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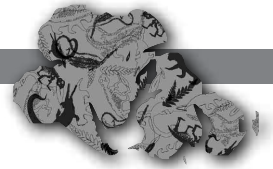
A LATE NORIAN–RHAETIAN COELOPHYSID NEOTHEROPOD (DINOSAURIA, SAURISCHIA) FROM THE QUEBRADA DEL BARRO FORMATION, NORTHWESTERN ARGENTINA

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Abstract. Coelophysoids are the most abundant theropod dinosaurs known from the Late Triassic through Early Jurassic and represent the earliest major radiation of Neotheropoda. Within Coelophysoidea *sensu lato*, the most stable clade is Coelophysidae, which are small theropods characterized by long necks, and light and kinetic skulls. Coelophysids are the most abundant basal non-Tetanurae neotheropods known worldwide; however, until recently, they were unknown from South America. We report here a new coelophysid neotheropod, *Lucianovenator bonoi* gen. et sp. nov., from the late Norian–Rhaetian Quebrada del Barro Formation, northwestern Argentina. A phylogenetic analysis recovered *Lucianovenator bonoi* nested into the monophyletic group Coelophysidae in an unresolved clade, together with *Coelophysis rhodesiensis* and *Camposaurus arizonensis*. The presence of *Lucianovenator* in the late Norian–Rhaetian of Argentina increases the poor and scarce record of Triassic South American neotheropods, suggesting that the virtual absence of theropods in the fossil record during the Rhaetian is probably a taphonomic/stratigraphic bias instead of a decline in diversity and abundance after the Norian. Finally, the new finding corroborates the American endemism of coelophysid neotheropods in the Late Triassic and their worldwide distribution during the Early Jurassic, supporting the extreme faunal homogeneity hypothesized for Early Jurassic continental biotas.

Key words. Dinosauria. Saurischia. Theropoda. Coelophysidae. Norian. Marayes.

Resumen. UN NEOTERÓPODO COELOPHYSIDO (DINOSAURIA, SAURISCHIA) DEL NORIANO TARDÍO–RETICO DE LA FORMACIÓN QUEBRADA DEL BARRO, NOROESTE DE ARGENTINA. Coelofisoideos son los dinosaurios terópodos más abundantes conocidos desde el Triásico Tardío al Jurásico Temprano y representan la más importante radiación temprana de Neotheropoda. Dentro de Coelophysoidea *sensu lato* el clado más estable es Coelophysidae, pequeños terópodos caracterizados por su largo cuello y cráneo liviano y quinético. Los coelofísidos son los neoterópodos basales no-Tetanurae más abundantes conocidos en todo el mundo, pero hasta hace poco tiempo eran desconocidos para América del Sur. Presentamos aquí un nuevo neoterópodo coelofísido, *Lucianovenator bonoi* gen. et sp. nov., proveniente de la Formación Quebrada del Barro (Noriano tardío–Rético), del noroeste de Argentina. El análisis filogenético recupera a *Lucianovenator bonoi* anidado en el grupo monofilético Coelophysidae, en un clado sin resolver junto con *Coelophysis rhodesiensis* y *Camposaurus arizonensis*. La presencia de *Lucianovenator* a finales del Noriano–Rético de Argentina aumenta el escaso registro de neoterópodos triásicos de América del Sur, sugiriendo que la virtual ausencia de terópodos en el registro fósil durante el Rético es más un sesgo tafonómico/estratigráfico que una disminución en su diversidad y abundancia después del Noriano. Por último, el nuevo hallazgo evidencia un endemismo americano en el Triásico Tardío y una distribución global durante el Jurásico Inferior de neoterópodos coelofísidos, coincidiendo con el supuesto de una homogeneidad extrema de las faunas hipotetizada para las biotas continentales del Jurásico Temprano.

Palabras clave. Dinosauria. Saurischia. Theropoda. Coelophysidae. Noriano. Marayes.

THE coelophysoids are the most abundant theropod dinosaurs known from the Late Triassic through the Early Jurassic. They were small to medium sized (up to 6 meters in length) carnivorous forms representing the earliest major radiation of Neotheropoda. Coelophysoidea traditionally included a large number of species (Holtz, 1994; Padian *et al.*, 1999); nevertheless, some of them (*e.g.*, *Dilophosaurus*, *Zupaysaurus*) are now considered successive sister-taxa of Tetanurae (Rauhut, 2003; Ezcurra and Brusatte, 2011; Nesbitt and Ezcurra, 2015; Rauhut *et al.*, 2016). No matter the diversity of opinions about its monophyly or paraphyly, or about its members, the most stable clade within coelophysoids is Coelophysidae. Coelophysids are small (up to 3 meters in length) bipeds characterized by their long necks, and light and kinetic skulls, which are the most abundant basal non-Tetanurae neotheropods known worldwide.

They are known from Africa (Raath, 1969), Asia (You *et al.*, 2014) and North America (Colbert, 1989; Rowe, 1989; Tykoski, 1998; Ezcurra and Brusatte, 2011; Nesbitt and Ezcurra, 2015), and were previously unknown from South America. Recently, two Argentinean coelophysids were simultaneously reported: one from the late Norian–Rhaetian Quebrada del Barro Formation (Martínez *et al.*, 2016) and the other from the mid-Norian Los Colorados Formation (Ezcurra, 2017). Here, we describe the former one.

GEOLOGICAL SETTINGS

The holotype of the new taxon (PVSJ 906) and the referred material (PVSJ 899, PVSJ 1004, PVSJ 1013, PVSJ 1084) were found in the "Quebrada del puma" locality, corresponding to the upper levels of the late Norian–Rhaetian Quebrada del Barro Formation. The Quebrada del Barro Formation crops out in northwestern Argentina and forms part of the continental Triassic–Jurassic Marayes-El Carrizal Basin (Fig. 1).

The Marayes-El Carrizal Basin, as the neighboring Ischigualasto-Villa Union Basin, corresponds to a series of extensional basins developed during the lower Mesozoic along the southwestern edge of Pangea (Spalletti, 1999). Stratigraphically, the basin is formed by the Marayes Group (Bossi, 1976; Colombi *et al.*, 2015) and is composed of, from base to top, the Esquina Colorada (Middle Triassic), the Carrizal (upper Carnian–lower Norian), the Quebrada del Barro (upper Norian–Rhaetian) and the Balde de Leyes (Lower Jurassic) formations (Fig.1.1).

The Quebrada del Barro Formation has a variable thickness ranging between 600 and 1400 m even though in the "Quebrada del puma" locality, where all the specimens reported here were found, it is only exposed at the upper 200 m of the section because the lower section is covered by recent sediments. The unit is formed by coarse sandstones and conglomerates interbedded with sandy-claystone with sabulitic clasts (Fig. 1.2). The depositional environment has been recently reinterpreted as a distributive fluvial system in which fluvial channels with a large range of sinuosity form a complex deposit with mudflows dominated by floodplains and terminal splays that are formed by heterolithic sandstone and mudstone accumulations (Colombi *et al.*, 2014, 2015). A late Norian–Rhaetian age is suggested for this unit based on the faunal assemblage known from the upper section of the Quebrada del Barro Formation; which is composed of opisthodontian sphenodonts, tritheledontid cynodonts, basal sauropodomorph dinosaurs, lagerpetid dinosauromorphs, coelophysoid neotheropods, pterosaurs, stem testudinatans and diverse pseudosuchians (Martínez *et al.*, 2015).

MATERIALS AND METHODS
Terminology

We use the term "basal" for the lower diverging nodes on a cladogram of a considered lineage with respect to the later diverging branches, which are often more derived. We employ traditional, or "Romerian", anatomical and directional terms over veterinarian alternatives (Wilson, 2006). "Anterior" and "posterior", for example, are used as directional terms instead of the veterinarian alternatives "rostral" or "cranial" and "caudal".

Phylogenetic Methods

In order to determine the phylogenetic position of the new specimen within Dinosauria, we added the new taxon to the original dataset of Nesbitt *et al.* (2009) later modified by Ezcurra and Brusatte (2011), and Nesbitt and Ezcurra (2015). In addition, we also included the new taxon in the dataset of You *et al.* (2014), in their description of the theropod *Panguraptor lufengensis*. We maintained the original scoring of character states for all the taxa in the previous datasets except for those of *Eodromaeus*, which were partially modified changing 57 character-states (see Phylogenetic Results section, and Supplementary Information). We follow the same criteria used by the authors in the original analysis of Nesbitt *et al.* (2009) as regards the choice of the outgroup and the order of the multistate characters 17, 30, 67, 128, 174, 184, 213, 219, 231, 236, 248, 253, 254, 273, 329, and 343.

