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BASAL SAUROPODOMORPHS FROM THE ISCHIGUALASTO FORMATION

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ABSTRACT—Basal sauropodomorphs from the Ischigualasto Formation include *Eoraptor lunensis*, *Panphagia protos*, and *Chromogisaurus novasi*. Few comparisons have been made between these taxa, because *Eoraptor* was only recently reassessed as a basal sauropodomorph and because *Panphagia* and *Chromogisaurus* were described nearly simultaneously. We describe in detail the fully prepared bones of the holotype of *Chromogisaurus novasi*, examine the evidence for its taxonomic distinction, and analyze the phylogenetic relationships among basal sauropodomorphs. Our results support *Chromogisaurus novasi* as a valid genus and species and provide weak phylogenetic evidence favoring a series of stem taxa at the base of Sauropodomorpha. The analysis positions *Panphagia* as the basal-most sauropodomorph, followed by *Eoraptor*, *Pampadromaeus*, and a clade that includes *Chromogisaurus* and *Saturnalia*.

RESUMEN—Los sauropodomorfos basales de la Formación Ischigualasto incluyen *Eoraptor lunensis*, *Panphagia protos* y *Chromogisaurus novasi*. Pocas comparaciones se han hecho entre estos taxones, porque *Eoraptor* fue reevaluado recientemente como sauropodomorfo basal y porque *Panphagia* y *Chromogisaurus* se describieron de forma casi simultánea. Describimos en detalle los huesos totalmente preparados del holotipo de *Chromogisaurus novasi*, examinamos la evidencia de su distinción taxonómica, y analizamos la relación filogenética entre sauropodomorfos basales. Nuestros resultados apoyan a *Chromogisaurus novasi* como un género y especie válido y proporcionan débil soporte filogenético favoreciendo un arreglo parafilético en la base de Sauropodomorpha. El análisis posiciona a *Panphagia* como el sauropodomorfo más basal, seguido de *Eoraptor*, *Pampadromaeus* y un clado que incluye a *Chromogisaurus* y *Saturnalia*.

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

INTRODUCTION

Basal sauropodomorphs are represented in two of the oldest dinosaur-bearing geologic units, namely the Ischigualasto Formation of Argentina (Ezcurra et al., 2008; Ezcurra, 2010; Martínez and Alcober, 2009; Martínez et al., 2011) and the Santa Maria Formation of Brazil (Langer et al., 1999; Cabreira et al., 2011). For many years dinosaurs were thought to comprise a relatively small proportion of the archosaurs in the Ischigualasto fauna, including only the ornithischian *Pisanosaurus* (Casamiquela, 1967) and the theropods *Herrerasaurus* (Reig, 1963; Sereno and Novas, 1992) and *Eoraptor* (Sereno et al., 1993). Sauropodomorphs had yet to be recorded.

In recent years, however, four new dinosaurs have been described, including the basal sauropodomorphs *Panphagia protos* (Martínez and Alcober, 2009) and *Chromogisaurus novasi* (Ezcurra, 2010), the herrerasaurid theropod *Sanjuansaurus gordilloi* (Alcober and Martínez, 2010), and the basal theropod *Eodromaeus murphi* (Martínez et al., 2011). All of these dinosaurs were recovered from the *Scaphonyx-Exaeretodon-Herrerasaurus* biozone, which is dated to approximately 231 Ma (Rogers et al., 1993; Martínez et al., 2011).

The similar morphology and near-synchronous, independent description of the two aforementioned sauropodomorphs, *Panphagia* (Martínez and Alcober, 2009) and *Chromogisaurus* (Ezcurra, 2010), leave their validity an open question. Prior to a detailed comparison, we completely prepared the holotype and only known specimen of *Chromogisaurus*. The recent reinterpretation of *Eoraptor* as a basal sauropodomorph closely related to *Panphagia* (Martínez et al., 2011) underscored the need to effectively compare these three contemporaneous basal sauropodomorphs. Although missing data are a problem for all

taxa considered except *Eoraptor* and *Saturnalia*, we analyzed the phylogenetic relationships among known basal sauropodomorphs.

METHODS

Comparative Specimens

Comparisons were made using the holotypic specimens of *Chromogisaurus* (PVSJ 845), *Panphagia* (PVSJ 874), and *Sanjuansaurus* (PVSJ 605), holotypic and referred specimens of *Eodromaeus* (PVSJ 534, 561, 562), *Eoraptor* (PVSJ 512, 559), *Saturnalia* (MCP 3844-PV, 3845-PV, 3846-PV), and *Guaibasaurus* (MCN PV 2355, 2356, UFRGS PV 0725T), and referred specimens of *Herrerasaurus* (PVSJ 373, 380, 407). Other comparisons were based on published figures.

Photography

Some bone surfaces of *Chromogisaurus* (PVSJ 845) were painted with neutral gray acrylic paint to remove color distractions prior photography.

Anatomical and Taxonomic Terminology

We employ traditional, or 'Romerian,' anatomical and directional terms over veterinarian alternatives (Wilson, 2006). 'Anterior' and 'posterior,' for example, are used as directional terms rather than the veterinarian alternatives 'rostral' or 'cranial' and 'caudal.' We also follow recent recommendations regarding the identification of vertebral laminae (Wilson, 1999).

We used the phylogenetic definitions for basal taxa within Dinosauria proposed by Sereno (2005a, 2005b, 2007). Sauropodomorpha, for example, has a stem-based definition in opposition to Theropoda and does not require the monophyly of Saurischia or Prosauropoda, as do other definitions (e.g., Galton and Upchurch, 2004). In this way, Sauropodomorpha is defined as

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the most inclusive clade containing *Saltasaurus loricatus* but not *Passer domesticus* or *Triceratops horridus*.

Institutional Abbreviations—**MCN**, Museu de Ciencias Naturais, Rio Grande do Sul, Brazil; **MCP**, Museo de Ciencias e Tecnología, Porto Alegre, Brazil; **PVSJ**, Instituto y Museo de Ciencias Naturales, Universidad Nacional de San Juan, San Juan, Argentina; **UFRGS,** Universidade Federal de Rio Grande do Sul, Porto Alegre, Brazil.

SYSTEMATIC PALEONTOLOGY

DINOSAURIA Owen, 1842
SAURISCHIA Seeley, 1887
SAUROPODOMORPHA Huene, 1932
CHROMOGISAURUS Ezcurra, 2010
CHROMOGISAURUS NOVASI Ezcurra, 2010
(Figs. 4–8, 9A–E, 10–13, 14A–E, 15)

Type Specimen—PVSJ 845, partial skeleton comprising one anterior and two mid-caudal vertebrae, anterior chevron, glenoid region of the left scapulocoracoid, right ilium lacking preacetabular process, acetabular portion of the left ilium, shaft of the right femur and proximal and distal ends of the left femur, complete right tibia and proximal end of the left tibia, right fibula lacking proximal and distal ends and proximal end of the left fibula, right metatarsal 2, right digit III phalanges, and unidentified bone fragments.

Type Locality—Cancha de Bochas, Hollada de Ischigualasto, Ischigualasto Provincial Park, San Juan Province, Argentina.

Age and Distribution—The horizon is located at the southern outcrops of the Ischigualasto Formation, 40 m above the base of the unit in the Cancha de Bochas Member (sensu Currie et al., 2009). The holotypic location belongs to the lower *Scaphonyx-Exaeretodon-Herrerasaurus* biozone (Martínez et al., 2011). The mid-Carnian age is based on a radioisotopic date near the base of the formation (Rogers et al., 1993) that was recently recalibrated to 231.4 Ma (Martínez et al., 2011).

Revised Diagnosis—Basal sauropodomorph diagnosed by the following combination of features (asterisk indicates an autapomorphy): marked posterior projection of the iliac postacetabular process; incipient perforation of the iliac portion of the acetabulum; low lateral projection of the iliac supraacetabular crest; strongly concave acetabular surface of the supraacetabular crest; femoral lateral condyle smaller than the medial condyle; medial surface of the proximal end of the fibula with an elongate rugosity adjacent to the anterior margin of the shaft*; metatarsal 2 with strongly dorsoventrally asymmetric distal condyles*.

DESCRIPTION

We offer alternative identifications for several elements described by Ezcurra (2010), based on comparisons with other basal saurischians from the Ischigualasto Formation, namely, *Eoraptor* (Sereno et al., 1993), *Panphagia* (Martínez and Alcober, 2009), and *Eodromaeus* (Martínez et al., 2011).

Reidentification of Ulna, Ischium, and Metatarsal

Lower Jaw Fragment—Originally described as the proximal end of the right ulna (Ezcurra, 2010), this fragment is clearly not an ulna because it is formed of four different bones instead of only one (Fig. 1). It is reidentified here as the posterior end of a right lower jaw, possibly of the rhynchosaur *Scaphonyx* (Fig. 1). Measuring 29.5 mm in length, the sutured bones that form the fragment preserves the right articular and posterior ends of the angular, surangular, and prearticular.

The surangular comprises most of the lateral surface of the preserved piece (Fig. 1A), as in the rhynchosaurs *Scaphonyx* (Sill, 1970) and *Hyperodapedon* (Benton, 1983; Langer and Schultz, 2000) (Fig. 2A). The surangular forms the dorsal one-half of the lateral surface, with the ventral one-half formed by the angular, as in the basal dinosaurs *Eoraptor*, *Panphagia*, *Herrerasaurus*, *Tawa* (Nesbitt et al., 2009), and *Lesothosaurus* (Galton, 1978; Knoll, 2002). In the fragment in question, the surangular wraps around the posterior end of the retroarticular process (Fig. 1C), as also occurs in *Scaphonyx* and *Hyperodapedon* (Fig. 2C). The posteroventral surface of the surangular is eroded, exposing the internal texture of the bone. Ezcurra (2010) interpreted this feature as the strongly striated surface of the olecranon.

The posterior portion of the prearticular is broken and eroded (Fig. 1B). It contacts the angular ventrally, the surangular posteriorly, and the articular dorsally. The prearticular forms the medial wall of the adductor fossa and covers most of the medial aspect of the articular, as in *Scaphonyx* and *Hyperodapedon* (Fig. 2B). In basal dinosaurs, in contrast, more of the articular is exposed dorsal to the prearticular (e.g., *Panphagia*, *Herrerasaurus*, *Lesothosaurus*). The angular forms the ventral margin of the posterior end of the lower jaw, extending to the extremity of the retroarticular process (Fig. 1B). The prearticular-surangular suture is not clear. The articular has a subquadrate articular surface as seen in dorsal view and is relatively small (Fig. 1C). The small size of the articular relative to the posterior end of the lower jaw is similar to that in *Scaphonyx* and *Hyperodapedon* (Fig. 2C) and unlike the proportionately larger articular socket in basal dinosaurs (e.g., *Panphagia*, *Eoraptor*, *Herrerasaurus*). Posterior to the articular, a deep fossa opens dorsally on the retroarticular process (Fig. 1C), as in *Hyperodapedon* (Benton, 1983).

The posterior end of the lower jaw is stout, transversely flattened, and dorsoventrally high (Fig. 1A, B), resembling *Scaphonyx* (Sill, 1970) and *Hyperodapedon* (Fig. 2A, B), but differing markedly from the slender proportions and low profile of the comparable portion of the lower jaw of the dinosauriform *Silesaurus* (Dzik, 2003) and basal dinosaurs. This holds for the basal sauropodomorphs *Panphagia*, *Eoraptor*, *Adeopapposaurus* (Martínez, 2009), and *Pantydraco* (Galton and Kermack, 2011), the basal theropods *Eodromaeus*, *Herrerasaurus* (Sereno and Novas, 1994), *Tawa* (Nesbitt et al., 2009), and *Coelophysis* (Raath, 1977), and the basal ornithischians *Pisanosaurus* (Casamiquela, 1967) and *Heterodontosaurus* (Crompton and Charig, 1962).

Chevron—Originally described as metatarsal 5 (Ezcurra, 2010), this bone is reidentified here as an anterior chevron (Fig. 6). The morphology in support of the new interpretation includes the 'Y'-shaped proximal end with a pair of articular facets, a hemal canal, and the laterally compressed, distally expanding shaft (see Description).

