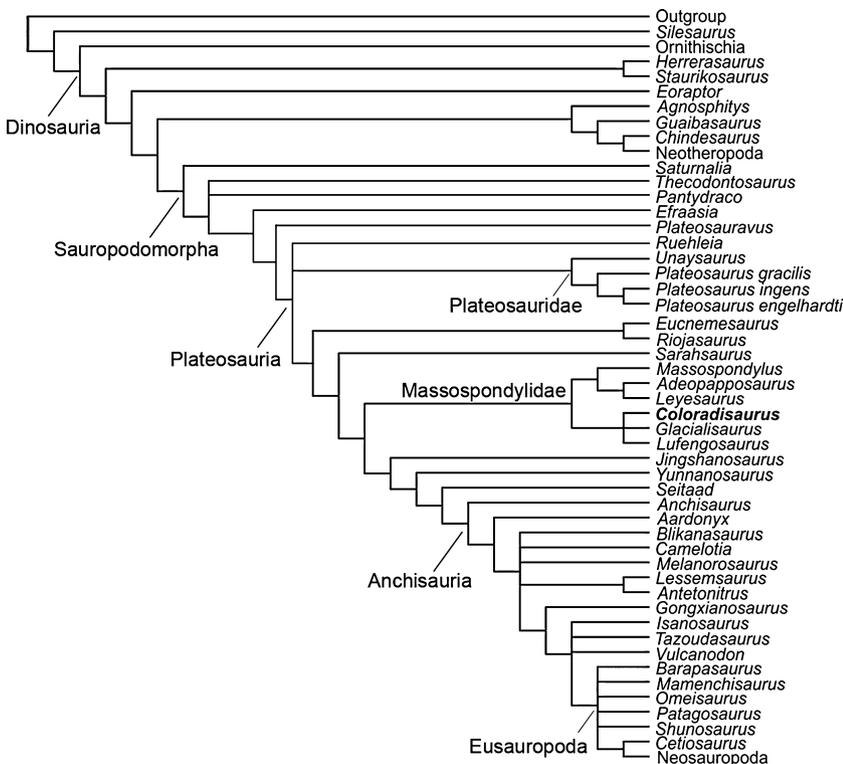
Additionally, eight characters provided by Smith and Pol (2007) and two new characters were added to this data set (see Appendix S1). Postcranial information on *Coloradisaurus* had already been incorporated by Yates *et al.* (2010) based on PVL 5904, although several scorings were changed (Apaldetti *et al.* 2011) or added based on the description provided in this contribution (see Appendices S1 and S2). The modified data set of 363 characters and 52 taxa was analysed with equally weighted parsimony in TNT (Goloboff *et al.* 2008a,b) using a heuristic search with 1000 replicates of Wagner trees followed by TBR branch swapping. The tree search resulted in 36 most parsimonious trees (length = 1277, CI = 0.330, RI = 0.670) found 540 times out of the thousand replicates. The strict consensus of the MPTs is shown in Figure 17.

Upchurch *et al.* (2007). This data set was modified with the addition of *Glacialisaurus*, *Adeopapposaurus*, *Seitaad*, *Sarahasaurus* and *Leyesaurus*, using the character scorings for this matrix provided in the original descriptions of these taxa and based on a first hand study of the latter taxon (CA, pers. obs.). The eight characters proposed by Smith and Pol (2007) and the other two new characters proposed in this work were also included in this data set (see Appendix S1). Character scorings for *Coloradisaurus* were completed as the original data matrix had almost no postcranial information for this taxon (see Appendices S1

and S3). The modified data set of 302 characters and 39 taxa was analysed using the outgroup constraints and character ordering defined by Upchurch *et al.* (2007). The analysis resulted in 20 most parsimonious trees (length = 848, CI = 0.364, RI = 0.632) found 330 times out of the thousand replicates. The reduced strict consensus of the MPTs is shown in Figure 18 (see below and Appendix S1 for further details).