The new dataset of 47 taxa and 343 characters was analyzed under equally weighted parsimony using TNT 1.1 (Goloboff *et al.*, 2008a, b). A heuristic tree search strategy was conducted performing 1,000 replications of Wagner trees (with random addition sequence) followed by TBR (tree bisection and reconnection) branch swapping (holding 10 trees per replicate). Zero length branches among the recovered most parsimonious trees (MPTs) were collapsed
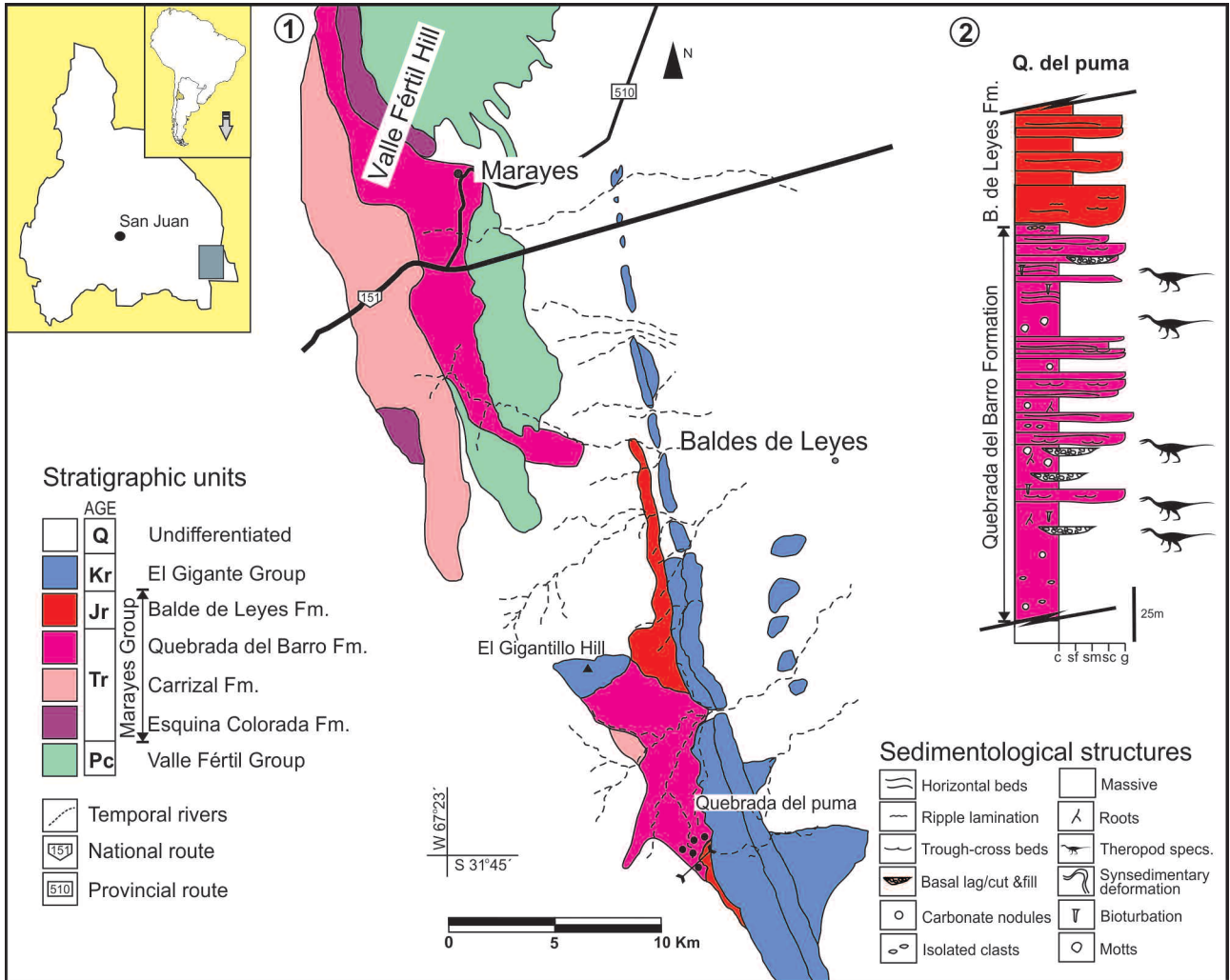
Figure 1. 1–2, Location and geology of the Marayes-El Carrizal Basin. **1,** Geological map of the Marayes-El Carrizal Basin; **2,** stratigraphic section of the upper levels of the Quebrada del Barro Formation at the "Quebrada del puma" locality, type locality of ***Lucianovenator bonoi*** gen. et sp. nov. Black circles indicate the finding sites, located between 60 and 160 m below the top of the Quebrada del Barro Formation. Modified from Martínez *et al.* (2015).

(*i.e.*, rule 3 of Swofford and Begle, 1993; Coddington and Scharff, 1994). Branch support of clades was calculated by examining the most parsimonious trees in which the monophyly of a given group is rejected (Bremer, 1994) and using GC frequencies in one of a thousand replicates of bootstrap analyses (Goloboff *et al.*, 2003). Some alternative phylogenetic hypotheses, such as placing the new taxon in alternative positions among basal Theropoda, have been used to test the support of its position using monophyly constraints in TNT (see Supplementary Information).

Institutional Abbreviations. **PVSJ,** Instituto y Museo de Ciencias Naturales, San Juan, Argentina.

SYSTEMATIC PALEONTOLOGY

Archosauria Cope, 1869 *sensu* Gauthier and Padian, 1985
Theropoda Marsh, 1881 *sensu* Gauthier, 1986
Neotheropoda Bakker, 1986 *sensu* Sereno, 1998
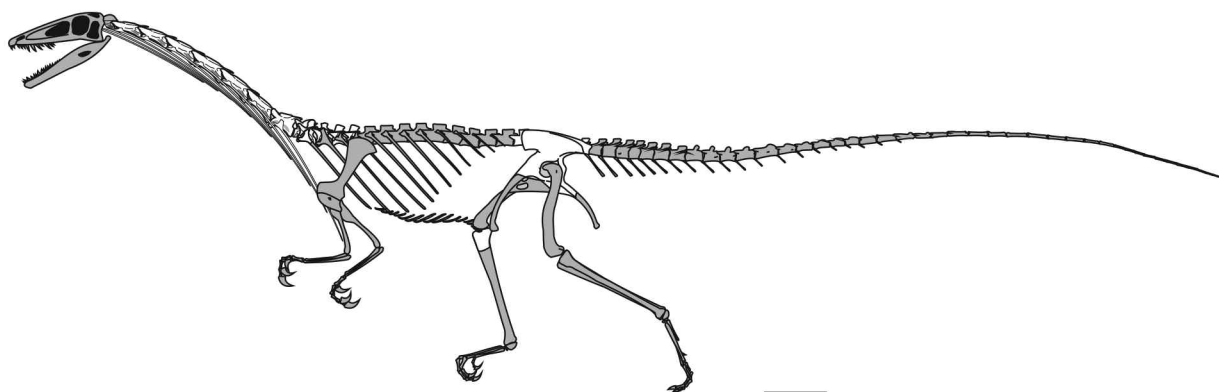Coelophysoidea Nopcsa, 1928 *sensu* Holtz, 1994
Coelophysidae Nopcsa, 1928, *sensu* Holtz, 1994

***Lucianovenator bonoi*, gen. et sp. nov.**
Figures 2–10, Table 1

Etymology. The generic name honors Don Luciano Leyes, in-

Figure 2. *Lucianovenator bonoi* gen. et sp. nov., skeletal reconstruction drawing. Known bones filled in white. Reconstruction of the unknown bones based on *Coelophysis bauri*. Scale bar= 20 cm.

habitant of the small town Balde de Leyes, who in 2001 called the attention of RNM about "some white bones buried in their lands"; *venator*, hunter (Latin). The specific name honors Tulio del Bono, main authority of the Secretaría de Ciencia, Técnica e Innovación of the Government of San Juan, who is strongly collaborating and helping to develop our paleontology research in the San Juan Province.

Diagnosis. Basal neotheropod dinosaur diagnosed according to the following combination of apomorphies (autapomorphies with asterisk): cervical neural arches with a series of three deep fossae, two blind pockets located within the prezygapophyseal centrodiapophyseal fossa, and the third, communicating with the internal cavity of the neural arch, located within the centropostzygapophyseal fossa; anteroposteriorly elongated fossa on the edge of the posterior centrodiapophyseal lamina that progressively increases in depth and size from C3 to C9*; length of the anterior cervical ribs equivalent to five cervical centra.

Type material. PVSJ 906, an articulated vertebral sequence from the third cervical vertebra to the fourth dorsal vertebra, sacrum composed of five co-ossified vertebrae articulated to the last dorsal and the first caudal, pelvis lacking distal end of pubis and ischium.

Referred material. PVSJ 899, sacrum composed of five co-ossified vertebrae articulated to the pelvis and lacking the distal ends of pubis and ischium, first caudal vertebra; PVSJ 1013, sacrum composed of five co-ossified vertebrae lacking most of the neural arches and sacral ribs; PVSJ 1084,

sacrum composed of five co-ossified vertebrae articulated to the pelvis and lacking the distal ends of pubis and ischium.

Possible referred material. PVSJ 1004, proximal end of right tibia.

Type Locality and Horizon. "Quebrada del puma" locality, Caucete Department, San Juan Province, Argentina (Fig. 1). The fossiliferous locality belongs to the southern outcrops of the late Norian–Rhaetian Quebrada del Barro Formation of the Marayes-El Carrizal Basin (Bossi, 1976; Colombi *et al.*, 2015). The reddish muddy-sandstones of the horizon including PVSJ 906 are located 60 meters below the top of the formation (Fig. 1).

Stratigraphic occurrence. Late Norian–Rhaetian based on the faunal assemblage composed of opisthodontian sphenodonts, tritheledontid cynodonts, basal sauropodomorph dinosaurs, lagerpetid dinosauromorphs, coelophysoid neotheropods, pterosaurs, stem testudinatans and diverse pseudosuchians (Martínez *et al.*, 2015).

Description
Cervical column

PVSJ 906 preserved an articulated series from the posterior half of the third to the 10th cervical vertebrae (Cv3 to Cv10). Several fractures and some damages on the neural spines affect the sequence. Otherwise, the neck is very well-preserved and enables a detailed description (Fig. 3). Almost the complete series of right cervical ribs is attached to the vertebrae in an approximately natural position.