Bone Fragments of Unknown Identity and Affinity—One bone piece originally assigned to the type specimen was identified as a probable section of the ischial shaft (Ezcurra, 2010). The squared section and massive size of the bone (Fig. 3) does not closely resemble the triangular section and slender proportions of the ischium in basal saurischians (e.g., *Eoraptor*, *Saturnalia*, *Eodromaeus*). Two other bone pieces originally included as part of the holotype have similar size, cross-sectional shape, and surface detail, suggesting that they may belong to the same bone (Fig. 3). The bone surface of these three pieces, however, does not preserve the fine, subparallel fractures and adhering hematite that characterize the other bones of the holotype. The sharp longitudinal ridge (Ezcurra, 2010:fig. 7B) is interpreted here as postmortem crushing, displacing one side with respect to the other. The identification of these pieces and their association with the other bones of the holotype remain uncertain.
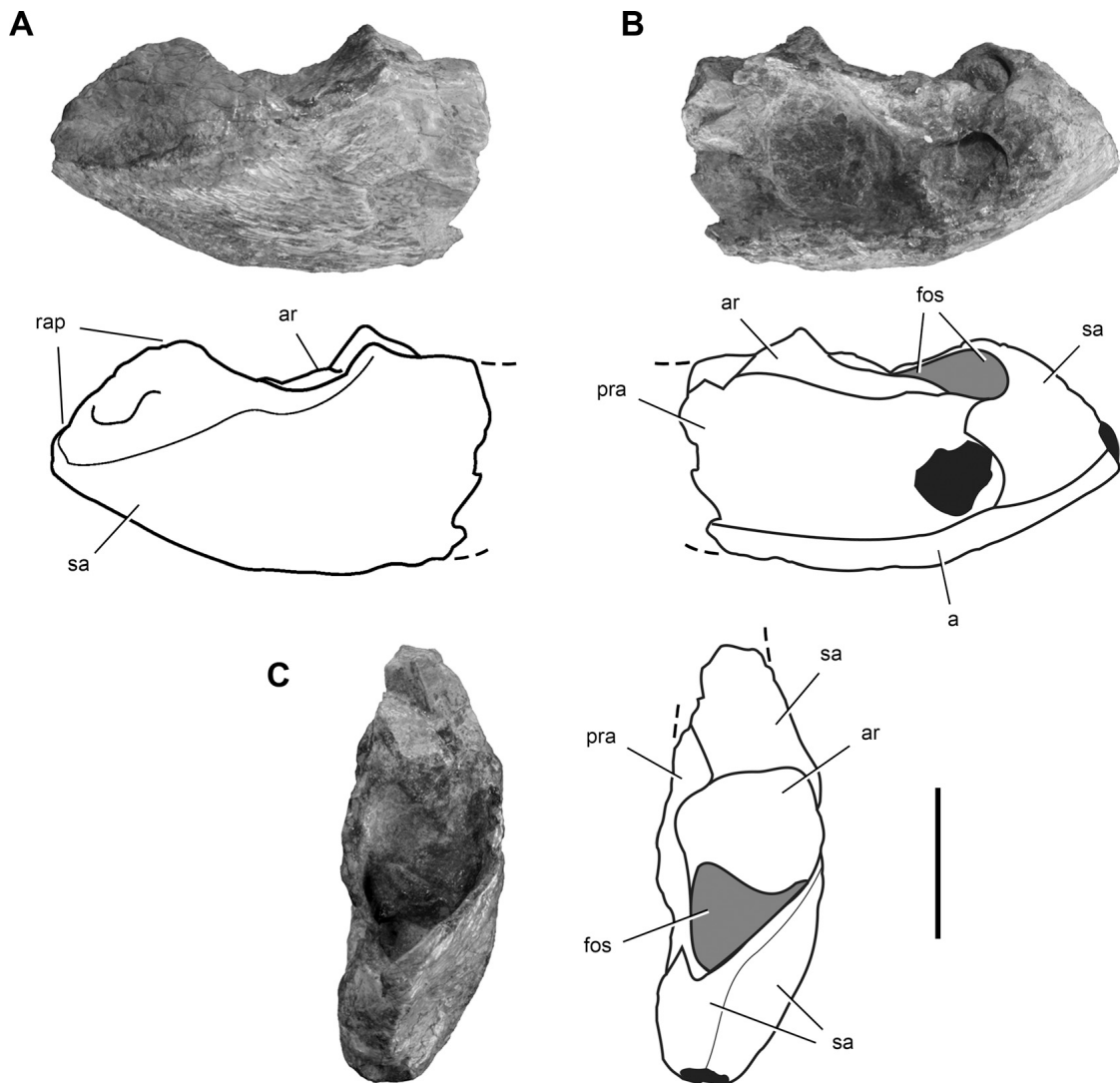
FIGURE 1. Photographs and line drawings of the posterior end of the right lower jaw of a possible rhynchosaur in lateral (**A**), medial (**B**), and dorsal (**C**) views. This specimen was originally included in the holotypic specimen of *Chromogisaurus novasi* (PVSJ 845) by Ezcurra (2010). Dark tone indicates broken areas; light tone indicates cavities. **Abbreviations**: **a**, angular; **ar**, articular; **fos**, fossa; **pra**, prearticular; **rap**, retroarticular process; **sa**, surangular. Scale bar equals 1 cm.

Description

Caudal Vertebrae—Three caudal vertebrae of *Chromogisaurus* are preserved. Based on general proportions, size of the transverse processes, and location and size of the neural spines, the first is likely to be in the range of caudal vertebrae 4–6 (Fig. 4) and the other two in the range of caudal vertebrae 14–16 (Fig. 5). The posterior-most mid-caudal vertebra (Fig. 5F, G) was not reported in the original description (Ezcurra, 2010). All of the centra are spool-shaped and strongly transversely compressed (Figs. 4D, 5C). In lateral view, the caudal centra are subrectangular with parallel anterior and posterior margins (Figs. 4A, B, 5A).

The mid-caudal centra of *Chromogisaurus* are slightly shorter (2%) than the anterior caudal centrum. The anterior and posterior faces of the caudal centra are oval, strongly concave, and bordered by a prominent external rim (Figs. 4E, F, 5D, E). The ventral surface of the anterior centrum is convex without any groove or keel (Fig. 4D), differing from the mid-caudal vertebrae, which have a longitudinal groove (Fig. 5C). The articular facets for the chevrons are small (Figs. 4A, B, 5A).

The neural arches of caudal vertebrae of *Chromogisaurus* are gracile, differing from the more robust neural arches present in *Panphagia* and *Eoraptor*. The transverse process of the anterior caudal vertebra is flattened and located in the middle of the centrum (Fig. 4C–F). The dorsolaterally directed transverse processes of the caudal vertebrae of *Chromogisaurus* are subtriangular and taper distally (Figs. 4C, D, F, 5F, G). They are relatively long in *Chromogisaurus*, constituting 82% of the length of the centrum (Ezcurra, 2010). The transverse processes of the distal-most mid-caudal vertebra are flat, strap-shaped, nearly horizontal, and directed posterolaterally (Fig. 5F, G). In the anterior and mid-caudal vertebrae of *Chromogisaurus*, pre- and postzygapophyses extend slightly beyond the ends of the centrum (Ezcurra, 2010; Figs. 4A, B, 5A), as in *Eoraptor*, *Panphagia*, and *Eodromaeus*. In *Herrerasaurus* and *Sanjuansaurus*, in contrast, the postzygapophyses terminate flush with the posterior rim of the centrum. In
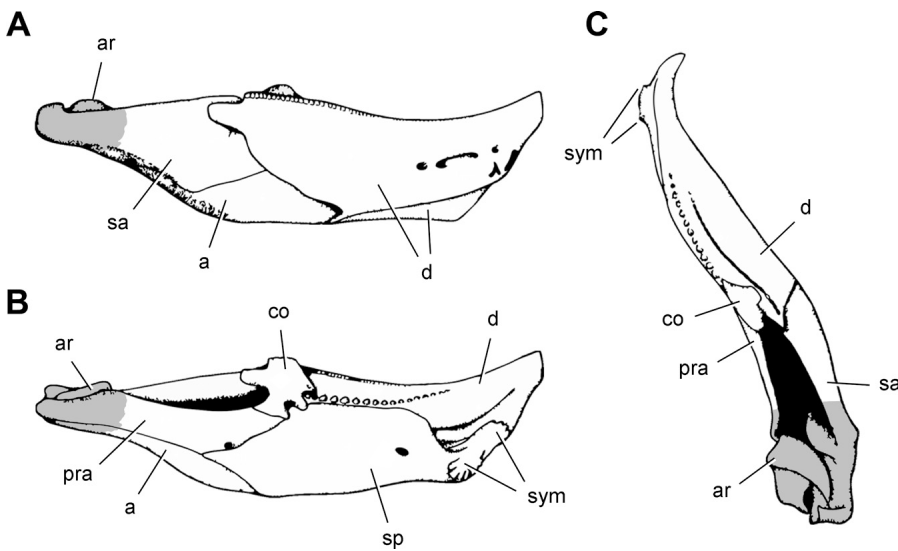
FIGURE 2. Reconstruction of the right lower jaw of the rhynchosaur *Hyperodapedon gordoni* in lateral (**A**), medial (reversed) (**B**), and dorsal (**C**) views (from Benton, 1983). **Abbreviations**: **a**, angular; **ar**, articular; **co**, coronoid; **d**, dentary; **pra**, prearticular; **sa**, surangular; **sp**, splenial; **sym**, symphysis. Gray tone indicates the region of the mandible preserved in the posterior end of the lower jaw in Figure 1.

Chromogisaurus, the zygapophyseal articular surfaces are oval and taper distally. Hyposphene-hypantrum articulations are unknown in caudal vertebrae of *Chromogisaurus* (Ezcurra, 2010). As in other basal dinosaurs, a deep median notch separates the postzygapophyses (Figs. 4F, 5E; contra Ezcurra, 2010). The neural arch of the anterior caudal has a weakly developed interpostzygapophyseal lamina (Ezcurra, 2010; Fig. 4A), a feature unknown in other dinosaurs from the Ischigualasto Formation. All the neural spines are damaged, although they seem to be anteroposteriorly wide, extending along two-thirds of their respective neural arches. The height of the neural spine of the mid-caudal vertebrae appears to be one-third of the height of the neural arch (Fig. 5A, D, E). The tall spine originally reported for mid-caudal vertebrae (Ezcurra, 2010:fig. 4) is an artifact of preservation; a thin fragment of bone was pressed against the neural spine.

Chevron—The single preserved chevron of *Chromogisaurus* is from the proximal end of the tail probably in the range of caudal vertebrae 4–6 (Fig. 6), based on its large size, lateral shape, size of the articular facets, and distal anteroposterior expansion, and in comparison with the chevrons of *Eoraptor*. It lacks portions of both proximal and distal ends. Its length is approximately 2.5 times the height of the centrum of the anterior caudal vertebra (Fig. 5E). The proximal end is 'Y'-shaped with two distinct articular facets. The anterior facet faces anterodorsally, and the smaller, posterior facet faces posterodorsally (Fig. 6B–D). The orientation of the anterior facet suggests that the chevron shaft was inclined at approximately 45° to the longitudinal axis of the tail. Due to transverse compression, the anterior opening of the hemal canal has been closed (Fig. 6C). The shaft is laterally compressed, straight, and anteroposteriorly expanded at its distal end.

Scapulocoracoid—The left glenoid region is the only preserved portion of the scapula and coracoid, which are joined along a fused suture (Fig. 7). The scapular glenoid is an oval-shaped concavity with its long axis oriented dorsoventrally (Fig. 7D). The scapular glenoid faces posteroventrally and somewhat laterally, as in *Panphagia*, *Eoraptor*, and *Saturnalia* (Langer et al., 2007). A fossa is located dorsal to the posterodorsal rim of the glenoid (Fig. 7B, D), as in *Eoraptor*, *Panphagia*, and *Eodromaeus*. Shallow medial and lateral depressions are present just anterior to the posterodorsal border (Fig. 7B, C). The rim of the glenoid is sharp (Fig. 7B, D). Not enough of the coracoid is preserved to comment on its form.

Ilium—The right ilium is the more complete, lacking only the preacetabular process; the distal end of the right pubic peduncle is weathered laterally (Fig. 8A–D). Only a central piece of the left ilium is preserved (Fig. 8E). The ilium is vertically deep with a relatively long postacetabular process, as in other basal sauropodomorphs (e.g., *Eoraptor*, *Adeopapposaurus*). In lateral view, the dorsal margin of the iliac blade is straight and curves ventrally as it approaches the preacetabular process (Fig. 8A, B). In dorsal view, the iliac blade is gently curved with acetabular processes diverging laterally (Fig. 8C), as in other basal sauropodomorphs (e.g., *Eoraptor*, *Saturnalia*, *Adeopapposaurus*). A broad, triangular depression covers much of the lateral aspect of the ilium dorsal to the supraacetabular crest (Ezcurra, 2010), as is also present in *Saturnalia* (Langer, 2003). The posterior projection at the base of the ischial peduncle is poorly developed.

The supraacetabular crest is a well-developed, raised shelf (Fig. 8A, C, D). Although the pubic peduncle is partially damaged, the crest seems to continue to its distal end (Fig. 8A). The supraacetabular crest has a sinuous curve in lateral view (Fig. 8A). A ventral flange partially closes the acetabulum in *Chromogisaurus* (Ezcurra, 2010; Fig. 8A, B), but its arched ventral margin suggests that the acetabulum had a central unossified gap.

The pubic peduncle is long, with its distal end facing anteroventrally (Fig. 8A, C). The distal end of the pubic peduncle has a subtriangular cross-section with slightly concave medial, dorsolateral, and ventrolateral borders. The broader and shorter ischial peduncle has its distal articular surface oriented more ventrally (Ezcurra, 2010; Fig. 8A, B). The distal end of the ischial peduncle is subtriangular, with flat medial and slightly convex posterior and lateral margins (Fig. 8D). The antitrochanter is smooth, poorly developed, and positioned on the anteroventral corner of the peduncle (Ezcurra, 2010).

The long postacetabular process tapers distally to a rounded end in lateral view, which has sustained some weathering. As was noted by Ezcurra (2010), the lateral surface bears a thick and trapezoidal rugose area, which tapers anteriorly along the dorsolateral border of the iliac blade (Fig. 8A). The well-developed brevis shelf does not join the supraacetabular crest (Fig. 8A). The posteromedial shelf is moderately developed and similar in transverse width to the brevis shelf in dorsal or ventral view (Fig. 8C, D). In cross-section at midlength, the postacetabular process has an
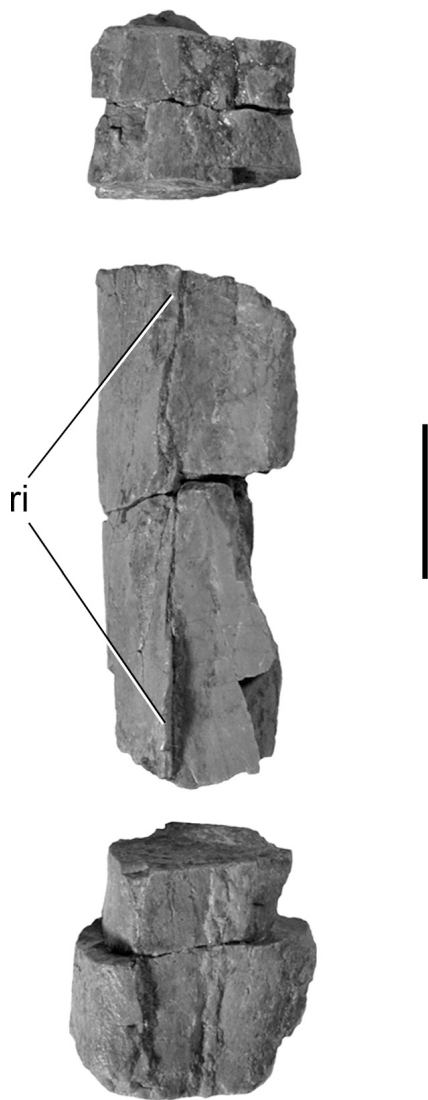
FIGURE 3. Bone fragments of unknown affinity and identity in dorsal view. These fragments were originally identified as a possible portion of the ischial shaft and included in the *Chromogisaurus novasi* holotype (PVSJ 845) by Excurra (2010). **Abbreviations**: **ri**, ridge. Scale bar equals 1 cm.

inverted 'V'-shape. The posteromedial shelf extends anteroventrally and dissipates as a rounded ridge on the medial surface of the iliac blade dorsal to the supraacetabular crest. Only the base of the preacetabular process is preserved (Fig. 8A, B). The ventral margin is thicker than the dorsal margin, so that the broken cross-section of the process is subtriangular. The ventral margin of the process is everted dorsal to the level of the supraacetabular crest.