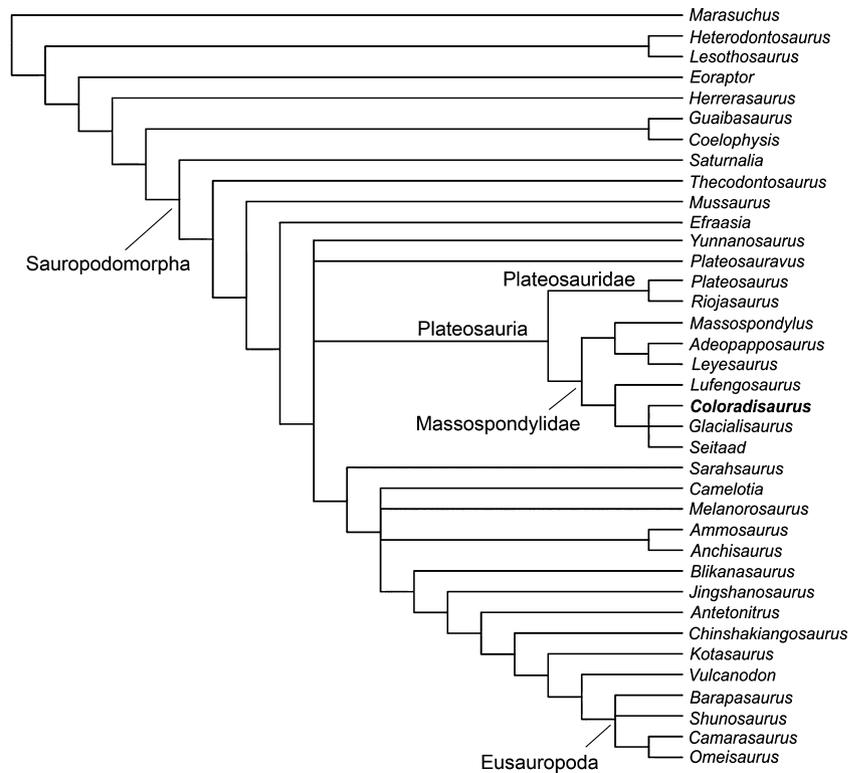
*The close affinities of Coloradisaurus and Lufengosaurus*

Yates *et al.* (2010). The strict consensus tree depicts *Coloradisaurus* forming part of a polytomy with *Lufengosaurus* and *Glacialisaurus* (Fig. 17). These taxa are allied to *Massospondylus*, *Adeopapposaurus* and *Leyesaurus* forming the monophyletic clade Massospondylidae (Fig. 17). The affinities of *Coloradisaurus* and *Lufengosaurus* were also obtained in previous analyses of this data matrix (Yates 2007a, Yates *et al.* 2010) and the inclusion of *Glacialisaurus* in this clade was also retrieved by Smith and Pol (2007). The clade formed by *Coloradisaurus*, *Lufengosaurus* and *Glacialisaurus* is supported by four unambiguous synapomorphies, all of which are from the postcranial skeleton and can be scored for *Coloradisaurus* based on PVL 5904. These are: the ventrolateral flange on plantar surface of metatarsal II in proximal view is well developed and extends further laterally than the ventromedial flange



**FIG. 17.** Strict consensus tree of the phylogenetic analysis based on the modified version of the data matrix of Yates *et al.* (2010).

**FIG. 18.** Reduced strict consensus tree of the phylogenetic analysis based on the modified version of the data matrix of Upchurch *et al.* (2007).



(character 354.1); distal surface of the tibiofibular crest wider lateromedially than deep anteroposteriorly (character 356.1); presence of a facet on the proximolateral corner of metatarsal II for articulation with the medial distal tarsal (character 357.1); and metatarsal III with its posterior border broadly exposed in plantar view (character 358.1). In some of the most parsimonious trees, other two synapomorphies support this clade: axial postzygapophyses that overhang the posterior margin of the axial centrum (character 125.0) and the presence of a craniocaudal expansion of the distal pubis that is >15 per cent of the length of the pubis (character 267.2).

This clade is supported by a Bremer support value of 2 and has bootstrap frequencies below 50 per cent (as with most other sauropodomorph nodes in this analysis). These support values are relatively low but alternative phylogenetic placements of *Coloradisaurus* that separate this taxon from *Lufengosaurus* imply a minimum of four extra steps. This increase in tree length, however, is not significant as measured by a Templeton test ( $p = 0.4795$ ). The best alternative placements of *Coloradisaurus* that are moderately suboptimal include the placement of this taxon as closer to *Massospondylus* or to *Sarahsaurus* (four extra steps), or to *Seitaad* (six extra steps) than to *Lufengosaurus*. More basal placements of *Coloradisaurus* within Plateosauria (e.g. closer to *Riojasaurus* or *Plateosaurus*), as well as more derived positions (e.g. within Anchisauria), are suboptimal and imply at least 14 extra

steps within the context of this data set (not significantly longer by the Templeton test;  $p < 0.05$ ).