TABLE 1 – Measurements (mm) of the holotype (PVSJ 906) and referred specimens of Lucianovenator bonoi *gen. et sp. nov.*

Bone measurement	PVSJ 906	PVSJ 899	PVSJ 1013	PVSJ 1084	PVSJ 1004
C3 centrum length	26.3d	—	—	—	—
C4 centrum length	49.8	—	—	—	—
C5 centrum length	54.7	—	—	—	—
C6 centrum length	57.0	—	—	—	—
C7 centrum length	56.6	—	—	—	—
C8 centrum length	54.0	—	—	—	—
C9 centrum length	52.8	—	—	—	—
C10 centrum length	40.8	—	—	—	—
D1 centrum length	38.0	—	—	—	—
D2 centrum length	31.6	—	—	—	—
D3 centrum length	32.0	—	—	—	—
D4 centrum length	31.3	—	—	—	—
LD (last dorsal) centrum length	37.1	—	—	—	—
S1 centrum length	36.2	14.9d	14.4d	—	—
S2 centrum length	28.6	25.9	18.5	—	—
S3 centrum length	26.3	22.2	16.3	—	—
S4 centrum length	30.2	21.7	20.5	26.2	—
S5 centrum length	32.0	25.9	21.7	25.3	—
Ca1 centrum length	32.6	24.8	—	—	—
Iliac blade length	145.6	75.5d	—	119.8d	—
Iliac blade height above acetabulum	56.4	40.3	—	47.3	—
Ilium, width of pubic peduncle	23.1	16.6	—	—	—
Tibia prox. end, anteroposterior length	—	—	—	—	33.8

Incomplete measurements due damages are indicating by d. Em dash indicates unknown.

Cervical vertebrae. The body of each cervical vertebrae is elongate and strongly compressed, both ventrally and laterally, with a weak ventral keel, and the anterior and posterior faces anterodorsal-posteroventrally directed (Fig. 3). Centrum length increases from the fourth (although presumably from the axis, the fourth is the first fully preserved cervical vertebra) to the sixth cervical vertebra. The posterior vertebrae become progressively shorter, with the tenth vertebra being the shortest in the cervical series (Tab. 1). Very elongated mid-cervical vertebrae (more than three times longer than the height at the posterior articular surface) are present in coelophysid neotheropods and the early theropod *Eodromaeus* Martínez, Sereno, Alcober, Colombi, Renne, Montañez, and Currie, 2011. The articular faces are sub-circular while the anterior ones are weakly concave and almost flat, and the posterior ones are deeply concave. Among basal theropods, cup-like posterior faces are present in *Sanjuansaurus* Alcober and Martínez, 2010, although in *Herrerasaurus* Reig, 1963 and *Eodromaeus*, the faces are weakly concave. In coelophysids, in which this surface is visible, and in other basal neotheropods, the posterior face is deeply concave (*e.g., Coelophysis rhodesiensis* Raath, 1969;

Coelophysis bauri Cope, 1889; "*Syntarsus*" *kayentakatae* Rowe, 1989; the yet-to-be-named Shake-N-Bake taxon; *Dilophosaurus* Welles, 1954; *Ceratosaurus* Marsh, 1884; tetanurans; Raath, 1977; Tykoski, 2005). In transverse section, the cervical vertebrae of *Lucianovenator* present two kidney-shaped internal pneumatic cavities of camerate structure in the neural arch and a large sub-circular neural channel in the centrum (Fig. 3.5).

In all preserved cervical vertebrae, the parapophyses are located at the ventralmost level of the anterior border, with no evidence of progressive posterodorsal displacement (Fig. 3.1–2). The median ventral keels extend along the anterior two thirds of the centrum andare weakly developed (except for the third vertebra, in which the median ventral keel is very pronounced), decreasing posteriorly along the cervical series toward an incipient crest in the tenth cervical vertebra.
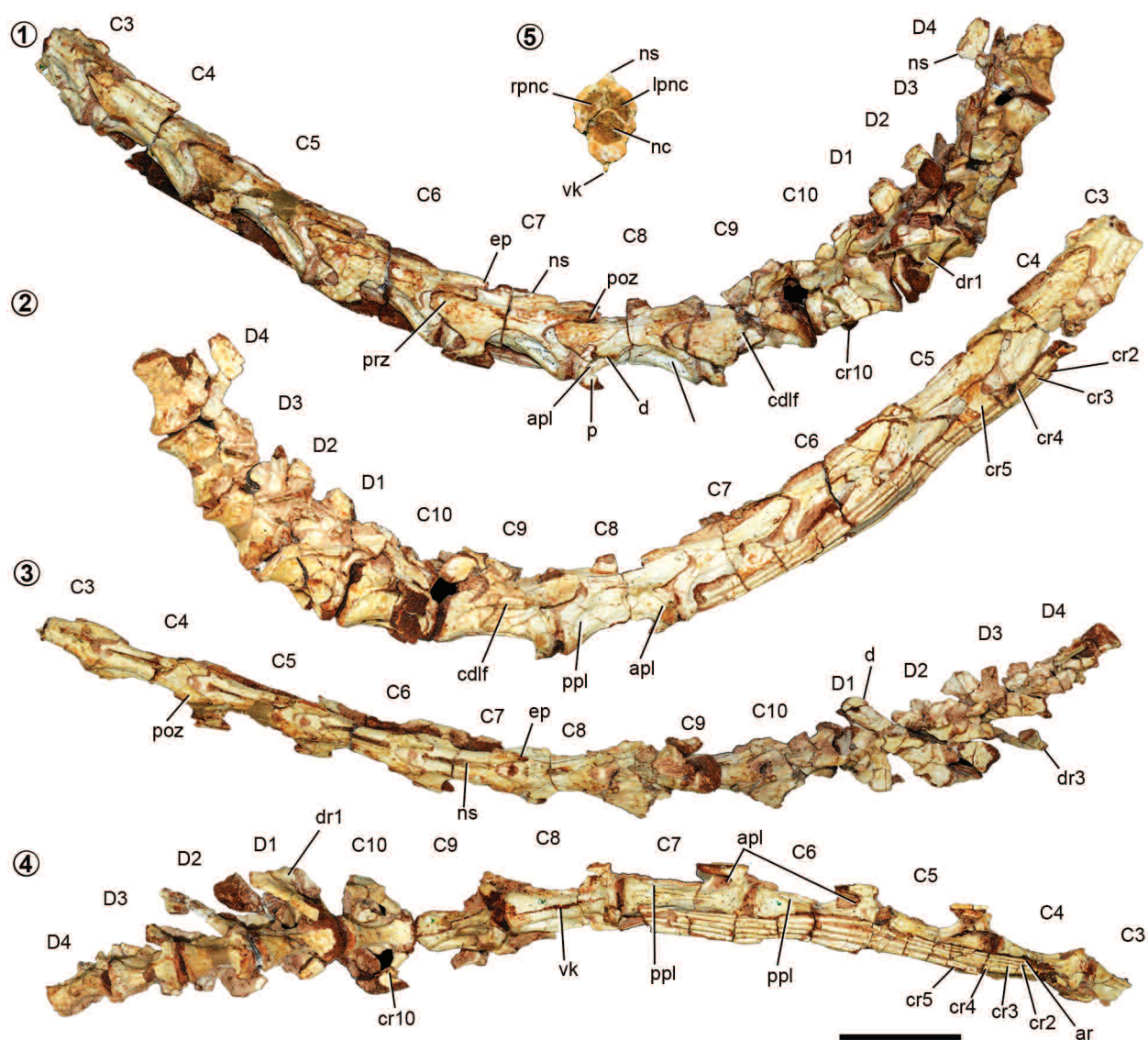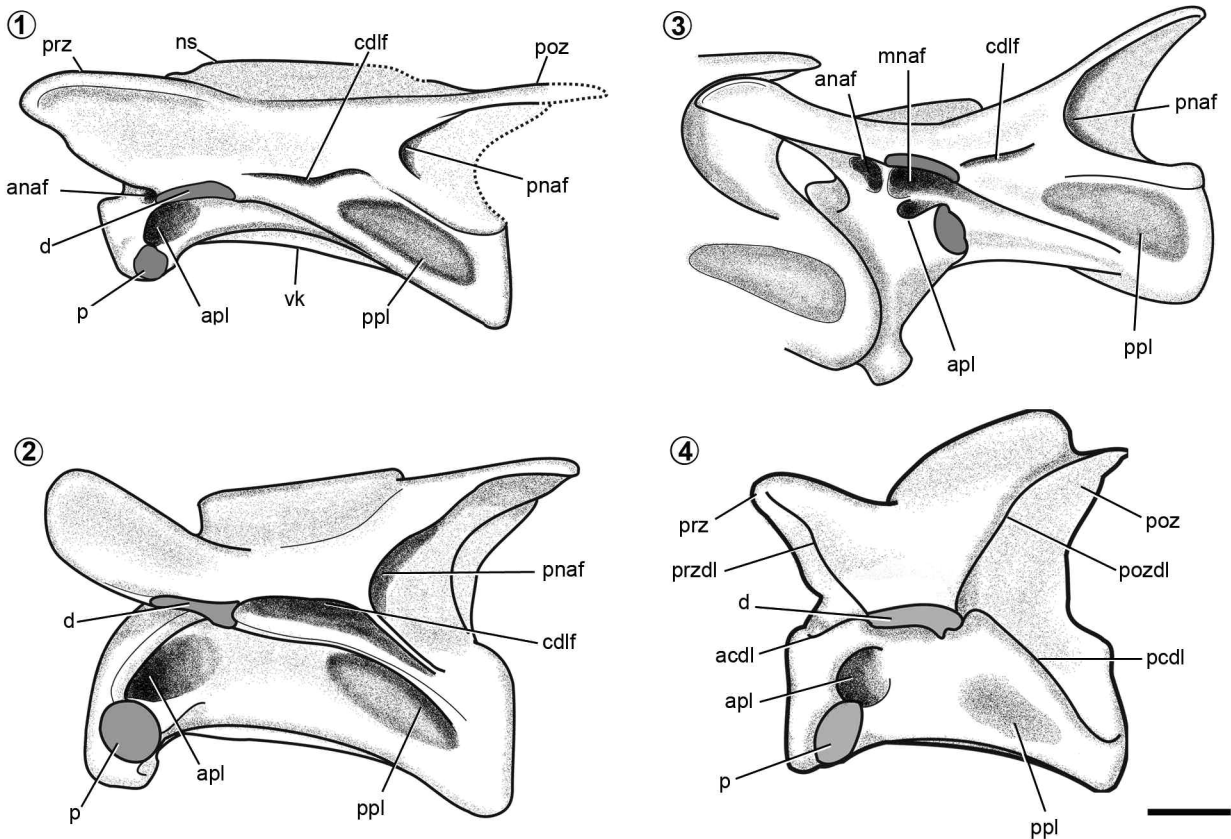

Figure 3. *Lucianovenator bonoi* gen. et sp. nov., cervical and anterior dorsal vertebrae of the holotypic specimen, **PVSJ** 906. **1,** Left lateral view; **2,** right lateral view; **3,** dorsal view; **4,** ventral view; **5,** cross-section of the fourth cervical vertebra in anterior view. Abbreviations: **apl,** anterior pleurocoel; **ar,** atlantal rib; **cdlf,** centrodiapophyseal lamina fossa; **cr2-10,** cervical rib 2 to 10; **Cv3-10,** cervical vertebrae 3 to 10; **d,** diapophyses; **D1-4,** dorsal vertebrae 1 to 4; **dr1-4,** dorsal rib 1 to 4; **ep,** epipophyses; **lpnc,** left pneumatic cavity; **nc,** neural channel; **ns,** neural spine; **p,** parapophysis; **poz,** postzygapophysis; **ppl,** posterior pleurocoel; **prz,** prezygapophysis; **rpnc,** right pneumatic cavity; **vk,** ventral keel. Scale bar= 50 mm.