Femur—Although both femora are incomplete (Figs. 9A–E, 10, 11), they overlap to allow an estimate of the form and length (ca. 170 mm) of the bone. The femur is gracile—its minimum circumference-to-length ratio equals 0.28—and slightly shorter than the tibia (Fig. 9F). In lateral view, the shaft of the femur has a sigmoid curve, as in other basal dinosaurs. In anterior view, it is straight with the femoral head rotated anteromedially. The shaft of the right femur of *Chromogisaurus* is transversely crushed, which may have flattened the medial projection of the head (com-

pare Fig. 9C and F). The proximal surface of the femoral head is kidney-shaped, as in most other basal dinosaurs, but it faces dorsally and is almost straight in posteromedial view (Fig. 9C, D). The proximal surface bounded by sharp edges, between which lies a groove extending anteromedially from the greater trochanter (Fig. 9E), as in basal dinosaurs such as *Eoraptor* (PVSJ 855), *Saturnalia*, *Herrerasaurus*, and *Staurikosaurus* (Galton, 1977). The greater trochanter is developed as a prominent ridge (Fig. 9A, D, E). The anterior surface of the femoral neck bears a sharp ridge that extends from the anteromedial end of the head and tapers distally (Fig. 9B, C). The trochanteric shelf extends along the lateral aspect of the proximal end, dissipating on its posterior aspect dorsal to the fourth trochanter (Ezcurra, 2010; Fig. 9).

A deep, elliptical fossa is present ventral the trochanteric shelf on both femora (Figs. 9A, 10A), which was considered an autapomorphy by Ezcurra (2010). Careful observation of the better-preserved left femur reveals compressional fractures surrounding each fossa (Fig. 9A). A similar fossa is present in some specimens of *Eodromaeus* (PVSJ 534, PVSJ 562), which also shows evidence of postmortem transverse compression (Fig. 9F). We regard this structure as an artifact of crushing and collapse of the internal lumen of the femoral shaft.

A prominent, crescentic fourth trochanter projects from the proximal half of the femoral shaft (Fig. 9A, B, D, E). The distal portion of the fourth trochanter is damaged on both sides. Whether the trochanter extends distally to end with an asymmetric profile, as in many basal saurischians (e.g., *Eoraptor*, *Saturnalia*, *Herrerasaurus*, *Staurikosaurus*, *Eodromaeus*), cannot be determined. A marked rugose scar for insertion of the M. caudofemoralis longus (Langer, 2003) is present on the medial aspect of the fourth trochanter and extends distally as a shallow striated fossa (Fig. 9B).

The distal end of the left femur, although partially broken, has a nearly subcircular shape as preserved (Fig. 11E). The medial border is flat, and the medial (tibial) condyle is oval and anteroposteriorly longer than the lateral condyle. The posterior surface is marked by a deep popliteal fossa that separates the condyles (Figs. 9F, 11D). At the distal end of the femur, a large rugose attachment scar is present facing anteriorly (Fig. 11C).

Tibia—The right tibia and proximal end of the left tibia are preserved, both of which have been flattened transversely (Fig. 12). The tibia is slender and measures 175 mm long. The tibiofemoral ratio is 1.03, similar to the values of *Eoraptor* (Sereno et al., 2013) and *Eodromaeus* (Martínez et al., 2011). The proximal articular surface is subtriangular and deeply concave, which has been exaggerated by transverse compression (Fig. 12E). As noted by Ezcurra (2010), the lateral condyle is located slightly anterior to the medial condyle (Fig. 12E). A median notch separates the proximal condyles (Fig. 12D, I). A low and symmetrical cnemial crest forms the anterior margin of the proximal end (Fig. 12A–C, E, H). A very pronounced longitudinal tuberosity is present on the lateral surface posterior to the concavity formed adjacent to the cnemial crest (Ezcurra, 2010; Fig. 12A, G). The shaft of the tibia is straight (Fig. 12A–D). The distal end has been transversely compressed postmortem, so that its transverse width is only about 40% of its anteroposterior depth (Fig. 12F). The medial tip of the posterolateral process projects distally (Fig. 12A–C). A groove on the lateral aspect of the distal end separates the posterolateral flange from the shaft of the tibia (Fig. 12A). As in other basal dinosaurs, the distal articular surface of the tibia is split between a broad astragalar articular surface and a convex 'L'-shaped surface formed by the posterolateral flange (Fig. 12F).

Fibula—Portions of both fibulae are preserved. On the right side, both the proximal and distal ends are broken away (Fig. 13A, B). On the left side, the proximal end is well preserved (Fig. 13C–F). The fibula is narrower transversely than the tibia;
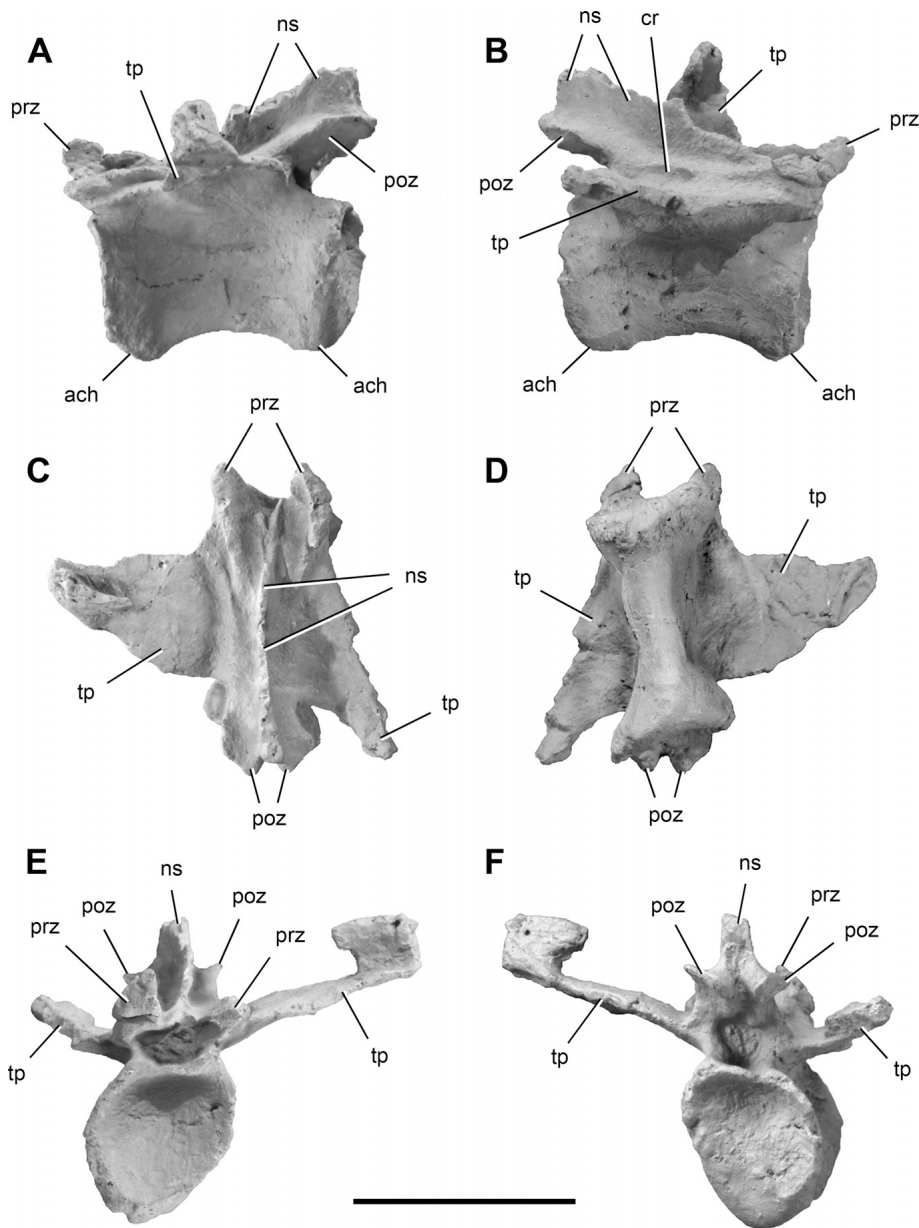
FIGURE 4. Proximal caudal vertebra of *Chromogisaurus novasi* (PVSJ 845) in left lateral (**A**), right lateral (**B**), dorsal (**C**), ventral (**D**), anterior (**E**), and posterior (**F**) views. **Abbreviations**: **ach**, articular surface for a chevron; **cr**, crest; **ns**, neural spine; **poz**, postzygapophysis; **prz**, prezygapophysis; **tp**, transverse process. Scale bar equals 2 cm.

the anteroposterior width of the midshaft is almost two-thirds that of the tibia. The proximal end is anteroposteriorly expanded to a depth approximately three times its maximum width. The proximal surface is posteriorly concave and slightly anteriorly convex (Fig. 13F). The medial border of the proximal end is straight, although the medial surface becomes concave below the border. In lateral view, the anterior border of the proximal end of the fibula is convex, and the posterior border is slightly concave, as in many other basal saurischians. The anterior prominence of the anterior border is well marked (Fig. 13A–D). Two attachment scars are visible on the medial surface (Fig. 13C). The first is an oblique ridge extending anterodistally from the posterior corner of the proximal end of the fibula and is similar to that of *Saturnalia* (Langer, 2003), *Eodromaeus* (PVSJ 562), and *Herrerasaurus*. The second is a more rugose ridge located parallel to and near the anterior border of the fibula, converging distally with the aforementioned ridge

(Fig. 13C). As in many other dinosaurs (e.g., *Saturnalia*, *Eoraptor*, *Eodromaeus*, *Herrerasaurus*, *Sanjuansaurus*), a rugosity is present along the anterolateral border of the proximal end (Fig. 13D, E), probably for the insertion of the M. iliofibularis (Bittencourt and Kellner, 2009). The lateral surface of the proximal end is anterior and posteriorly concave and slightly convex at the middle. The shaft of the fibula gradually decreases in anteroposterior depth distally (Fig. 13A, B). The lateral surface of the shaft is convex and has a crest, or anterior trochanter (Fig. 13A), presumably for attachment of the M. iliofibularis (Langer, 2003). An elongate concavity extends for most of the length of the medial surface of the shaft due to postmortem collapse of the central lumen of the tibia (Fig. 13B).

Metatarsal 2—Only one metatarsal of *Chromogisaurus* is preserved. The metatarsal is difficult to identify with certainty, given the absence of its proximal end. Ezcurra (2010) regarded the
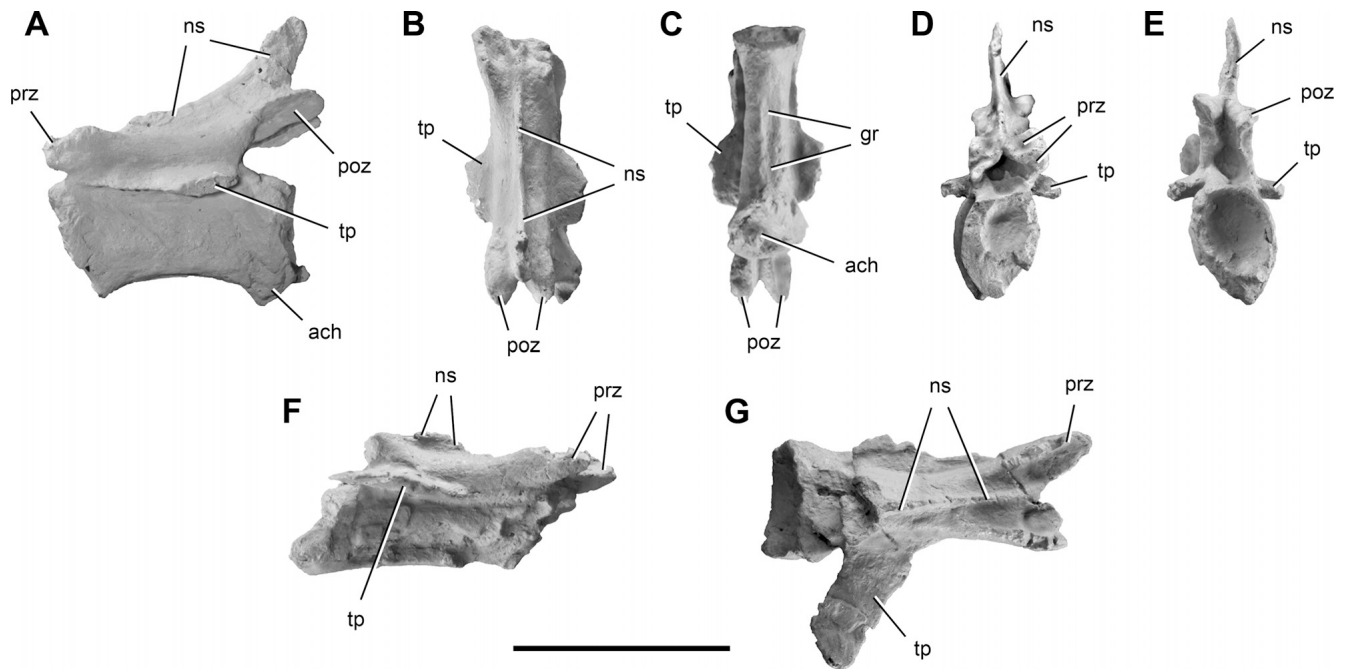
FIGURE 5. Mid-caudal vertebrae of *Chromogisaurus novasi* (PVSJ 845). The anterior-most preserved mid-caudal vertebra in left lateral (**A**), dorsal (**B**), ventral (**C**), anterior (**D**), and posterior (**E**) views. The posterior-most preserved mid-caudal vertebra in right lateral (**F**) and dorsal (**G**) views. Anterior is towards top in **B** and **C** and to the right in **G**. **Abbreviations**: **ach**, articular surface for a chevron; **gr**, groove; **ns**, neural spine; **poz**, postzygapophysis; **prz**, prezygapophysis; **tp**, transverse process. Scale bar equals 2 cm.