Upchurch *et al.* (2007). The strict consensus of this analysis is highly collapsed (see Appendix S1), but a reduced strict consensus (after pruning *Lessemsaurus* and *Gyposaurus* from the MPTs) shows that all topologies depict *Coloradisaurus* forming a polytomy with *Seitaad* and *Glacialisaurus*, with *Lufengosaurus* as the sister taxon of this clade. These four taxa are placed as the sister group of the clade formed by *Massospondylus*, *Adeopapposaurus* and *Leyesaurus* (Fig. 18). This clade is recognized as Massospondylidae and resembles the results obtained for the data set of Yates *et al.* (2010) in the sense that *Coloradisaurus* and *Lufengosaurus* are as close to each other and to massospondylids than to plateosaurids. The clade formed by *Coloradisaurus*, *Seitaad* and *Glacialisaurus* is supported by a single unambiguous synapomorphy in the modified version of the data set of Upchurch *et al.* (2007), which refers to the minimum shaft widths of metatarsal III and IV divided by minimum shaft width of metatarsal II that is more than 0.6 (character 276.1). This clade shares with *Lufengosaurus* eight unambiguous synapomorphies, three of which are cranial features and five are postcranial characters revealed by PVL 5904 for *Coloradisaurus*. The five synapomorphies from postcranium include the four hindlimb characters mentioned above for the previous analysis (characters 293.1, 295.1, 296.1 and

297.1 in this data set) plus the absence of ossified proximal carpals (character 178.1; unknown in *Coloradisaurus*).

In this analysis, the *Lufengosaurus* + (*Coloradisaurus* + *Seitaad* + *Glacialisaurus*) clade is poorly supported, with minimal Bremer support and bootstrap frequencies below 50 per cent (see Appendix S1). In contrast to the other data set, only two extra steps are required in this data matrix to separate *Coloradisaurus* from *Seitaad* or *Glacialisaurus*. The most parsimonious alternative placement of *Coloradisaurus*, as in the previous analysis, is obtained when this taxon is placed closer to other massospondylids than to plateosaurids. Placing *Coloradisaurus* as sister to *Plateosaurus* + *Riojasaurus* results in suboptimal trees with seven extra steps (not significantly longer than the MPTs by the Templeton test;  $p = 0.5$ ).

#### *Coloradisaurus* and *Lufengosaurus*: massospondylids or plateosaurids?

Both data sets show a congruent result in the close relationship of *Coloradisaurus* and *Lufengosaurus* and on the inclusion of these taxa within Massospondylidae. In the data set modified from Yates *et al.* (2010), Massospondylidae is depicted as closer to Anchisauria than to Plateosauridae (Fig. 17) and is supported by seven unambiguous synapomorphies. Four of the synapomorphic features of Massospondylidae are cranial features and three synapomorphies are postcranial characters: anterior cervical centra length exceeding four times the anterior centrum height (character 131.2), the presence of laterally expanded tables at the midlength of the dorsal surface of the neural spines of the pectoral and cervical vertebrae (character 149.2; unknown in *Coloradisaurus*) and the presence of a symmetrical fourth trochanter of the femur (character 294.2). Most of the cranial synapomorphic characters of Massospondylidae retrieved in this analysis are present in the holotype specimen of *C. brevis* (see Appendix S1).

The modified matrix of Upchurch *et al.* (2007) also retrieved to *Coloradisaurus* and *Lufengosaurus* (together with *Seitaad* and *Glacialisaurus*) clade as massospondylids but this clade is placed as the sister clade to Plateosauridae, depicting Plateosauria as a group basal to Anchisauria (Fig. 18). Massospondylidae is supported in this analysis by five unambiguous synapomorphies, but only two are postcranial features: lateral margins of the pubic apron have a concave profile in anterior view (character 220.1) and length of the ungual on pedal digit III divided by length of the ungual on pedal digit II lesser than 0.85 (character 291.1). Most of the cranial synapomorphic features of Massospondylidae retrieved in this analysis are craniomandibular characters present in the holotype specimen of *C. brevis* (see Appendix S1). As noted earlier, in this analysis,

Massospondylidae includes *Seitaad*, although with four extra steps, *Seitaad* is retrieved on a derived position as closer to Anchisauria than massospondylids (not significantly longer than the MPTs by the Templeton test;  $p = 0.5$ ).

In this data set, Plateosauridae and Massospondylidae conform a monophyletic core of 'prosauropods' (Plateosauria), which is supported by four unambiguous synapomorphies (see Appendix S1). Only one of them is postcranial: cranial process of the ilium is relatively large and has a broad triangular outline in lateral view (character 205.1), and in some of the most parsimonious trees, other synapomorphy support this clade: concave area on the lateral surface of the ilium restricted to the dorsal half of the blade (Character 210.1).