Weak cervical ventral keels are usual among coelophysoids, other basal neotheropods and the early theropods *Sanjuansaurus* and *Eodromaeus*. In contrast, ventral keels are more pronounced in the early theropods *Herrerasaurus* and *Tawa* Nesbitt, Smith, Irmis, Turner, Downs, and Norell, 2009.

All cervical centra present two pleurocoels or deep fossae on each lateral surface, one anterior and another one posterior (Fig. 3.1–2). The anterior pleurocoel is located posterodorsal to the parapophysis (Fig. 4). It is a sub-elliptical deep and blind fossa in Cv3, with the major axis anteroventrally-posterodorsally oriented. In the successive vertebrae, the fossa become progressively wider although maintaining their depth (Fig. 4.1–4). The posterior pleurocoel is an ovoid blind fossa larger than the anterior one, which is located in the posterior half of the centrum, near

its ventral margin (Fig. 3.1, 4). The ventral border of this fossa is represented by a rod-like lamina extending from the mid-length of the centrum toward its posteroventral corner. In contrast with the anterior pleurocoels, the posterior pleurocoels keep their shape and size (one third of the centrum length) along the entire cervical series, although their depth increases from Cv3 to Cv8 and decreases in depth in Cv9 and Cv10 (Fig. 3.1). The features of the anterior and posterior pleurocoels in PVSJ 906 are similar to those present in most coelophysids, such as "*Syntarsus*" *kayentakatae* (Tykoski, 1998), *Coelophysis bauri* (Colbert, 1989) and *Coelophysis rhodesiensis* Raath, 1969, but different from those of *Panguraptor lufengensis* You, Azuma, Wang, Wang, and Dong, 2014, in which the pleurocoels are deep in Cv4 and Cv5 but weakly developed in Cv6 and Cv7.

Figure 4. *Lucianovenator bonoi* gen. et sp. nov. (**PVSJ** 906), cervical vertebrae. **1,** Fourth cervical vertebra in left lateral view; **2,** ninth cervical vertebra in left lateral view; **3,** fourth cervical vertebra in left antero-ventrolateral view; **4,** tenth cervical vertebra in left lateral view. Abbreviations: **acdl,** anterior centrodiapophyseal lamina; **anaf,** anterior neural arch fossa; **apl,** anterior pleurocoel; **cdlf,** centrodiapophyseal lamina fossa; **d,** diapophyses; **mnaf,** median neural arch fossa; **ns,** neural spine; **p,** papapophysis; **pcdl,** posterior centrodiapophyseal lamina; **pnaf,** posterior neural arch fossa; **poz,** postzygapophysis; **pozdl,** postzygodiapophyseal lamina; **ppl,** posterior pleurocoel; **prz,** prezygapophysis; **przdl,** prezygodiapophyseal lamina; **vk,** ventral keel. Scale bar= 10 mm.

All cervical neural arches are low and fused to the centra, which is characterized by low blade-like neural spines, stout prezygapophyses medially connected by an intra-prezygapophyseal lamina and thin postzygapophyses with long epipophyses overhanging their rear margin (Figs. 3.1–3, 4.1–3). The pre- and post- zygapophyses are at the same level and nearly horizontal, up to the sixth vertebra. From the seventh vertebra onwards, they are anterodorsally and posterodorsally oriented, respectively. The postzygapophyses are more elevated with respect to the prezygapophyses and both have more inclined articular facets (Fig. 4.1–2).

From Cv3, the first incompletely preserved cervical vertebra, to Cv9, the prezygapophyses extend beyond the anterior margin of the centra (18% of the anterior centrum length) and have flat articular facets with a strong dorsomedial slope. From the lateral edge, a prezygodiapophyseal lamina extends posteroventrally to the diapophysis. An anterior and a posterior centrodiapophyseal lamina are present (Fig. 4.1–3). The diapophyses are laterally reduced but anteroposteriorly elongated, and located close to the parapophyses (Fig. 4.1). The postzygapophyses are thinner than the prezygapophyses and project beyond the posterior margin of the centra (20% of centrum length), with faces directed outwardly and long epipophyses projecting posteriorly (Figs. 3, 4.1–3). Ventral to the postzygapophyses, the neural arches present a thin bone lamina covering the anterior extent on the posterolateral surface and, under this lamina, a deep centropostzygapophyseal fossa opens posteriorly (Fig. 4.1–3). The neural spines are thin, low, anteroposteriorly long and without expanded distal ends. From Cv3 onwards, the posterior centrodiapophyseal lamina is progressively more laterally expanded and, at the same time, a progressively deeper anteroposteriorly directed fossa is developed on its edge. This fossa forms a deep blind pocket in Cv9 (Fig. 4.2), a character not present in other basal theropods. In addition to these fossae, PVSJ 906 presents two pairs of deep fossae located on the prezygapophyseal centrodiapophyseal fossa (Fig. 4.3). One pair of fossae, sub-triangular in shape and blind although very deep, is located posterolateral to the prezygapophyses and lateral to the anterior opening of the neural canal (Fig. 4.3). The second pair is an anteroposteriorly large and blind deep fossa, located immediately posterior to the first one (Fig.

4.3). PVSJ 906 has another pneumatic feature within the centropostzygapophyseal fossa; that is, a deep pocket which communicates with the internal cavity of the neural arch (Fig. 4.3). The first and the third aforementioned fossae are similar and located in the same position as those present in "*Syntarsus*" *kayentakatae* (Tykoski, 1998) but different from those of *Coelophysis bauri*, in which both fossae are communicated with the internal cavities of the centrum (Colbert, 1989). The series of three aligned fossae presents, in the cervical neural arches of PVSJ 906, two anterior blind ones and a posterior one communicating with the internal pneumatic cavity of the neural arch, which is a combination of characters not reported in other neotheropods.

The morphology of the tenth cervical vertebra (Cv10) is quite different (Fig. 4.4). The centrum is similar in shape to the anterior centra, and differs mostly in its length (20% shorter than the preceding) and its less developed ventral keel and posterior pleurocoel. The major changes, comparing with the preceding vertebrae, are located in the neural arch. The pre and postzygapophyses of Cv10 are strongly laterodorsally oriented and do not extend much beyond the margins of the centrum (Fig. 4.4). The laterally directed diapophyses are long and thin laminae which are delta-shaped in dorsal view. The diapophyses, as in the preceding cervical vertebrae, are anteroposteriorly expanded although broader, more robust and located far dorsolaterally from the parapophyses. In the neural arch of Cv10, the prezygodiapophyseal, the postzygodiapophyseal, the anterior centrodiapophyseal, the posterior centrodiapophyseal, the centroprezygoapophyseal and the centropostzygodiapophyseal laminae are very well-developed and delimit a set of corresponding deep fossae (Fig. 4.4). The neural spine is thin and low, and anteroposteriorly long, with a thin distal end.

Cervical ribs. As in other coelophysoids, the cervical ribs are long, slender and posteriorly oriented in an imbricate pattern (Figs. 3.2–4, 5.2). As with the cervical vertebrae, the first nine cervical ribs are similar but become increasingly robust posteriorly and substantially differ from the tenth cervical rib. The ribs of Cv3 to Cv9 are extremely long and extend up to the length of the following four vertebrae; thus, each rib is as long as five cervical vertebrae (Figs. 3.2, 4, 5.2). The anterior process of each cervical rib, except for the tenth, is acute, long and extends beyond the anterior margin of the
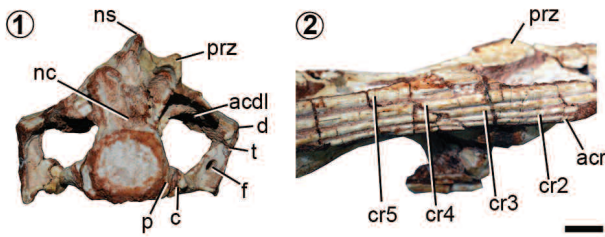
Figure 5. *Lucianovenator bonoi* gen. et sp. nov. (**PVSJ** 906), cervical vertebrae and ribs. **1,** Tenth cervical vertebra in left anterolateral view; **2,** fifth cervical vertebra in ventral view. Abbreviations: **acdl,** anterior centrodiapophyseal lamina; **acr,** atlantal cervical rib; **c,** capitulum; **cr2-5,** cervical rib 2 to 5; **d,** diapophysis; **f,** foramen; **nc,** neural canal; **ns,** neural spine; **p,** parapophysis; **prz,** prezygapophysis; **t,** tuberculum. Scale bar= 10 mm.

centrum and as far as the prezygapophysis. Both the capitulum and the tuberculum are fused with the parapophysis and the diapophysis, respectively. The capitulum is short, subcilindrical and mediolaterally oriented. The tuberculum is laminar, lateromedially flat and almost dorsally oriented. All cervical ribs extend parallel to the neck in juxtaposition to the following, maintaining the same diameter (3 millimeters) along 80% of its length, from where they begin to taper. Extremely long and parallel cervical ribs are present in most coelophysoids, although this length, equivalent to five cervical centra, is only reported in "*Syntarsus*" *kayentakatae* (Tykoski, 1998).