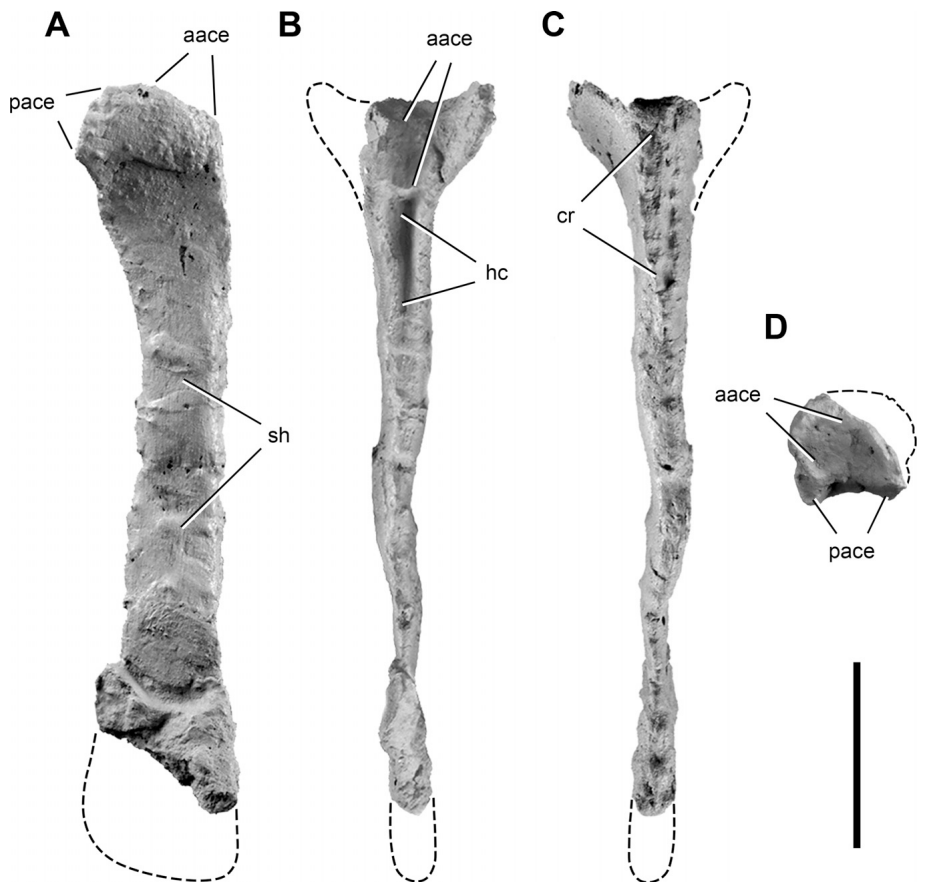FIGURE 6. Anterior chevron of *Chromogisaurus novasi* (PVSJ 845) in right lateral (**A**), anterior (**B**), posterior (**C**), and proximal (**D**) views. Dashed line indicates missing portions of proximal and distal ends. **Abbreviations**: **aace**, anterior articular surface for centrum; **cr**, crest; **hc**, hemal canal; **pace**, posterior articular surface for centrum; **sh**, shaft. Scale bar equals 1 cm.
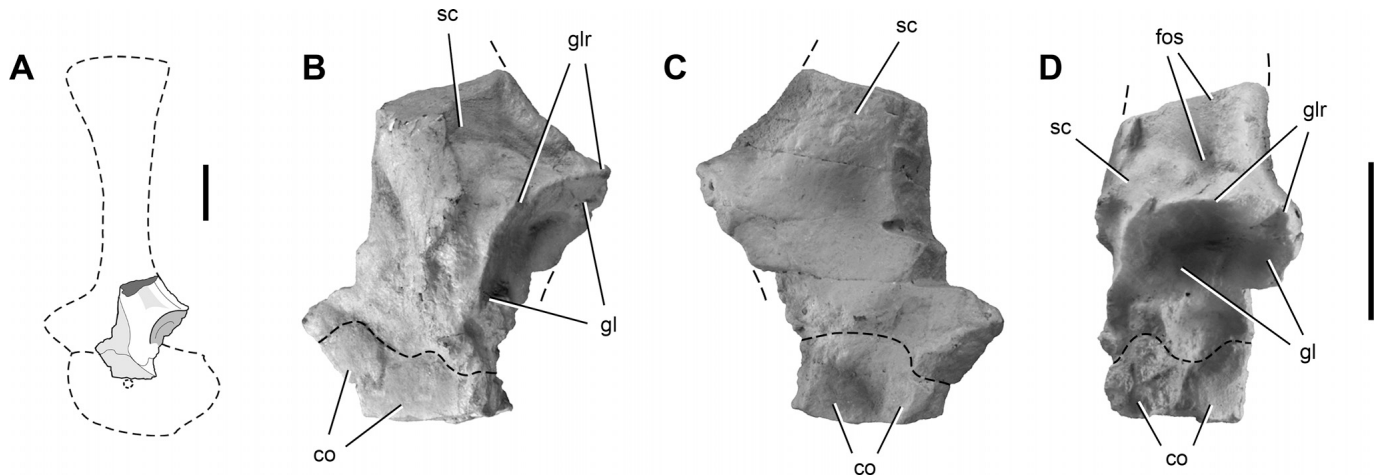
FIGURE 7. Proximal portion of the left scapulocoracoid of *Chromogisaurus novasi* (PVSJ 845) in left lateral (**A**, **B**), medial (**C**), and posterior (**D**) views. Dashed lines indicate fused scapulocoracoid suture and the continuation of preserved margins. **Abbreviations**: **co**, coracoid; **fos**, fossa; **gl**, glenoid; **glr**, glenoid rim; **sc**, scapula. Scale bars equal 1 cm (left scale bar for **A** only).
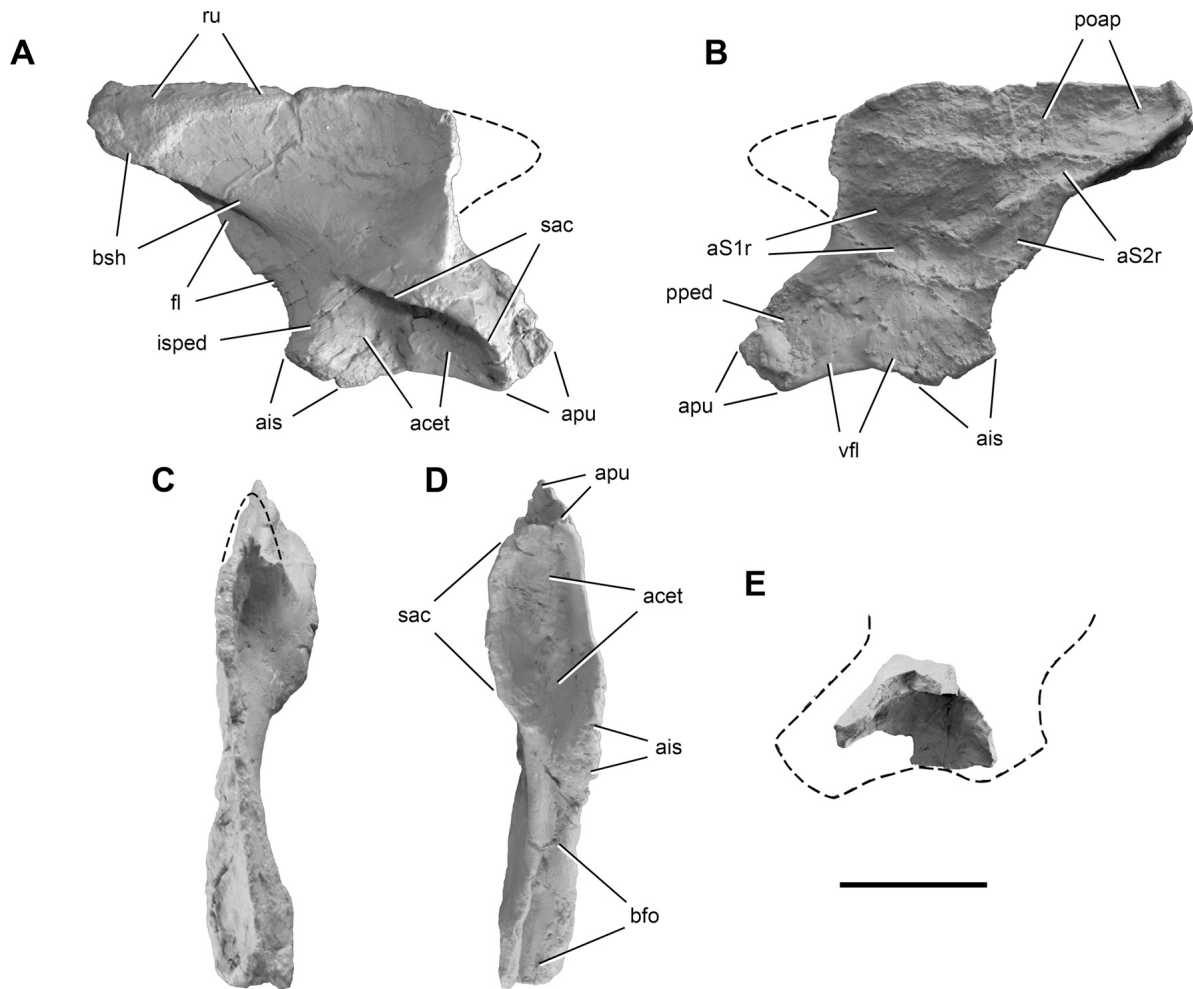
FIGURE 8. Ilia of *Chromogisaurus novasi* (PVSJ 845). Right ilium in lateral (**A**), medial (**B**), dorsal (**C**), and ventral (**D**) views. Fragmentary left ilium in lateral view (**E**). Dashed lines indicate the continuation of preserved margins. **Abbreviations**: **acet**, acetabulum; **ais**, articular surface for the ischium; **apu**, articular surface for the pubis; **aS1r**, articular surface for sacral 1 rib; **aS2r**, articular surface for sacral 2 rib; **bfo**, brevis fossa; **bsh**, brevis shelf; **fl**, flange; **isped**, ischial peduncle; **poap**, postacetabular process; **pped**, pubic peduncle; **ru**, rugosity; **sac**, supraacetabular crest; **vfl**, ventral flange. Scale bar equals 3 cm.