*Character support.* Although both data sets retrieved *Coloradisaurus* and *Lufengosaurus* as massospondylids, this clade has been allied with both plateosaurids and anchisaurians. The degree of support for alternative placements of these two taxa, however, is markedly different for the two data sets.

Within the context of the modified data set of Yates *et al.* (2010), the most parsimonious topologies that depict *Coloradisaurus* and *Lufengosaurus* as more closely related to *Plateosaurus* than to *Massospondylus* are remarkably suboptimal, implying 20 extra steps (found to be significant by the Templeton test, as the  $p$ -values range between 0.013 and 0.087). On the other hand, within the context of the modified analysis of Upchurch *et al.* (2007), the most parsimonious topologies that depict *Coloradisaurus* and *Lufengosaurus* as closer to Plateosauridae than to Massospondylidae imply seven extra steps (not significantly longer than the MPTs by the Templeton test;  $p = 0.5$ ).

The small difference in tree length for trees that depict *Coloradisaurus* and *Lufengosaurus* as part of massospondylids or plateosaurids in the second analysis highlights the underlying differences in current data sets (and results) for basal sauropodomorph dinosaurs. Therefore, depending on the character sampling used, the massospondylid affinities of *Coloradisaurus* and *Lufengosaurus* are either strongly or moderately supported by the character data. Although both data sets agree on the massospondylid affinities of the *Coloradisaurus* and *Lufengosaurus*, further studies are needed to thoroughly understand the relationships among massospondylids and plateosaurids.

As noted previously, the position of *Coloradisaurus* and *Lufengosaurus* represents only part of the topological incongruences among recently published phylogenetic hypotheses of basal plateosaurian sauropodomorphs. These incongruences also include the affinities of a growing number of recently described taxa that have an uncertain position among nonsauropod sauropodomorphs (e.g. *Seitaad*, *Sarhsaurus* and *Jingshanosaurus*). For instance, in the results obtained here, the massospondylid affinities of sev-

eral recently described taxa are disputed (e.g. *Seitaad* and *Sarhsaurus*), as discussed by Apaldetti *et al.* (2011). Further studies on these recently described taxa are needed to assess with confidence their status and phylogenetic affinities.

## CONCLUSIONS

The new information provided by PVL 5904 increases our knowledge of the anatomy of basal sauropodomorphs from the Los Colorados Formation, which represents one of the most diverse Late Triassic sauropodomorph assemblages in the world. *Coloradisaurus* was a small and gracile basal sauropodomorph that contrasts with the much more robust *Riojasaurus*, the even larger basal sauropod *Lessemsaurus* and the new unnamed form PULR136 (Ezcurra and Apaldetti 2011), all of which were found in the uppermost section of Los Colorados Formation. The existence of four taxa with slightly different body plans in this unit suggests these sympatric basal sauropodomorphs may have had ecological differences, providing another case of niche partitioning (Barrett 2000) for sauropodomorph dinosaurs in the terrestrial ecosystems during the Late Triassic. The specimen described here reveals the postcranial anatomy of *Coloradisaurus brevis*, allowing a more extensive characterization and autapomorphy-based diagnosis of this taxon.

The postcranial anatomy of PVL 5904 also bears phylogenetic information that provides support for the close relationships of *Coloradisaurus* and *Lufengosaurus*, such as the distal expansion of the pubis, the shape of the tibiofibular crest of the femur, and the shape of the proximal surface of the metatarsus. The results obtained here show that in the two data sets analysed postcranial features are critical for allying *Coloradisaurus* and *Lufengosaurus* as sister taxa. Cranial features of *Coloradisaurus*, instead, include a mix of derived characters shared with both massospondylids and plateosaurids that are relevant for postulating this clade as more closely related either to *Massospondylus* or to *Plateosaurus*. The close affinities of *Coloradisaurus* and *Lufengosaurus* and their position within Massospondylidae are congruent in the two data sets used in this study, although the character support for their phylogenetic placement differs likely due to the distinct character and taxon sampling regimes of both data matrices. These results highlight some of the current conflict in the phylogeny of basal sauropodomorphs and further studies are needed to confidently assess not only the phylogenetic relationships of *Lufengosaurus* and *Coloradisaurus* but also to thoroughly test the affinities of other recently described nonanchisaurian sauropodomorphs.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Phylogenetic analyses and results.

**Appendix S2.** Scoring of *Coloradisaurus* (modified from Yates *et al.* 2010).

**Appendix S3.** Scoring of *Coloradisaurus* (modified from Upchurch *et al.* 2007).

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