The tenth cervical rib is more robust, with a longer capitulum and tuberculum, and an anterior process that is only a small protuberance (Figs. 3.4, 5.1). The capitulum projects anteromedially and increases its diameter toward the end. The tuberculum is a long, mediolaterally thin lamina of bone projecting anterodorsally. The capitulum and the tuberculum are medially connected by a thin lamina of bone. The left rib has a sub-circular foramen on the surface of this lamina, which is a character not present in the right rib (Fig. 5.1). Only the anterior portion of the shaft, which is lateromedially flat instead of cylindrical and projects posteriorly, is preserved.

Dorsal column

PVSJ 906 preserves the first four dorsal vertebrae articulated to the neck while the last dorsal vertebra is articulated to the sacrum. The anterior sequence has some damage on the right side that mostly affects the neural

arches. The last dorsal is fractured but almost complete.

Dorsal vertebrae. The bodies of the dorsal vertebrae are elongate although much shorter than the cervical ones. The dorsal centra are ventrally and laterally compressed, and lack a ventral keel (Figs. 3.1–4, 6). The first dorsal vertebra (D1) is 10% shorter than the last cervical but 20% longer than D2 (Tab. 1). From D2 to D4 (the only preserved anterior dorsal centrum) the centra are similar in length (Figs. 3.1–4, 6.1–3). The last dorsal centrum is longer than the first one. The anterior and posterior faces of the dorsal centra are sub-circular, weakly concave and at right angle with respect to the median axis of the centra. Both articular surfaces (anterior and posterior) are similar in size in the anterior dorsal vertebrae but, in the last dorsal, the posterior articular face is much larger than the anterior one (Fig. 7.5). Dorsal centra lack the posterior pleurocoels present in cervical centra. D1 and D2 still have a deep anterior pleurocoel located posterodorsal to the parapophysis (Fig. 6.1–2); in D3, it is a shallow fossa and, in D4, the centrum lacks pleurocoels (Fig. 6.3). The presence of anterior pleurocoels only in the anterior dorsal vertebrae is reported in other neotheropods (*e.g., "Syntarsus" kayentakatae, Dilophosaurus, Carnotaurus* Bonaparte, 1985; Tykoski, 1998). The parapophyses are located at the level of the anteroventral border of the centrum in D1, with a progressive slightly posterodorsal displacement from D2 to D3 (Fig. 6.1–3). D4 is the first dorsal vertebra with the parapophyses located on the neural arc (Fig. 6.3). In contrast, in *Coelophysis rhodesiensis*, the parapophysis is located in the neural arc in D1 (Raath, 1977).

All neural arches are robust, tall (twice as tall as the centrum) and fused to the centrum. The prezygapophyses extend well beyond the anterior margin of the centra (40% of the anterior centrum length) and are roughly triangular in lateral view (Fig. 6.3). Their articular facets are sub-circular and dorsomedially sloped in the two first dorsal vertebrae but, from the third vertebra back, they face dorsally. The transverse processes are sheet-like and strongly backswept (Figs. 3.3, 6). The postzygapophyses do not project beyond the posterior margin of the centra. The sub-circular articular facets are ventrolaterally sloped in the two first dorsal vertebrae and ventrally oriented in the subsequent ones. The neural spines of at least the two most anterior dorsal vertebrae (the third one is broken) are anteroposteriorly
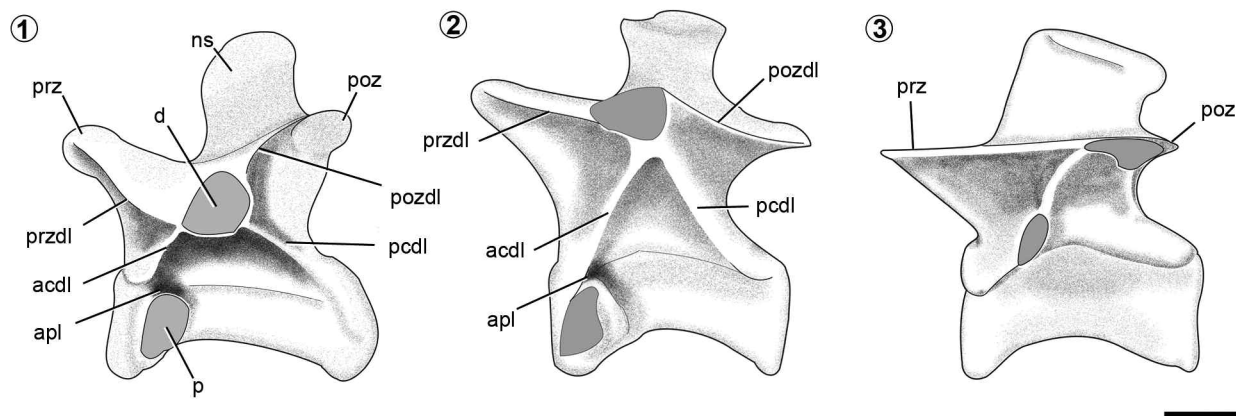
Figure 6. *Lucianovenator bonoi* gen. et sp. nov. (**PVSJ** 906), dorsal vertebrae in left lateral view.**1,** First dorsal vertebra; **2,** second dorsal vertebra; **3,** fourth dorsal vertebra. Abbreviations: **acdl,** anterior centrodiapophyseal lamina; **apl,** anterior pleurocoel; **d,** diapophyses; **ns,** neural spine; **p,** parapophysis; **pcdl,** posterior centrodiapophyseal lamina; **poz,** postzygapophysis; **pozdl,** postzygodiapophyseal lamina; **prz,** prezygapophysis; **przdl,** prezygodiapophyseal lamina. Scale bar= 10 mm.

short, with spine tables on their distal ends (Figs. 3.3, 6.1–2). The spine tables are posteriorly wider and result in a triangular shape in dorsal view. The neural spine of the fourth vertebra is anteroposteriorly long and square-shaped in lateral view, and has an expanded distal end although not configuring a spine table (Fig. 6.3). From D1 to D4 (all preserved anterior dorsal vertebrae), the neural arches possess well-developed prezygadiapophyseal, postzygadiapophyseal, anterior centrodiapophyseal, posterior centrodiapophyseal, centroprezygapophyseal and centropostzygapophyseal laminae delimiting deep fossae (Fig. 6.1–3). In contrast to the anterior dorsal vertebrae, the last dorsal vertebra does not have any laminae or fossae (Fig. 7.5). The transverse process is shed-like anteroposteriorly wide, with a sharp distal end, and is roughly triangular in dorsal view. The neural spine is tall and anteroposteriorly wide, with concave anterior and posterior borders in lateral view, and ends in a spine table.

Dorsal ribs. PVSJ 906 preserves the proximal end of the first and second dorsal ribs as well as the capitulum of the third (Fig. 3). The dorsal ribs lack anterior processes and each has a large capitulum and tuberculum, of which the former is larger. The capitulum projects ventroanteromedially and the tuberculum anterodorsally. A thin lamina of bone connects both processes. The preserved small anterior portion of the shaft is mediolaterally flat and projects posteroventrolaterally.

Sacrum

Four sacra have been found, all with articulated sacral vertebrae and of different sizes. The smallest one (approximately 98 mm in length; PVSJ 1013) preserves the four anterior centra and the anterior half of the fifth but lacks most of the neural arches and ribs (Fig. 7.1–2). The second in size (approximately 107 mm in length; PVSJ 899) preserves the posterior half of S1, the following four sacral centra and almost complete neural arches and ribs (Fig. 7.3). The third specimen (129 mm in length; PVSJ 1084) preserves the complete sacrum (Fig. 7.4). The last one belongs to the holotype (PVSJ 906), which is the largest (154 mm in length) and the most complete specimen (Fig. 7.5, 8). The following description is mostly based upon PVSJ 906, unless noted.

As in other coelophysids, the sacrum has five completely co-ossified sacral centra. In ventral view, the centra are almost cylindrical with a weak widening of their articular faces except for S1 and S5, in which the anterior and the posterior faces, respectively, are much wider (Fig. 7.1–5). The ventral surfaces present a shallow longitudinal fossa, which is more pronounced in the smaller specimens (Figs. 7.2, 8.4).

The sacral neural arches including transverse processes form an almost continuous and fused structure (Figs. 7.3, 8.1). The sacral ribs are shared between coalescent sacral vertebrae. S1 retains the kind of dorsal transverse process located up on the neural arch. The transverse processes are laminar and contact the ilium at the level of the preacetabu-

lar process of the ilium. The primordial sacral vertebrae are S3 and S4, whic bear the true sacral ribs located close to the ventral border of the respective centrum. The rib of S2 attaches to the medial wall of the ilium just behind the preacetabular process, whereas the rib of S4 attaches at the rise of the postacetabular process. S3 has the shortest centrum and its transverse process is located up in the neural arch, contacting laterally the iliac lamina. S5 has a laminar transverse process that contacts the ilium at the rear portion of its postacetabular process. In dorsal view, the transverse processes form a nearly continuous shed of bone only interrupted by a wide hollow between the S4 and S5, which contacts the ilium near the dorsal border (Fig. 9.1). The neural spines have strongly mediolaterally expanded distal ends and are completely fused to each together (Fig. 8.2).

Caudal column

Only the first caudal vertebra is preserved in PVSJ 906, PVSJ 1084, and PVSJ 899, in all specimens attached to the sacrum. The best preserved one is from the former specimen.