FIGURE 9. Femora of *Chromogisaurus novasi* and *Eodromaeus murphi*. Proximal end of the left femur of *Chromogisaurus novasi* (PVSJ 845) in lateral (**A**), medial (**B**), anterior (**C**), posterior (**D**), and proximal (**E**) views. Proximal end of the left femur of *Eodromaeus murphi* (PVSJ 562) in lateral view (**F**). Dashed lines indicate the continuation of preserved margins. *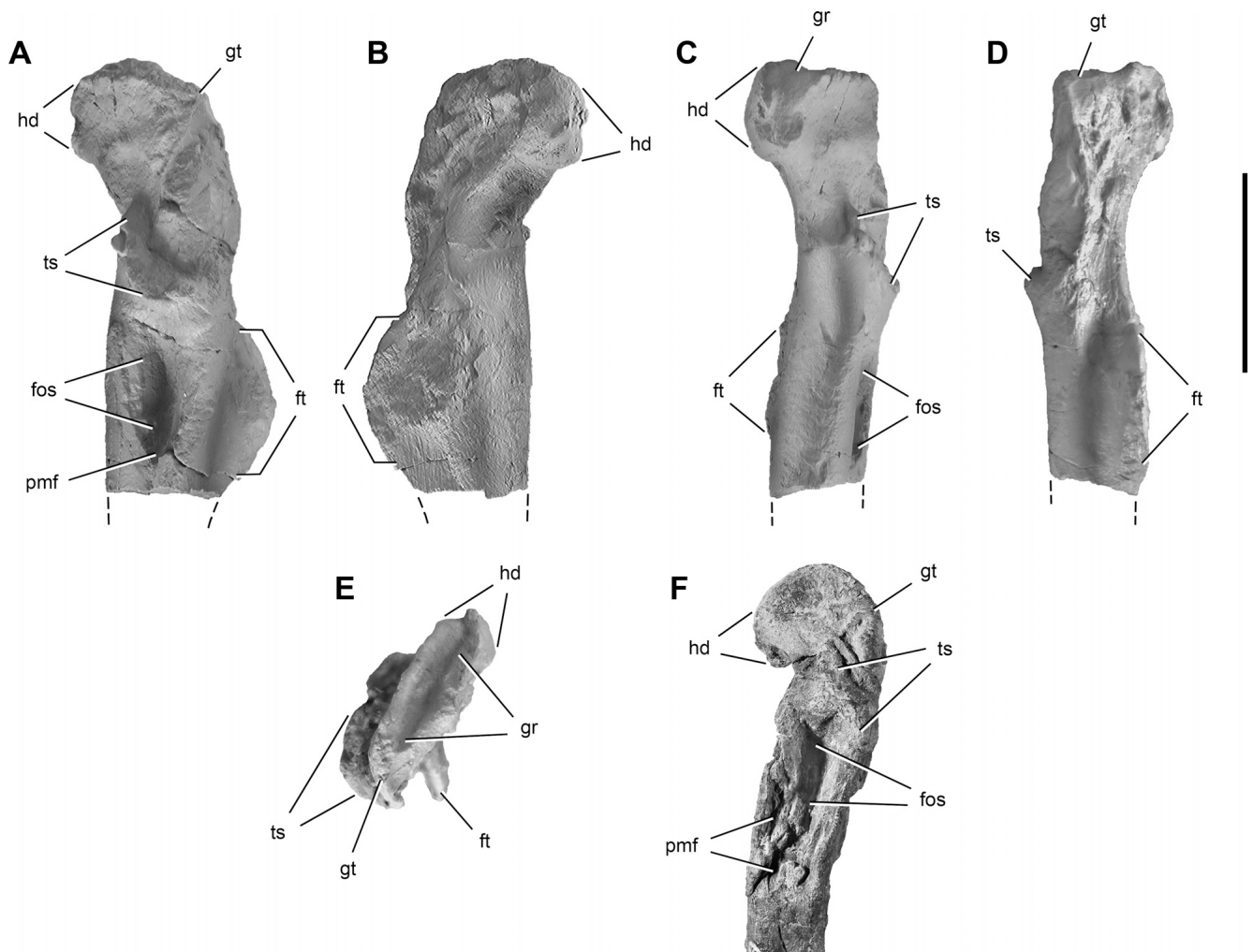*Abbreviations**: **fos**, fossa; **ft**, fourth trochanter; **gr**, groove; **gt**, greater trochanter; **hd**, head; **pmf**, postmortem fracturing; **ts**, trochanteric shelf. Scale bar equals 3 cm.

metatarsal and phalanges as pertaining to left pedal digit II. The size and marked asymmetry between its distal condyles clearly indicate that the metatarsal could only pertain to either metatarsal 2 or 4. The distal end is most similar to metatarsal 2 of other basal dinosaurs (e.g., *Eoraptor*, *Saturnalia*, *Herrerasaurus*). The distal end of metatarsal 4 is typically more asymmetric and divergent, and its lateral condyle is narrower. When identified as metatarsal 2, the asymmetry of the condyles indicates that it is from the right pes and not the left as proposed (Ezcurra, 2010). The greater distal extension of the lateral condyle of metatarsal 2 diverts the phalanges of pedal digit II medially from a sagittal axis, spreading the weight-supporting digits of the pes (Fig. 14F).

The shaft of metatarsal 2 is parallel-sided and does not change much in diameter along its length. In dorsal view, there is a distinct lateral curvature to the shaft (Fig. 14A), as in *Saturnalia*, *Eoraptor*, and *Herrerasaurus*. In cross-section, the metatarsal is subtriangular at midshaft with medial, anterior, and posterolateral surfaces. A shallow fossa on the dorsal surface of the distal one-third of the metatarsal is probably postmortem deformation

(Fig. 14A). The distal end is transversely broad, with a more distally developed lateral condyle and a larger lateral collateral ligament pit (Fig. 14A, B, D). An asymmetrical, deep, and broad extensor depression is located dorsal to the distal ginglymus. The narrow medial distal condyle protrudes posteriorly and forms a prominent posterolateral edge, which is similar to, although narrower than, that in *Sanjuansaurus* (Fig. 14E, F). As was noted by Ezcurra (2010), this condition contrasts with the more symmetrical morphology of the distal condyles in other basal dinosaurs (e.g., *Eoraptor*, *Saturnalia*, *Herrerasaurus*).

Pedal Phalanges—The articulated pedal phalanges may belong to right pedal digit III, rather than left pedal digit II as proposed by Ezcurra (2010). The most distinctive feature in support of this attribution is the asymmetry of the ungual. The ventromedial border of the ungual of digit III tends to be sharper than the border on the opposite side (e.g., *Herrerasaurus*, *Adeopapposaurus*). Only the distal tip of the ungual is lacking (Fig. 15A–D). The first phalanx (phalanx III-2) is longer than the second (phalanx III-3). The lateral, medial, and ventral surfaces
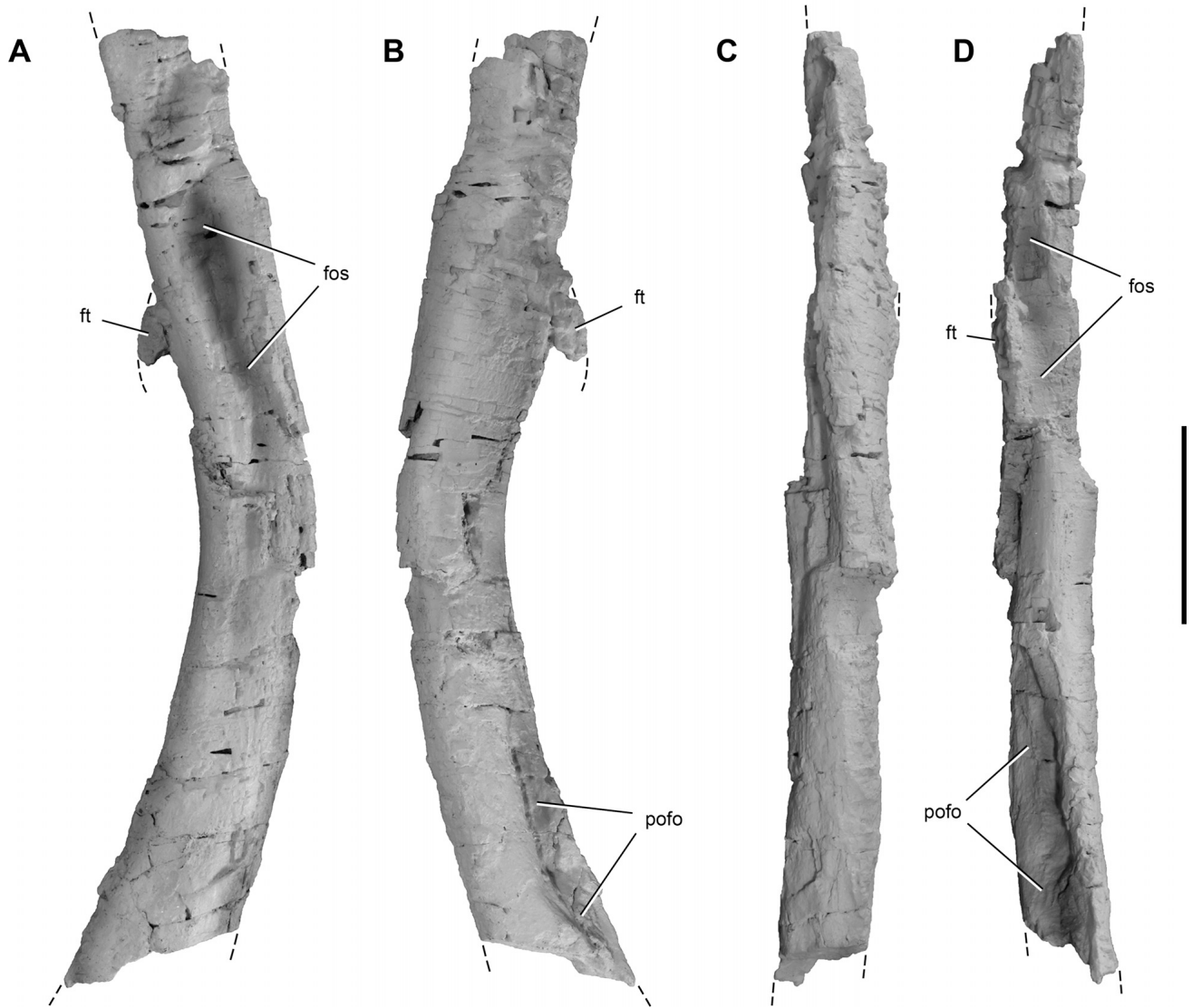
FIGURE 10.   Right femoral shaft of *Chromogisaurus novasi* (PVSJ 845) in lateral (**A**), medial (**B**), anterior (**C**), and posterior (**D**) views. Dashed lines indicate the continuation of preserved margins. **Abbreviations**: **fos**, fossa; **ft**, fourth trochanter; **pofo**, popliteal fossa. Scale bar equals 3 cm.

FIGURE 11.   Distal end of the left femur of *Chromogisaurus novasi* (PVSJ 845) in lateral (**A**), medial (**B**), anterior (**C**), posterior (**D**), and distal (**E**) views. **Abbreviations**: **fos**, fossa; **lco**, lateral condyle; **mco**, medial condyle; **pofo**, popliteal fossa; **ru**, rugosity. Scale bar equals 3 cm.
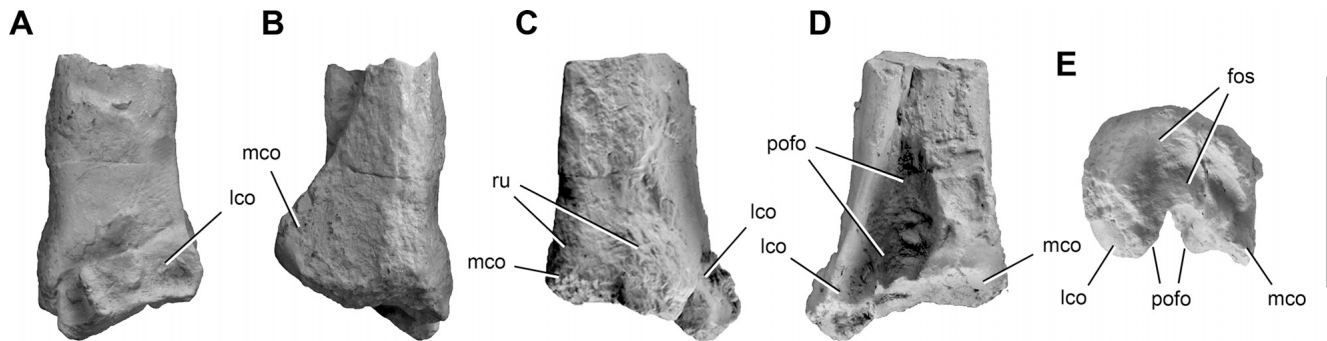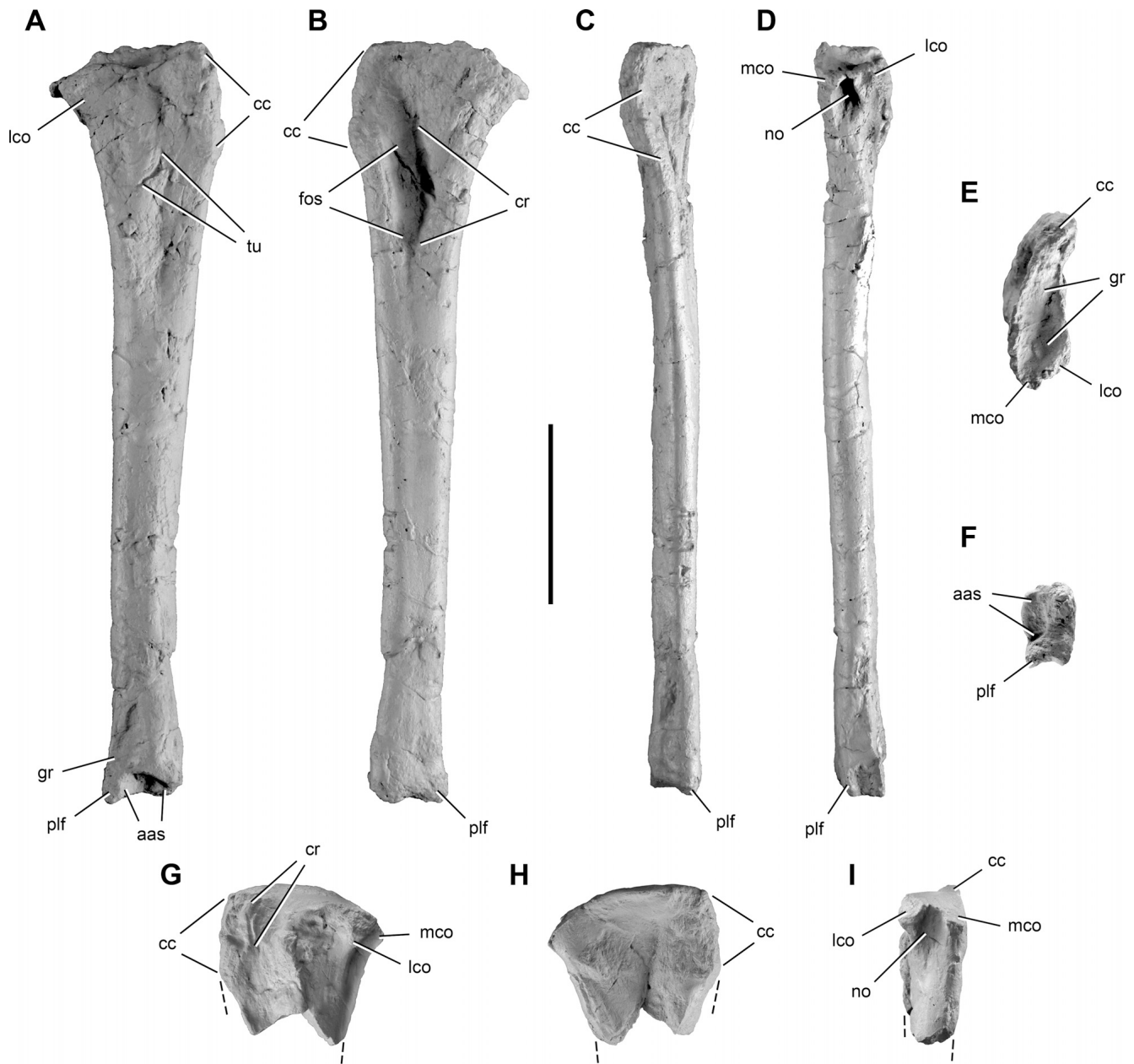
FIGURE 12. Tibiae of *Chromogisaurus novasi* (PVSJ 845). Right tibia in lateral (**A**), medial (**B**), anterior (**C**), posterior (**D**), proximal (**E**), and distal (**F**) views. Proximal end of the left tibia in lateral (**G**), medial (**H**), and posterior (**I**) views. Anterior is towards top in **E** and **F**. Dashed lines indicate the continuation of preserved margins. **Abbreviations**: **aas**, articular surface for the ascending process of the astragalus; **cc**, cnemial crest; **cr**, crest; **fos**, fossa; **gr**, groove; **lco**, lateral condyle; **mco**, medial condyle; **no**, notch; **plf**, posterolateral flange; **tu**, tuberosity. Scale bar equals 4 cm.

are concave, and the dorsal surface is flat. The proximal ends are transversely slightly wider than the corresponding distal ginglymus, as in *Eoraptor* and *Saturnalia*. Dorsal intercondylar processes are present on both non-ungual phalanges (Fig. 15A, C), and they are better developed than in *Eoraptor* and *Saturnalia* (MCP 3844-PV). The medial collateral ligament pits are somewhat more dorsally oriented than corresponding lateral pits.