The first caudal vertebra is anteroposteriorly slightly shorter than the last sacral (Fig. 8.4). The centrum is ventrally and laterally constricted. The ventral surface is excavated by a longitudinal groove that is more developed in the larger specimens. The neural arch is tall, without additional accessory laminae nor spinal fossae. The transverse processes are very thin laminae directed laterally and ending in sharp edges. The prezygapophyses extend beyond the anterior border of the centrum and are located at the same level as the transverse processes. The neural spine is not preserved in any of the specimens.
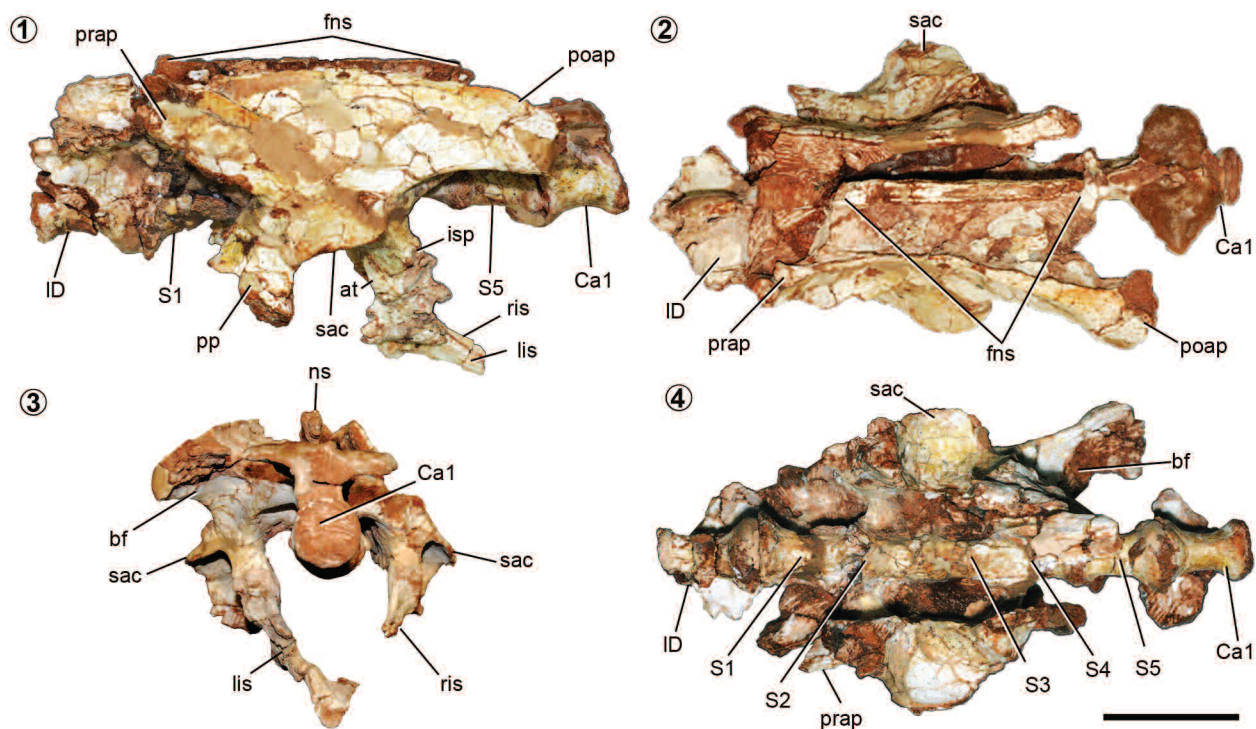
Pelvis

Three incomplete pelves of different sizes were found. All three specimens have firmly fused together pelvic bones. PVSJ 899 preserves both ilia, and lacks most of the preacetabular processes and the proximal end of both pubes and ischia (Fig. 7.3). PVSJ 1084 preserves the left ilium, lacking the preacetabular process, the right ilium, lacking the postacetabular process, and the proximal end of both ischia (Fig. 7.4). PVSJ 906 preserves the left ilium, lacking the anterior tip of the preacetabular process, the right ilium, lacking part of the postacetabular process, and
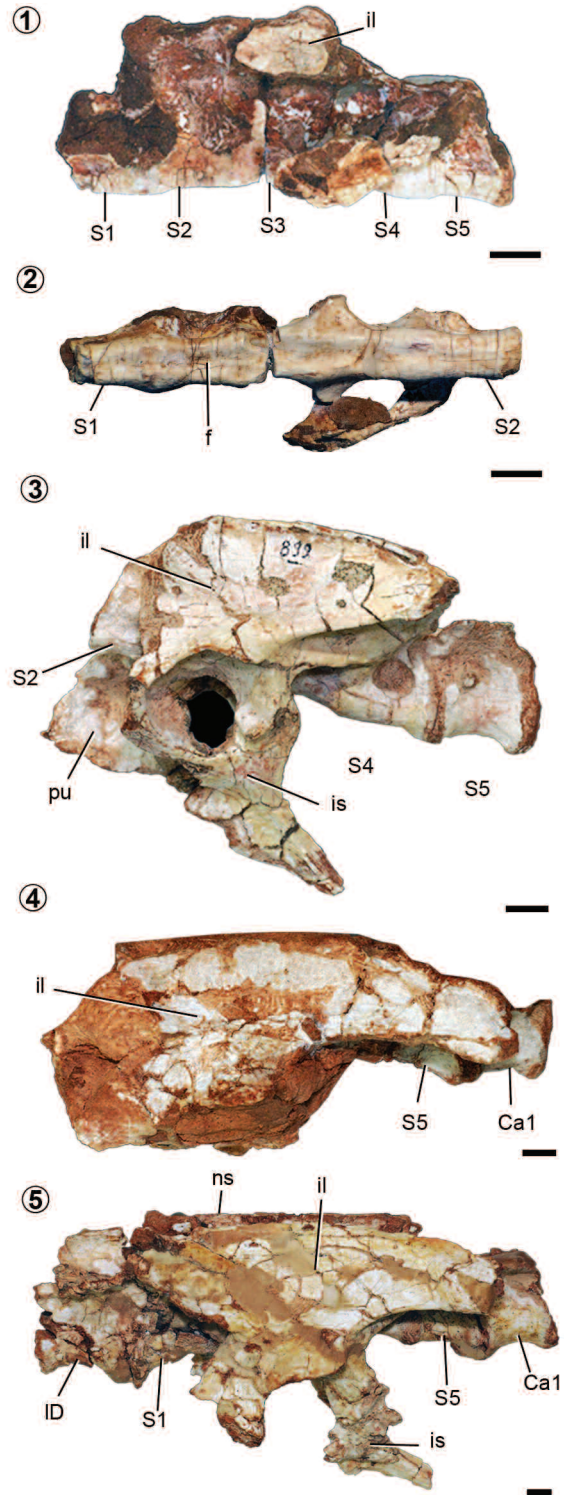
Figure 7. Sacra and pelvis of different specimens of *Lucianovenator bonoi* gen. et sp. nov. **1,** Sacrum of referred specimen **PVSJ** 1013 in left lateral view; **2,** sacrum of referred specimen **PVSJ** 1013 in ventral view; **3,** sacrum and pelvis of referred specimen **PVSJ** 899 in left lateral view; **4,** sacrum and pelvis of referred specimen **PVSJ** 1084 in left lateral view; **5,** sacrum and pelvis of holotypic specimen **PVSJ** 906 in left lateral view. Abbreviations: **Ca1,** first caudal vertebra; **f,** fossa; **ID,** last dorsal vertebra; **il,** ilium; **is,** isquium; **ns,** neural spine; **pu,** pubis; **S1-5,** sacral vertebrae 1 to 5. Scale bars= 10 mm.

Figure 8. Sacrum and pelvis *Lucianovenator bonoi* gen. et sp. nov. (**PVSJ** 906). **1,** Left lateral view; **2,** dorsal view; **3,** posterior view; **4,** ventral view. Abbreviations: **at,** antitrochanter; **bf,** brevis fossa; **Ca1,** first caudal vertebra; **fns,** fused neural spines; **ID,** last dorsal vertebra; **isp,** ischial peduncle; **lis,** left isquium; **ns,** neural spine; **poap,** postacetabular process; **pp,** pubic peduncle; **prap,** preacetabular process; **ris,** right isquium; **sac,** supraacetabular crest; **S1-5,** sacral vertebrae 1 to 5. Scale bar= 50 mm.

the proximal end of the right ischium (Figs. 7.5, 8.1–4). The description below is mostly based on PVSJ 906, unless noted.

Ilium. The iliac blade is dorsoventrally tall, with thin but well-developed pre- and postacetabular processes. The dorsal border is weakly convex to almost straight in lateral view, and strongly laterally curved with medial convexity in dorsal view (Fig. 8.1–4).

The supraacetabular crest is well-developed and extends close to the pubic facet. As in other coelophysids and *Dilophosaurus*, this crest projects lateroventrally, hiding most of the dorsal and anterior region of the acetabulum in lateral view. The supraacetabular crest does not form a continuous structure with the brevis shelf (Figs. 7.3–4, 8.1). The acetabulum is fully perforated with a strongly concave ventral margin. Dorsal to the supraacetabular crest, the lateral surface of the iliac blade is broadly concave (Fig. 8.1).

The preacetabular process is laminar, dorsoventrally wide, square-shaped in lateral view and very long, and, as in other neotheropods, extends well beyond the level of the

pubic peduncle. The postacetabular process is long, posterolaterally oriented and presents, in lateral view, a notch at the posterior margin (Figs. 7.3, 9.3). A thick and trapezoidal rugose area extends along the dorsolateral border of the process, from a mid-point of the dorsal border of the iliac blade, and widens posteriorly (Fig. 8.2). This feature is present in coelophysids (*e.g.*, *Coelophysis bauri*, *C. rhodesiensis*, "*Syntarsus*" *kayentakatae*; Tykoski, 1998) and in several basal sauropodomorphs (*e.g.*, *Saturnalia* Langer, Abdala, Richter, and Benton, 1999, *Chromogisaurus* Ezcurra, 2010, *Adeopapposaurus* Martínez, 2009), but absent in the basal theropods *Eodromaeus* and *Tawa* as well as in the basal sauropodomorphs *Eoraptor* Sereno, Forster, Rogers, and Monetta, 1999 and *Panphagia* Martínez and Alcober, 2009. The ventral surface of the postacetabular process has a deep and wide brevis fossa that widens posteriorly in a fan-like fashion (Fig. 8.4).