The ungual (phalanx III–ungual) is slightly asymmetric, the ventromedial edge slightly sharper than its opposite (Fig. 15B). The ventral surface is only slightly arched proximodistally, and there

are marked grooves to each side for attachment of the ungual sheath. The ventral flexor tubercle is low and broad (Fig. 15B).

COMPARISONS AND PHYLOGENETIC POSITION

Comparisons

Chromogisaurus resembles closely the general morphology of basal-most sauropodomorphs from Argentina and Brazil (e.g., *Panphagia*, *Eoraptor*, *Saturnalia*, *Guaibasaurus*). The vertebral
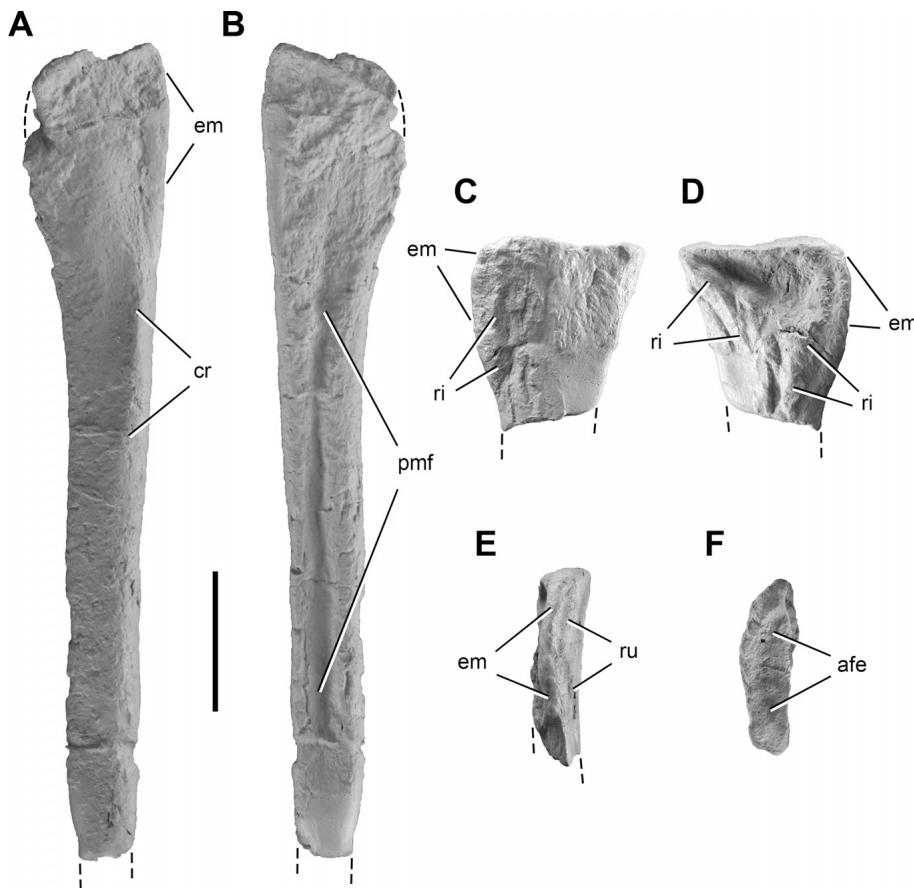
FIGURE 13. Fibulae of *Chromogisaurus novasi* (PVSJ 845). Right fibula in lateral (**A**) and medial (**B**) views. Proximal left fibula in lateral (**C**), medial (**D**), anterior (**E**), and proximal (**F**) views. Anterior is towards top in **F**. Dashed lines indicate the continuation of preserved margins. **Abbreviations**: **afe**, articular surface for the femur; **cr**, crest; **em**, eminence; **pmf**, postmortem fracturing; **ri**, ridge; **ru**, rugosity. Scale bar equals 2 cm.

centra of *Chromogisaurus* are transversely compressed (Figs. 4D, 5C), as in *Eoraptor*, and less compressed than in *Panphagia* and *Saturnalia* (MCP 3846-PV). In *Chromogisaurus*, centrum length is almost constant in the anterior one-third of the tail. In some other basal sauropodomorphs, caudal centrum length decreases distally in this portion of the tail (Table 1). In the basal theropod *Eodromaeus*, in contrast, caudal centrum length increases distally in the proximal caudal vertebrae (Table 1). In these same caudal vertebrae, depth decreases more markedly than in *Eoraptor*, although less so than in *Panphagia* and *Eodromaeus* (Table 1).

Chromogisaurus lacks a groove or keel on the ventral surface of the anterior caudal centra (Fig. 4D), as in *Eoraptor*, *Panphagia*, *Sanjuansaurus*, and *Herrerasaurus*. A groove is present in *Eodromaeus*. A groove is present in mid-caudal vertebrae in *Chromogisaurus* (Fig. 5C), as in *Panphagia*, *Eoraptor*, and *Eodromaeus*.

The neural arches of the caudal vertebrae of *Chromogisaurus* are more gracile than in *Panphagia* and *Eoraptor*. The transverse processes of the anterior caudal vertebra of *Chromogisaurus* are subtriangular and taper distally (Fig. 4C, D). In *Eoraptor* and *Panphagia*, in contrast, the comparable processes are leaf-shaped. The relative length of the transverse processes is less in *Chromogisaurus* (82% of centrum length) than in *Panphagia* (99%) and *Eoraptor* (111%). In the anterior and mid-caudal vertebrae of *Chromogisaurus*, pre- and postzygapophyses extend slightly beyond the ends of the centrum (Figs. 4A, B, 5A), as in *Eoraptor*, *Panphagia*, and *Eodromaeus*. In *Herrerasaurus* and *Sanjuansaurus*, in contrast, the postzygapophyses terminate flush with the posterior rim of the centrum. The neural spines extend along two-thirds of their respective neural arches. In *Panphagia*, in contrast, the spine base occupies less than one-half the length of the neural arch.

TABLE 1. Measurements (in mm) and ratios of anterior and mid-caudal vertebrae of several basal dinosaurs from the Ischigualasto Formation.

Taxon	Anterior caudal (4th)			Mid-caudal (14th)			Length difference	Depth difference
	Length	Depth	Ratio	Length	Depth	Ratio		
Chromogisaurus	21.6	14.3	1.51	21.2	11.2	1.89	−1%	−22%
Panphagia	21.4	16.5	1.30	19.7	9.4	2.10	−8%	−43%
Eoraptor	20.0	14.0	1.43	17.0	12.0	1.42	−15%	−14%
Eodromaeus	20.4	11.9	1.71	23.7	8.1	2.93	+13%	−32%

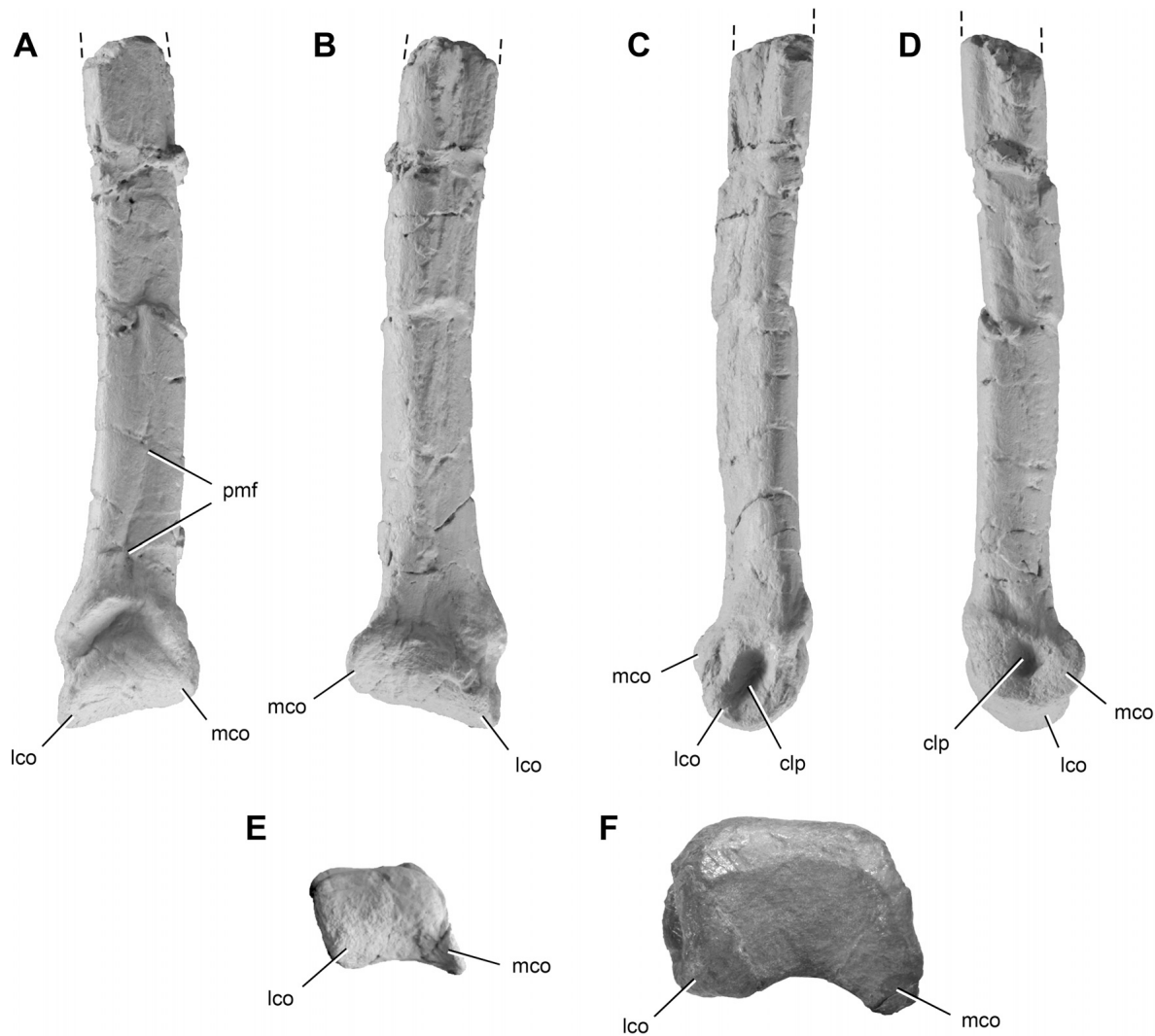Depth measurement was taken at the posterior end of the centrum.

FIGURE 14. Metatarsal 2 of *Chromogisaurus novasi* and *Sanjuansaurus gordilloi*. Right metatarsal 2 of *Chromogisaurus novasi* (PVSJ 845) in dorsal (**A**), ventral (**B**), lateral (**C**), medial (**D**), and distal (**E**) views. Left metatarsal 2 (reversed) of *Sanjuansaurus gordilloi* (PVSJ 605) in distal view (**F**). Dorsal is towards top in **E** and **F**. Dashed lines indicate the continuation of preserved margins. **Abbreviations**: **clp**, collateral ligament pit; **lco**, lateral condyle; **mco**, medial condyle; **pmf**, postmortem fracturing. Scale bar equals 1 cm.

The iliac blade is 65% of the maximum depth of the ilium, as in *Eoraptor* (66%), *Panphagia* (67%), and *Eodromaeus* (67%). The depth of the blade is somewhat shallower in *Saturnalia* (56%) and noticeably deeper in more derived sauropodomorphs, such as *Pantydraco* and *Adeopapposaurus*. In lateral view, the straight dorsal margin of the iliac blade is similar to that of *Saturnalia* but differs from the gently convex border of *Eoraptor* and *Eodromaeus*. The ischial peduncle does not project posteriorly, as in *Saturnalia* and *Guaibasaurus*. The peduncle projects more strongly posteriorly in *Panphagia*, *Eoraptor*, and more advanced basal sauropodomorphs (e.g., *Adeopapposaurus*).

The supraacetabular crest of *Chromogisaurus* extends to the distal end of the pubic peduncle (Fig. 8A), as in *Saturnalia*, *Eoraptor*, and *Eodromaeus*. In *Panphagia* and other sauropodomorphs such as *Adeopapposaurus*, the crest dissipates before the end of the pubic peduncle. The flange of the acetabulum has a straight ventral margin in *Saturnalia* and *Panphagia*, which closes the acetabulum to a greater degree than in *Chromogisaurus*. The pubic peduncle is directed more ventrally than in *Saturnalia*, *Panphagia*, and *Eoraptor*. The subtriangular distal end of the pubic peduncle of *Chromogisaurus* is similar than that of *Eoraptor* and *Saturnalia* (MCP 3846-PV), contrasting with the semicircular, or 'D'-shaped, cross-section of the peduncle of *Panphagia*.

There is a thick and trapezoidal rugose area along the dorsolateral border of the iliac blade (Fig. 8A), as in *Saturnalia* (Ezcurra (2010). The development of this muscle scar, which is presumably for attachment of the M. iliotibialis (Langer, 2003), varies in other sauropodomorphs (e.g., *Adeopapposaurus*), which may be related to maturity or body size.

The femur is slightly shorter than the tibia in *Chromogisaurus*, as in *Eoraptor*, *Pampadromaeus*, and *Eodromaeus*. In all other sauropodomorphs, the tibia is the shorter than the femur. The femoral shaft of *Chromogisaurus* is sigmoidal in lateral view, as in all other basal dinosaurs, but in anterior view it is straight,
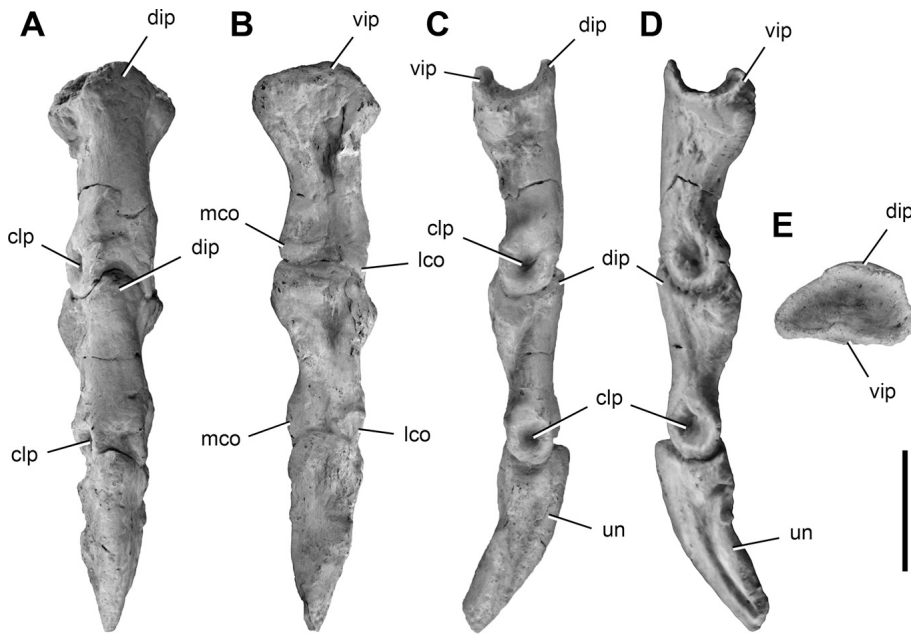
FIGURE 15. Articulated phalanges 2–4 of right pedal digit III of *Chromogisaurus novasi* (PVSJ 845) in dorsal (**A**), ventral (**B**), lateral (**C**), medial (**D**), and proximal (**E**) views. **Abbreviations**: **clp**, collateral ligament pit; **dip**, dorsal intercondylar process; **lco**, lateral condyle; **mco**, medial condyle; **un**, ungual; **vip**, ventral intercondylar process. Scale bar equals 1 cm.

which differs from the sigmoidal shaft in *Eoraptor*, *Saturnalia*, and *Eodromaeus*. The proximal surface of the femoral head faces dorsally and has a straight profile in posteromedial view (Fig. 9C, D), as in *Guaibasaurus* (Bonaparte et al., 2006:fig. 8; UFRGS PV 0725T). In other basal dinosaurs, in contrast, the proximal surface faces dorsomedially and has a convex profile in posteromedial view (e.g., *Saturnalia*, *Eoraptor*, *Eodromaeus*). The large and rugose attachment scar at the distal end of the femur is similar to that in *Guaibasaurus*, *Eodromaeus*, and *Herrerasaurus*.

The lateral condyle of the tibia is positioned slightly anterior to the medial condyle (Fig. 12E), as in *Eoraptor* and *Panphagia*. In *Saturnalia*, the lateral condyle is located even farther anteriorly. The symmetrical profile of the cnemial crest in lateral or medial view is similar to that in *Eoraptor*. In *Panphagia*, *Saturnalia*, and *Eodromaeus*, the apex of the crest is situated closer to its proximal end. The pronounced tibiofibular crest is similar to that in *Saturnalia*, *Eoraptor*, and *Eodromaeus*, and more marked than in *Panphagia*. The straight shaft of the tibia (Fig. 12A–D) most closely resembles that in *Eodromaeus* and differs from the slightly sinuous shaft in *Eoraptor* (PVSJ 559), *Saturnalia* (Langer, 2003:fig. 5C), and *Panphagia*. The posterolateral process of the tibia projects distally, similar to that in *Saturnalia* and *Eodromaeus*.

Taxonomic Status of *Chromogisaurus*

We were unable to verify several of the characters originally used by Excurra (2010) to differentiate *Chromogisaurus novasi* from other sauropodomorphs. These include the femoral fossa near the trochanteric shelf, which is here regarded as postmortem deformation, and the absence of a notch between the postzygapophyses in caudal vertebrae, which is present in the present material. We were able to confirm only one autapomorphy cited by Ezcurra (2010), the marked dorsoventral asymmetry of the distal condyles of metatarsal 2, although our interpretation of the siding of that bone is opposite to his. A second autapomorphy supporting the distinctiveness of *Chromogisaurus* is the rugose scar near, and parallel to, the anterior border of the fibula (Fig. 13C).

Although there are few autapomorphies in the available material of *Chromogisaurus*, other features distinguish this basal sauropodomorph from other basal dinosaurs from the Ischigualasto Formation (*Panphagia*, *Eoraptor*, *Eodromaeus*) and from the basal sauropodomorph *Saturnalia* from Brazil.

Chromogisaurus novasi differs from *Panphagia protos* in the following features: the caudal centra are more transversely compressed; the transverse processes of the anterior caudal vertebrae are subtriangular and distally tapered; the articular surfaces of caudal zygapophyses are oval; the caudal neural spines are anteroposteriorly broader; the iliac posteromedial shelf equals the brevis shelf in transverse width; the proximal articular surface of the tibia is concave; the tibial cnemial crest reaches its most prominent point well below the proximal margin; the lateral side of the cnemial crest has a rugose crest; the posterolateral flange of the tibia extends distally more prominently; and a more marked groove separates the posterolateral flange from the remainder of the distal end of the tibia.

Chromogisaurus novasi differs from *Eoraptor lunensis* in the following features: caudal vertebrae with more strongly concave articular faces; iliac blade with a straighter profile in lateral view; less prominent iliac supraacetabular crest; acetabulum with strongly concave dorsal articular surface; femoral head with proximal surface facing dorsally and straight in posteromedial view; femoral fibular condyle less developed than the tibial condyle; shaft of the tibia straight in anteroposterior and mediolateral views; medial tip of the posterolateral flange of the tibia distally protruding; and a more marked groove separating the posterolateral flange from the remainder of the distal end of the tibia.

Chromogisaurus novasi differs from the basal theropod *Eodromaeus murphi* in a number of features, the most salient of which are shorter mid-caudal vertebrae; caudal vertebrae with more strongly concave articular faces; anterior caudal centra without a ventral groove; caudal vertebrae without any development of hyposphene-hypantrum articulations; robust glenoid region of the scapulocoracoid; iliac blade with a straighter profile in lateral view; less prominent iliac supraacetabular crest; concave surface on the dorsal margin of the acetabulum; straight proximal surface
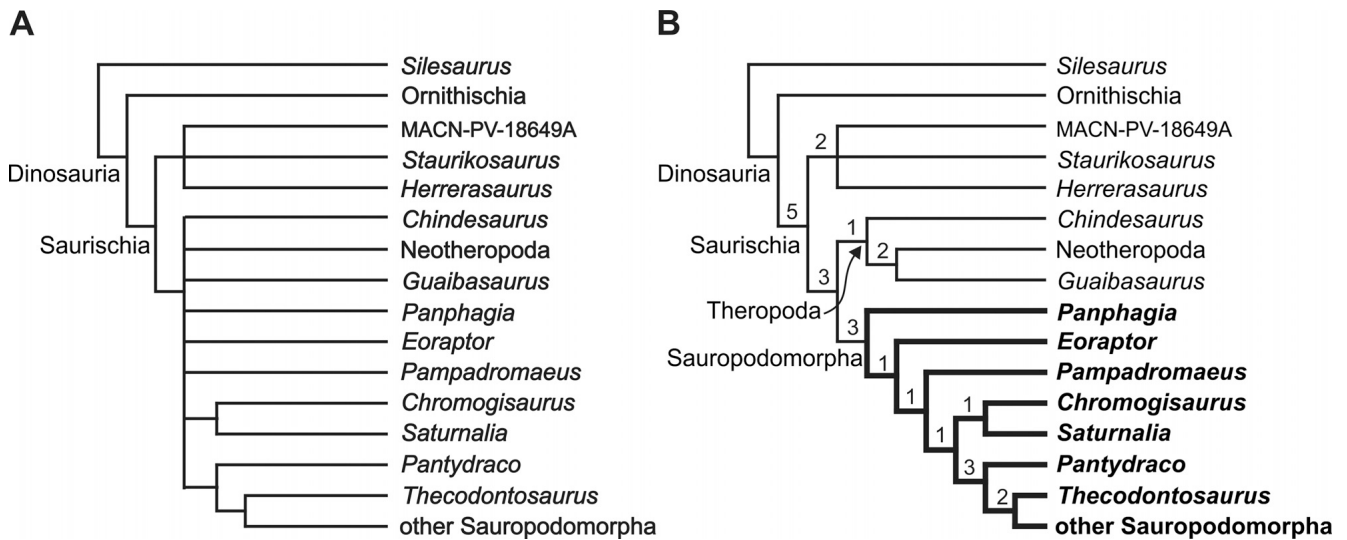
FIGURE 16. Simplified phylogenetic relationships of basal sauropodomorphs based on a data set of Ezcurra (2010). Strict consensus (**A**) and reduced consensus trees after the exclusion of *Agnosphytis* (**B**). Full black lines indicate Sauropodomorpha in **B**. Numbers within Sauropodomorpha indicate the decay indices.

of the femoral head facing dorsally in posteromedial view; fibular condyle of the femur less developed than the tibial condyle; the tibial cnemial crest reaches its most prominent point well below the proximal margin; the rugose crest on the lateral side of the cnemial crest; the posterolateral flange of the tibia protrudes distally; and a more marked groove separating the posterolateral flange from the remainder of the distal end of the tibia.

Chromogisaurus novasi differs from *Saturnalia tupiniquim* in the following features: caudal vertebrae with more strongly concave articular faces; strongly transversely compressed caudal centra; higher iliac blade of the ilium; pubic peduncle facing more ventrally; slightly concave ventral border of the acetabular wall; poorly developed supraacetabular crest of the ilium; strongly concave surface on the dorsal margin of the acetabulum; straight proximal surface of the femoral head facing dorsally in posteromedial view; fibular condyle of the femur less developed than the tibial condyle; subtriangular scar on the distal-most region of the anteromedial surface of the femur; lateral condyle of the tibia much posteriorly located; the tibial cnemial crest reaches its most prominent point well below the proximal margin; the rugose crest on the lateral side of the cnemial crest; the posterolateral flange of the tibia protrudes distally; and a more marked groove separating the posterolateral flange from the remainder of the distal end of the tibia.

Phylogenetic Analysis

Reanalysis Based on Ezcurra (2010)—To reexamine phylogenetic relationships among basal sauropodomorphs, we modified the data set originally published by Yates (2007) and later modified by Smith and Pol (2007) and Ezcurra (2010). We rescored *Chromogisaurus* based on the information presented above and added *Pampadromaeus* as a terminal taxon (Cabreira et al., 2011). The character-state scores for the basal sauropodomorphs *Eoraptor*, *Panphagia*, *Chromogisaurus*, and *Saturnalia* were reviewed and rescored (Appendices 1, 2, Supplementary Data).

The data set for reanalysis included 51 taxa and 378 characters. We used TNT 1.1 (Goloboff et al., 2008a, 2008b) in an equally weighted parsimony analysis that included a heuristic search of 1000 replicates of Wagner trees followed by tree bisection and reconnection (TBR) branch swapping. Following the original analysis of Yates (2007), a total of 36 characters were ordered. The analysis yielded 60 most parsimonious trees (MPTs) of 1192 steps (consistency index = 0.37; retention index = 0.69) (Fig. 16).

The strict consensus tree depicts a polytomy formed by *Eoraptor*, *Panphagia*, *Pampadromaeus*, the clade *Chromogisaurus* + *Saturnalia*, *Chindesaurus*, *Agnosphytis*, *Guaibasaurus*, and Neotheropoda (Fig. 16A). Following Ezcurra (2010), a reduced strict consensus was obtained after exclusion of the poorly known taxon *Agnosphitys* (Fraser et al., 2002) (Fig. 16B). In the reduced strict consensus, basal sauropodomorphs are depicted in a paraphyletic arrangement with *Panphagia* as the basal-most member, followed by *Eoraptor*, *Pampadromaeus*, and the clade that includes *Chromogisaurus* + *Saturnalia* as the sister clade of more derived sauropodomorphs (Fig. 16B).