The pubic peduncle has an anteroposteriorly elongated sub-triangular cross-section delimited by a concave acetabular gently convex lateral and almost flat medial sur-

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faces. This peduncle is directed anteroventrally and is greater in overall size and longer than the ischial peduncle (Figs. 8.1, 9.3). The ischial peduncle is expanded posteriorly although it does not form a posterior stub and it has a broad antitrochanter on the acetabular surface.

Pubis. Only the proximal end of the iliac peduncle and the dorsal part of the obturator process is preserved in PVSJ 899 and PVSJ 1084 (Fig. 7.3). The acetabular surface is concave (Fig. 9.3) and lateromedially thin at its ventral regional though, toward the zone of the iliac peduncle, it widens lateromedially. The pubic apron and puboischiadic plate are not preserved in any of the specimens.

Ischium. The best preserved ischia belong to PVSJ 899 (Fig. 7.3); nevertheless, they are incomplete, with the ventral border badly damaged and lacking most of the shafts and both distal ends. The iliac peduncle of the ischium is wide and tabular in lateral view. It is mediolaterally thin, sub-triangular in cross-section and delimited by flat medial and convex lateral surfaces. Close to the articular surface, the proximal end of the ischium is laterally expanded and forms the antitrochanter surface (Fig. 8.1). The anterior border of the iliac peduncle has a deep acetabular embayment (Fig. 9.3). On the lateral surface, 2 cm below to the ischio-iliac suture, a pronounced lateral crest runs distally from the iliac articulation down to the shaft (Fig. 9.3).

The pubic process is dorsoventrally wide and extends anteriorly to form most of the ventral surface of the acetabulum. The ventral border and the puboischiadic plate are damaged and thus preclude the determination of whether a ventral notch is present. The proximal portion of the shaft is mediolaterally thin and has a triangular cross-section that is as dorsoventrally deep as it is transversely broad.

Appendicular skeleton

The only part of the appendicular skeleton that is known is the proximal end of the right tibia (PVSJ 1004; Fig. 10). Although no parts of this specimen overlap with the holo-
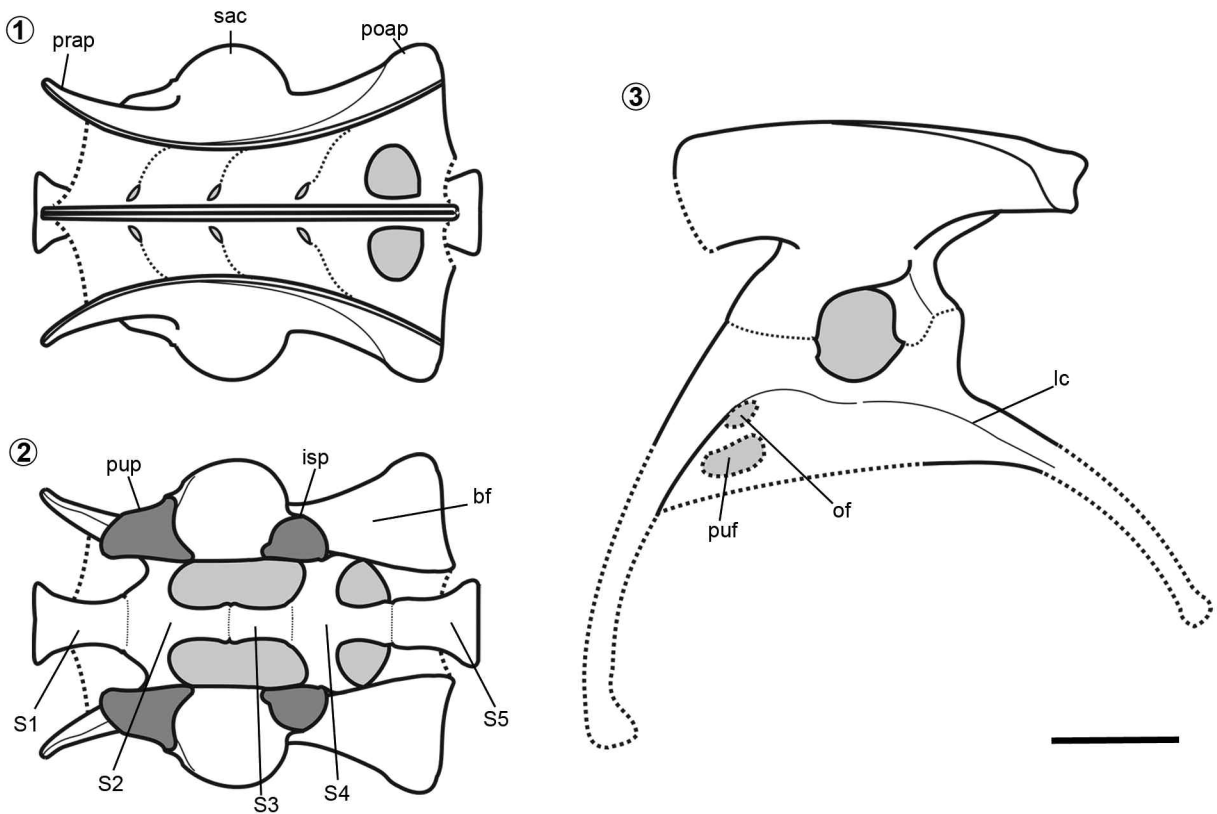
Figure 9. Reconstruction of the sacrum and pelvis of *Lucianovenator bonoi* gen. et sp. nov. **1,** Dorsal view; **2,** ventral view; **3,** left lateral view. Abbreviations: **bf,** *brevis fossa*; **isp,** ischial peduncle; **lc,** lateral crest; **of,** obturator foramen; **poap,** postacetabular process; **prap,** preacetabular process; **puf,** pubic fenestra; **pup,** pubic peduncle; **sac,** supraacetabular crest; **S1-S5,** sacral vertebrae 1 to 5. Scale bar= 50 mm.
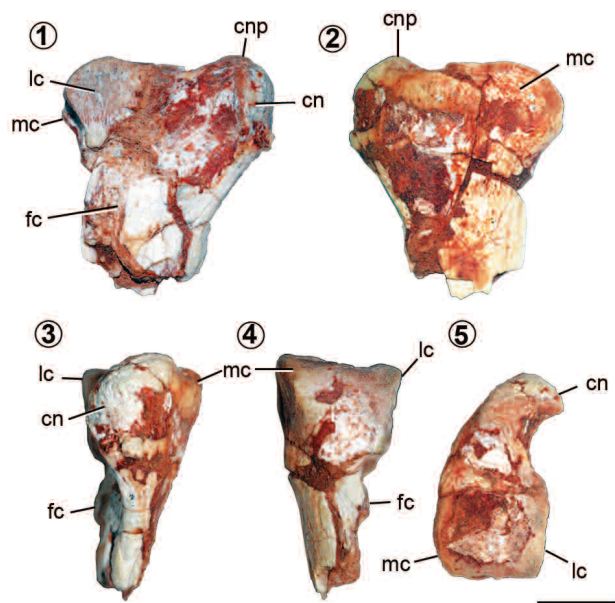
Figure 10. 1–5, Proximal end of the right tibia of possible referred specimen (**PVSJ** 1004). **1,** Lateral view; **2,** medial view, **3,** anterior view; **4,** posterior view; **5,** proximal view. Abbreviations: **cn,** cnemial crest; **cnp,** cnemial process; **fc,** fibular crest; **lc,** lateral condyle; **mc,** medial condyle. Scale bar= 10 mm.

type, we assigned it as a "possible referred specimen" because the bone clearly belongs to a neotheropod of the same size of the type and referred specimens and because no other neotheropod fossils were found in the stratigraphic unit. It has some damage on the lateral side and a partial crushing of the proximal part of the shaft. Otherwise, it is well-preserved. The proximal surface of the tibia is sub-triangular in proximal view, with an anteroposterior concavity delimiting aproximally expanded cnemial process (Fig. 10.1–2). The medial condyle is larger and slightly more proximally expanded than the lateral condyle (fibular condyle). The posterior borders of both condyles are at the same level and separated by a shallow cleft. The lateral margin of the lateral condyle is squared-off, although damages in this area cast doubts about the validity of this character (Fig. 10.5). The fibular crest is dorsoventrally oriented and extends along the lateral side of the proximal portion of the tibia (Fig. 10.1, 3–4). Again, the damage precludes the determination of whether this crest extends from the proximal articular surface or if it originates distal to the proximal margin of the tibia.

PHYLOGENETIC RESULTS

The phylogenetic affinities of *Lucianovenator bonoi* were tested through a cladistic analysis within the context of basal Theropoda and using the dataset recently published by Nesbitt and Ezcurra (2015), which is a modification of the datasets of Nesbitt *et al.* (2009) altered by Ezcurra and Brusatte (2011). We partially amended the original matrix by adding the recently published theropod *Panguraptor lufengensis*, based on the scoring of You *et al.* (2014), and modifying 57 character-states of the scoring for *Eodromaeus*, based on personal observations of the specimens housed in the PVSJ (see Supplementary Information). The resulting matrix includes 343 characters and 47 taxa.

Following the analysis of Nesbitt and Ezcurra (2015), we carried out our main analysis including the holotype of *Lepidus praecisio*. Yet, in order to establish a comparison with previous results, extra analyses were conducted, including one in which the holotype and the referred specimens were treated as a "combined" terminal and another one in which the holotype and the referred specimens were treated as two different terminals (see Supplementary Information).