The position of *Panphagia* as basal to other sauropodomorphs is supported by nine unambiguous synapomorphies: pterygoid wing of the quadrate extending for more than 70% of the total quadrate length (71:1); presence of postparietal fenestra between supraoccipital and parietals (74:1); supraoccipital wider than high (75:1); coarse serrations of the teeth angled upwards at 45° (114:1); absence of a postzygodiapophyseal lamina in cervical vertebrae 4–8 (142:1); weakly developed laminae in the neural arches of cervical vertebrae 4–8 (143:1); minimum width of the scapula less than 20% of its length (200:0); posterior end of the fibular condyle of the tibia anterior to the posterior margin of proximal articular surface (304:0); and strongly laterally curved iliac blade in dorsal view (372:1). Sauropodomorpha is well supported by a decay index of 3, although bootstrap confidence is below 50% (Fig. 16B).

The more derived position of *Eoraptor* is supported by three unambiguous synapomorphies: subtriangular cross-section of the ischial midshaft (274:1); supraacetabular crest of the ilium contacting the distal end of pubic peduncle (363:2); and subtriangular distal end of the ischium (377:1). *Pampadromaeus* and more derived sauropodomorphs share four unambiguous synapomorphies:

squamosal bordering the laterotemporal fenestra for more than 50% of its depth (62:0); length of the base of proximal caudal neural spines greater than half the length of the neural arch (184:1); transverse width of the distal humerus greater than 33% of its length (211:1); and length of the pubic peduncle of the ilium greater than twice the anteroposterior width of its distal end (252:1).

The *Chromogisaurus* + *Saturnalia* clade is supported by three unambiguous synapomorphies: presence of a caudosacral vertebra (178:1); strong trapezoidal rugosity for the origin of the M. flexor tibialis and iliotibialis on the postacetabular process of the ilium (362:1); and concave posterolateral corner of the distal end of the tibia (375:1). This clade is particularly weak, with a decay index of 1 and bootstrap frequency below 50% (Fig. 16B).

Comparisons with Recent Analyses—In the analysis of Ezcurra (2010), *Panphagia*, *Guaibasaurus*, and *Chromogisaurus* + *Saturnalia* joined a polytomy within the clade Guaibasauridae (Bonaparte et al., 1999; Ezcurra and Novas, 2009). In the present analysis, *Guaibasaurus* is recovered as a theropod, the sister taxon to Neotheropoda (Fig. 16B), a very tentative result for this poorly known taxon that mirrors previous analyses (e.g., Smith and Pol, 2007; Yates, 2007; Langer et al., 2011).

Eoraptor was originally viewed as a theropod (Sereno et al., 1993; Novas, 1996; Sereno, 1999; Rauhut, 2003; Yates, 2007; Ezcurra, 2010) or basal saurischian (Langer and Benton, 2006; Brusatte et al., 2010, 2011). Here *Eoraptor* is retrieved as a basal sauropodomorph (Fig. 16B), as in Martínez et al. (2011) and as discussed in detail in Sereno and Martínez (in review). The sauropodomorph affinity of *Eoraptor* is generated by alteration of several character states for this taxon (Appendix 2).

Ezcurra (2010) coined the subfamily Saturnaliinae to include *Saturnalia* plus *Chromogisaurus*. He based this clade on three synapomorphies: ulna with an extremely enlarged olecranon process; iliac postacetabular process with pointed posteroventral corner and rounded posterodorsal margin; and strong trapezoidal rugosity for the origin of the M. flexor tibialis and iliotibialis. Although we show that the ulna of *Chromogisaurus* is not preserved, our analysis also generates this clade (Fig. 16B), based on only one of the original synapomorphies: strong trapezoidal rugosity for the origin of the M. flexor tibialis and iliotibialis (362:1).

CONCLUSIONS

Most of the small-bodied (<15 kg) primary consumers from the Ischigualasto Formation appear to have been sauropodomorphs. This trophic niche was shared with at least one silesaurid (Martínez et al., 2013) and possibly the ornithischian *Pisanosaurus*, which is thus far known only from the upper levels of the formation. The three sauropodomorphs, *Panphagia*, *Eoraptor*, and *Chromogisaurus*, come from the *Scaphonyx-Exaeretodon-Herrerasaurus* biozone (Martínez et al., 2011) and thus were likely contemporaries sharing the same ecosystem. The presence in Brazil of the similar-age basal sauropodomorphs *Saturnalia* and *Pampadromaeus* suggests that these herbivores had achieved a level of diversity in southern Pangaea during the Carnian. A similar diversity of sauropodomorphs (three) is present in the overlying Los Colorados Formation, which was deposited about 15 million years later in the mid-Norian (Santi Malnis et al., 2011). The main difference between these sauropodomorphs is that in the Los Colorados Formation, they are the most abundant vertebrates and also attained large body size. The fossil record of sauropodomorphs across these two formations suggests that sauropodomorphs have been an important component from the emergence of dinosaurs, but that their size and abundance increased markedly in the Norian toward the end of the Triassic.

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APPENDIX 1. Character-state scores modified from the data matrix of Ezcurra (2010).

Chromogisaurus novasi

Character 215: state (?) instead of (2). *Chromogisaurus* was originally scored as having greatly enlarged olecranon process on the proximal ulna, with a separate ossification forming a strongly striated portion (2). As we demonstrate, the ulna is unknown in *Chromogisaurus*, and the element identified by Ezcurra (2010) as an ulna is actually part of a rhynchosaur mandible.

Character 374: state (1) instead of (?). The femoral head was scored as unknown in the original description (Ezcurra, 2010), but it can be scored. The head is strongly inturned,

oriented at less than 120° from the main axis of the femoral head, and distinctively separated from the shaft by a well-developed femoral neck.

Character 376: state (?) instead of (2). Although pedal digit II was originally described for *Chromogisaurus* (Ezcurra, 2010), we interpret it to be pedal digit III. Accordingly, we score pedal digit II as unknown in *Chromogisaurus*.

Eoraptor lunensis (see Sereno et al., 2013)

Character 24: state (1) instead of (0). The posterolateral process of the nasal overlaps the lacrimal in *Eoraptor*.

Character 71: state (1) instead of (?). The pterygoid wing occupies more than 70% of the length of the quadrate in *Eoraptor*.

Character 74: state (1) instead of (0). The postparietal fenestra between supraoccipital and parietals is present in *Eoraptor*.

Character 75: state (1) instead of (0). The supraoccipital of *Eoraptor* is wider than high.

Character 100: state (1) instead of (?). The first dentary tooth of *Eoraptor* is inset one tooth's width from the symphysis (Martínez et al., 2011).

Character 128: state (1) instead of (0). The lengths of middle to posterior cervical centra (cervicals 6–8) are greater than the length of the axial centrum in *Eoraptor*.

Character 142: state (1) instead of (?). The postzygodiapophyseal lamina is absent in cervical neural arches 4–8 of *Eoraptor*.

Character 143: state (1) instead of (?). The laminae of the cervical neural arches 4–8 are weakly developed low ridges in *Eoraptor*.

Character 200: state (0) instead of (1). The minimum width of the scapula is lesser than 20% of its length in *Eoraptor*.

Character 205: state (1) instead of (0). The length of the humerus of *Eoraptor* is 56% of the length of the femur.

Character 215: state (1) instead of (0). The olecranon process on the proximal ulna is absent in *Eoraptor*.

Character 234: state (1) instead of (?). The transverse axis of the distal end of the first phalanx of manual digit I is ventrolaterally twisted relative to its proximal end in an angle of 35° in *Eoraptor* (Martinez et al., 2011).

Character 238: state (0) instead of (1). The length of the penultimate phalanx of manual digit II is less than the length of the second metacarpal in *Eoraptor*.

Character 242: state (1) instead of (0). The length of the ungual of manual digit II is equal to the length of the ungual of manual digit I in *Eoraptor*.

Character 251: state (1) instead of (2). Although in the holotypic specimen of *Eoraptor* the acetabulum is hidden by the femur, the referred specimen PVSJ 754 has the acetabulum partially open.

Character 255: state (2) instead of (0). Length of the postacetabular process of the ilium. This character was originally scored by Yates (2007) as state (1)—less than 40% of the distance between the pubic and ischial peduncles. Ezcurra (2010) modified this character to state (0)—between 40% and 100%. This character is partially obscured in the holotypic specimen, but the referred specimen PVSJ 754 shows that its length is more than 100% of the distance between the peduncles (state 2).

Character 257: state (0) instead of (1). The anterior end of the brevis shelf is not connected to the supracetabular crest.

Character 274: state (1) instead of (0). The shape of the transverse section of the ischial shaft is triangular in *Eoraptor*.

Character 308: state (0) instead of (1). The posterolateral process of the distal end of the tibia does not make significant contact with the fibula.

Character 364: state (0) instead of (1). The subnarial gap (i.e., posterior part of premaxillary alveolar margin edentulous, resulting in an interruption of the upper tooth row) is absent in *Eoraptor*.

Character 365: state (0) instead of (1). The alveolar margin of the anterior-most maxilla is slightly convex in *Eoraptor*.

Character 369: state (1) instead of (0). The medial distal condyle of metacarpal I of *Eoraptor* is dorsoventrally smaller than the lateral distal condyle.

Character 371: state (1) instead of (2). The supraacetabular crest of the ilium in *Eoraptor* is a well-developed raised shelf, but does not flare lateroventrally to form a hood-like structure that hides the anterodorsal half of acetabulum in lateral view.

Character 372: state (1) instead of (0). The iliac blade in dorsal view curves strongly laterally with a deeply concave lateral border.

Character 373: state (1) instead of (0). The pubic shaft is nearly straight in *Eoraptor*.

Character 377: state (1) instead of (0). The distal outline of ischium in *Eoraptor* is subtriangular.

Character 378: state (1) instead of (0). The pubic shaft of *Eoraptor* is oriented anteroventrally, almost perpendicular to the longitudinal axis of the ilium.

Pampadromaeus barberenai

Character 13: state (1) instead of (0). The subnarial foramen in *Pampadromaeus* is present. It is small and positioned outside of narial fossa (Cabreira et al., 2011:fig. S3).

Panphagia protos

Character 47: state (1) instead of (0). *Panphagia* has a small and slender anterior process of the frontal intruding between the prefrontal and the nasal (see Martínez et al., 2013).

Character 74: state (1) instead of (0). The postparietal fenestra is present in *Panphagia* (see Martínez et al., 2013).

Character 131: state (0) instead of (1). The length of anterior cervical centrum (c4?) of *Panphagia* is less than 2.5 times the height of its anterior face (Martínez and Alcober, 2009).

Character 201: state (0) instead of (1). The posterior margin of the acromion process of the scapula of *Panphagia* rises from the blade at angle of 55° from the long axis of the scapula at its steepest point.

Character 252: state (0) instead of (1). The length of the pubic peduncle of the ilium in *Panphagia* is less than twice the anteroposterior width of its distal end.

Character 306: state (1) instead of (0). The transverse width of the distal tibia is greater than its anteroposterior length.

Character 363: state (1) instead of (2). The supraacetabular crest of the ilium extends along the pubic peduncle as a faint ridge, but does not contact its distal end.

Saturnalia tupiniquim

Character 200: state (0) instead of (1). The minimum width of the scapula of *Saturnalia* is less than 13% of its length

(Langer et al., 2007:table 1), but it was originally scored as being greater than 20%.

APPENDIX 2. Scorings of the basal dinosaurs *Chromogisaurus*, *Eoraptor*, *Pampadromaeus*, *Panphagia*, and *Saturnalia* for 378 characters from the data matrix of Ezcurra (2010). Scores in parentheses indicate that both states are present.

Chromogisaurus

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?????????1000??1100??1?????????????????????????0??????????
??????????????????????0????111002202????????????????????????
0??????1???10110??100000010100010????????????????????????
??0??0???000???10????????12???????11?11???

Eoraptor

0001?001?01010?00110001110100000100001101000 00?101100101
00?011000010011??11?1?????????????00000010???0?0?00?1
010000001?????110000000000?1011??000??00?00??00?000??00
000011??10???100??001?00?2000?0000??1?10??00101??????20?
00011?00010?00000101101001100 02201??0??00?0???10?1011?10
??0?01100001011000 00?1?0011010??1?0??0?????01????0?0???0
0?0010000000??000?0????1?02001110 11110011

Pampadromaeus

00???00211001?1?011??0??000?1000000?110?0?0?0??0?10?1??
0???10????111?1?????????????????0???00000000??0010?1001
01000000???????????????????1??????0?0?01??001?110?01000?
000000?0??0000?11?0??01????00?1010??1?????1?0?1?????????
?????????????????????00100111010202????????????????????0
0001111100110111 00?00?000??????010????????????????????
???????????????0??0???0??210011??11?1????

Panphagia

?0?????????1??????????0?1????????????????????0??1????????1
?1?0???????10?1?111???????????????????1?0?0?1010000?10?01
01000000???????000001 00011?01101?000?01???01?10000?0?00
00000??0???00???????????00?0??000???????????????????????
??????????????????0??0?110102201?00?0 00????1??0??10??
?????????????????0010001101 00???010?1010???????????????0
????????????????0??????01???????111?1?0?

Saturnalia

10????????????????????????1??1????00?100?0??????????????
????10?????1??00??0?0??0?0?0000????????01000?????00001
00000000???????001001 0010??01101?00000100001 100100 00000
000000001000101??0??1000?0??101011111000101 02?????????
?????????????????????00000111(01)02202100000001 0011001001
0000001001(01)0001011000100000001010001001 00101000000010
00000001011000?000?0010000000001 2?000???11111?11