The heuristic tree search resulted in 2 MPTs of 1066 steps (CI= 0.385, RI=0.692) found in 880 out of the 1000 replicates. As was reported by Nesbitt and Ezcurra (2015), in the strict consensus tree, *Eodromaeus murphi, Tawa hallae* and *Chindesaurus bryansmalli*, together with herrerasaurids, represent the most basal members of Theropoda (Fig. 11). The mid-Norian South American theropod *Zupaysaurus rougieri* is recovered as the sister-taxon of *Liliensternus lilienstermi* among a monophyletic clade more closely related to Averostra than to Coelophysidae (Fig. 11).

The strict consensus tree depicted the new taxon *Lucianovenator bonoi* in an unresolved clade together with *Coelophysis rhodesiensis* and *Camposaurus arizonensis* (Fig. 11). This clade is supported by one unambiguous synapomorphy: the presence of co-ossified prezygapophyses and complimentary postzygapophyses of sacral vertebrae (character 140.1). The Bremer support value for this clade is of 1 and the bootstrap frequency is below 50 per cent (see Supplementary Information).

The holotype of *Lepidus praecisio* was recovered as the sister-taxon of *Coelophysis bauri* and the both of those together, as the sister-clade of the polytomy of *Lucianovena-*

tor, *C. rhodesiensis* and *Camposaurus* (see Supplementary Information for synapomorphies supporting clades). The Asiatic *Panguraptor lufengensis* was depicted as the sister-taxon of the group comprised of these two clades and, together with *"Syntarsus" kayentakatae*, these encompass the taxonomic content of the clade Coelophysidae (Fig. 11). In this context, Coelophysidae is supported by 12 unambiguous synapomorphies (and a Bremer value of 1, and 27% of bootstrap frequencies), of which three are present in *Lucianovenator*: the presence of a rimmed depression on the posterior part of the cervical centrum (character 129.1), a sacral centrum co-ossified at the ventral edge (character 139.1) and the lateral surface of the postacetabular process of the ilium with a distinct posterior rim for the origin of the *M. iliofibularis* (character 341.1). Alternative phylogenetic placements of *Lucianovenator* within Coelophysidae require at least one or two extra steps whereas a minimum of eight extra steps are necessary to place it outside of Coelophysidae (see Supplementary Information).

DISCUSSION AND CONCLUSIONS

Since the group Coelophysoidea, usually defined as all the neotheropods more closely related to *Coelophysis bauri* than to *Ceratosaurus nasicornis* (Padian *et al.*, 1999), was coined (Nopcsa, 1928; Holtz, 1994), a large number of theropod dinosaurs were included within (*e.g.*, *Liliensternus*, *Dilophosaurus*, *Gojirasaurus*, "*Syntarsus*", *Zupaysaurus*, *Procompsognathus*, *Coelophysis*, *Camposaurus*; Fraas, 1913; Colbert, 1989; Carpenter, 1997; Tykoski, 1998, 2005; Arcucci and Coria, 2003; Carrano and Sampson, 2004; Ezcurra and Novas, 2007; Ezcurra and Brusatte, 2011). Nevertheless, in most recent analyses, some of these taxa (*e.g.*, *Dilophosaurus*) were found to be successive sister-taxa to Averostra (Ezcurra and Brusatte, 2011; Nesbitt and Ezcurra, 2015; Rauhut *et al.*, 2016) while some other (*e.g.*, *Liliensternus*, *Zupaysaurus*) were found together with Coelophysidae and the most basal Averostra in an unresolved arrangement at the base of Neotheropoda (Ezcurra and Brusatte, 2011; Nesbitt and Ezcurra, 2015). In our analysis, we recovered all the aforementioned conflictive taxa that were once included in Coelophysoidea as successive sister-taxa to Averostra (Fig. 11). This result depicts the natural group Coelophysidae as the first and the only node on the stem Coelophysoidea. In this context, the clade Coelophysidae, as in other analyses

(*e.g.*, Rowe and Gauthier, 1990; Sereno, 1999; Holtz, 2000; Tykoski, 2005; Carrano *et al.*, 2005; Ezcurra and Novas, 2007; Ezcurra and Nesbitt, 2011), persists as a robust natural group supported by many unambiguous synapomorphies (see Phylogenetic Results) as well as several ambiguous traits (*i.e.*, small size, long neck, highly kinetic elongated skulls). Accordingly, this analysis supports a basal split of Neotheropoda between the monophyletic stem Coelophysoidea and the stem that includes Averostra. The temporal vicinity of the late Carnian *Eodromaeus* (Martínez *et al.*, 2011) the sister taxa of Neotheropoda and the most basal members of the stem leading to the Averostra (*e.g.*, middle
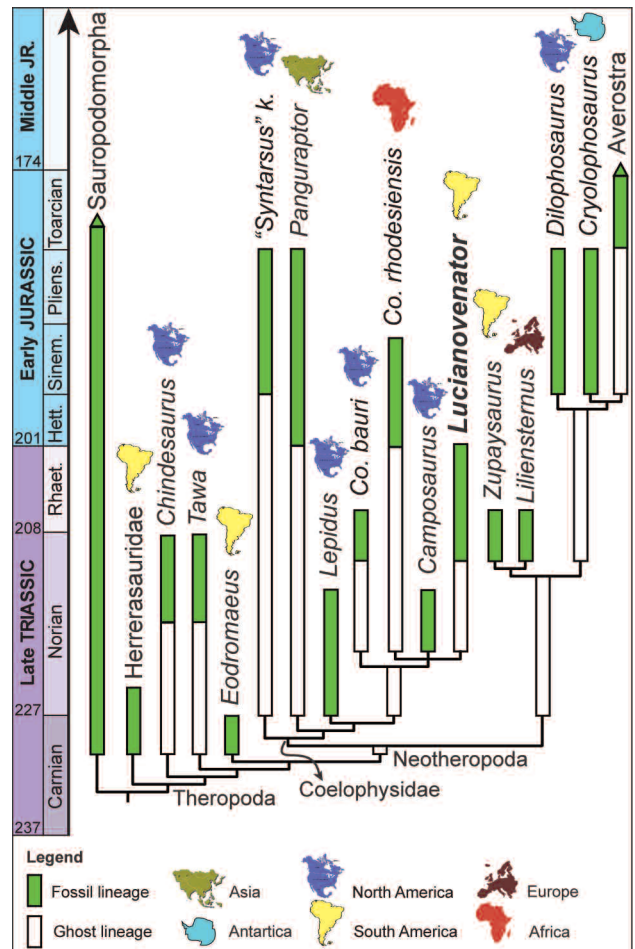
Figure 11. Chronostratigraphically calibrated strict consensus tree showing phylogenetic relationships of **Lucianovenator bonoi** gen. et sp. nov. among basal Theropoda. Maps above taxa indicate paleobiogeographic distribution during Late Triassic−Early Jurassic. Dataset of Nesbitt *et al.* (2009) modified by Ezcurra and Brusatte (2011) and Nesbitt and Ezcurra (2015), with the addition of **Panguraptor lufengensis** (You *et al.*, 2014).

Norian *Zupaysaurus*; Kent *et al.*, 2014) demand a short ghost lineage to support this result (Fig. 11).

To date, the Triassic indubitable record of Coelophysidae, as well as all early non-neotheropod theropod dinosaurs (*e.g.*, Herrerasauridae, *Chindesaurus*, *Eodromaeus*, *Tawa*), are restricted to Western Pangea. Although the oldest record of non-neotheropod theropods is from the Carnian of South America (*e.g.*, *Herrerasaurus*, *Sanjuansaurus*, *Eodromaeus*), they are certainly present in younger (Norian) North American strata (*e.g.*, *Chindesaurus*, *Tawa*). Among Neotheropoda, the earliest records are the coelophysids. Between them, the earliest known records are *Lepidus praecisio* from the early Norian, maybe late Carnian (Nesbitt and Ezcurra, 2015), and *Camposaurus arizonensis* (Hunt *et al.*, 1998; Ezcurra and Brusatte, 2011) from the early–middle Norian of North America. A little younger are the North American *Coelophysis bauri* (middle–late Norian) and the recently reported specimen from the middle Norian Los Colorados Formation of South America (Ezcurra, 2017). Finally, among the reliable record, the late Norian–Rhaetian *Lucianovenator bonoi* represents the youngest known Triassic coelophysid so far. During the Early Jurassic, the persistence of coelophysids in North America is represented by "*Syntarsus*" *kayentakatae* (Rowe, 1989; Tykoski, 1998) but, additionally, a wide distribution of coelophysids in other areas of Pangea during the Early Jurassic is documented by the Asian *Panguraptor lufengensis* (You *et al.*, 2014) and the African *Coelophysis rhodesiensis* (Raath, 1969). This distribution of early non-Neotheropoda theropods and coelophysid neotheropods, characterized by American endemism in the Late Triassic and worldwide distribution during the Early Jurassic, may support the hypothesized Late Triassic regionalism followed by extreme faunal homogeneity at the beginning of the Jurassic for continental biotas (Shubin and Sues, 1991). Nevertheless, the still poor and scarce record of coelophysids, and their phylogenetic relationships, may indicate that its wide distribution during the Early Jurassic represents a bias in the Late Triassic record.

The presence of *Lucianovenator* in the late Norian–Rhaetian (Martínez *et al.*, 2015) of Argentina increases the poor and scarce record of Triassic South American neotheropods that until now only included four specimens: *Zupaysaurus*, a putative coelorusaur (Bonaparte, 1971), another new coelophysid (Ezcurra, 2017) from the middle Norian Los Colorados Formation and a putative neotheropod from the Norian *Riograndia* Assemblage Zone of Brazil (Pinheiro, 2016). Moreover, the relative abundance of specimens of *Lucianovenator* within the faunal assemblage of the Quebrada del Barro Formation (2%; Martínez *et al.*, 2015), together with its age, suggests that the near absence of theropod fossil records during the Rhaetian (Carrano and Sampson, 2004; Galton and Upchurch, 2004) is probably a taphonomic/stratigraphic bias instead of a decline in diversity and abundance after the Norian.

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