Early archosauromorph remains from the Permo-Triassic Buena Vista Formation of northeastern Uruguay

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The Permo-Triassic archosauromorph record is crucial to understand the impact of the Permo-Triassic mass extinction on the early evolution of the group and its subsequent dominance in Mesozoic terrestrial ecosystems. However, the Permo-Triassic archosauromorph record is still very poor in most continents and hampers the identification of global macroevolutionary patterns. Here we describe cranial and postcranial bones from the Permo-Triassic Buena Vista Formation of northeastern Uruguay that contribute to increase the meagre early archosauromorph record from South America. A basioccipital fused to both partial exoccipitals and three cervical vertebrae are assigned to Archosauromorpha based on apomorphies or a unique combination of characters. The archosauromorph remains of the Buena Vista Formation probably represent a multi-taxonomic assemblage composed of non-archosauriform archosauromorphs and a 'proterosuchid-grade' animal. This assemblage does not contribute in the discussion of a Late Permian or Early Triassic age for the Buena Vista Formation, but reinforces the broad palaeobiogeographic distribution of 'proterosuchid grade' diapsids in Permo-Triassic beds worldwide.

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Martín D. Ezcurra[1,*], Pablo Velozo[2], Melitta Meneghel[3] & Graciela Piñeiro[2]

[1]School of Geography, Earth and Environmental Sciences, University of Birmingham, Edgbaston, Birmingham B15 2TT, UK. martindezcurra@yahoo.com.ar

[2]Departamento de Evolución de Cuencas, Facultad de Ciencias. Iguá 4225. CP. 11400. Montevideo, Uruguay. fossil@fcien.edu.uy

[3]Laboratorio de Sistemática e Historia Natural de Vertebrados, Facultad de Ciencias. Iguá 4225, CP. 11400. Montevideo, Uruguay. melitta@fcien.edu.uy

*Corresponding author: Martín D. Ezcurra: School of Geography, Earth and Environmental Sciences, University of Birmingham, Edgbaston, Birmingham B15 2TT, UK. martindezcurra@yahoo.com.ar

Introduction

Archosauromorpha is one of the major groups of diapsid reptiles, which includes around 10,000 species of living birds and crocodilians (Clements, 2007) and all extinct species more closely related to these extant groups than to lepidosaurs (Dilkes, 1998). The oldest known archosauromorphs are represented by four nominal species restricted to Upper Permian rocks of Europe and Africa (~~e.g.~~ *Protorosaurus speneri*, *Archosaurus rossicus*, *Eorasaurus olsoni*, *Aenigmastropheus parringtoni*; Meyer, 1830; Tatarinov, 1960; Sennikov, 1988, 1997; Gower & Sennikov, 2000; Gottmann-Quesada & Sander, 2009; Ezcurra, Scheyer & Butler, 2014). In the aftermath of the Permo-Triassic mass extinction, the archosauromorph fossil record is considerably more abundant and morphologically diverse, including members of Rhynchosauria, Prolacertiformes, Proterosuchidae and Archosauria (Charig & Reig, 1970; Charig & Sues, 1976; Carroll, 1976; Dilkes, 1998; Gower & Sennikov, 2000; Butler et al., 2011; Nesbitt, 2011; Ezcurra, Butler & Gower, 2013). The Permo-Triassic (latest Permian-earliest Triassic) archosauromorph record is crucial to understand the impact of the Permo-Triassic mass extinction on the group and their subsequent dominance in Mesozoic terrestrial ecosystems. However, the Permo-Triassic archosauromorph record is currently null or very meagre in several continents (~~e.g.~~ South America, North America, Australia, Antarctica) (Camp & Banks, 1978; Thulborn, 1979, 1986; Colbert, 1987; Smith et al., 2011; Ezcurra, Butler & Gower, 2013; Ezcurra, Scheyer & Butler, 2014; Ezcurra, 2014). In particular, the South American Permo-Triassic archosauromorph record is remarkably scarce, being restricted to isolated postcranial bones from the Early Triassic Sanga do Cabral Formation of southern Brazil (Dias-da-Silva, 1998; Langer & Schultz, 1997; Langer & Lavina, 2000; Da-Rosa et al., 2009; Dias-da-Silva & Da-Rosa, 2011 – the archosauriform *Koilamasuchus gonzalezdiazi* from the Quebrada de los Fósiles Formation of central-western Argentina [Bonaparte, 1981; Ezcurra, Lecuona & Martinelli, 2010] was recently redated as Middle-Late Triassic [Ottone et al., 2014]). Here, we increase the South American early archosauromorph record with the description of cranial and postcranial bones from the Permo-Triassic Buena Vista Formation of northeastern Uruguay.

Geological and palaeontological setting

The Buena Vista Formation crops out in northeastern Uruguay and consists of red-brownish sandstones, intercalated with thin layers of red-brownish mudstones and intraformational conglomerates deposited under continental fluvial conditions (Bossi & Navarro, 1991; Goso et al., 2001; Piñeiro & Ubilla, 2003). Most of the fossils collected from the Buena Vista Formation are found in the intraformational conglomerates and correspond to isolated bones to ocassionally articulated partial skeletons. The tetrapod fossil content of the Buena Vista Formation represents the Colonia Orozco Local Fauna and includes laidleriid (*Uruyiella liminea*), mastodonsaurid, rhinesuchid-like and dvinosaurian temnospondyls (Marsicano, Perea & Ubilla, 2000; Piñeiro, 2004; Piñeiro Marsicano & Lorenzo, 2007; Piñeiro, Marsicano & Damiani, 2007; Piñeiro et al., 2007; Piñeiro, Ramos & Marsicano, 2012), procolophonoid parareptiles (~~i.e.~~ *Pintosaurus magnidentis*; Piñeiro, 2004; Piñeiro, Rojas & Ubilla, 2004), probable varanopid and sphenacodontid synapsids (Piñeiro et al., 2003, 2013), and basal archosauromorphs (present study). The age of the Buena Vista Formation is poorly constrained because of the absence of index taxa and the presence of taxa that are documented in either Late Permian or earliest Triassic assemblages. Therefore, the age of this formation has been substantially debated. The Buena Vista Formation has been considered a lateral equivalent of the Sanga do Cabral Formation of southern Brazil based on lithostratigraphic similarities (Andreis, Bossi & Montardo, 1980; Bossi & Navarro, 1991). The Brazilian unit is considered late Induan−early Olenekian in age because of the presence of the index taxon *Procolophon* (Dias-da-Silva, Modesto & Schultz, 2006) and, as a result, the same age has been assigned to the Buena Vista Formation (Bossi & Navarro, 1991). However, subsequent authors have suggested an older age for the Buena Vista Formation, being closer to the Permo-Triassic boundary or even within the Late Permian based on its tetrapod fossil content (Piñeiro & Ubilla, 2003; Piñeiro et al., 2003; Piñeiro, 2004; Piñeiro, Rojas & Ubilla, 2004; Piñeiro Marsicano & Lorenzo, 2007; Piñeiro, Marsicano & Damiani, 2007; Piñeiro et al., 2007; Piñeiro, Ramos & Marsicano, 2012). In particular, the description of varanopid synapsids would favour a Permian age (Piñeiro et al., 2003), but recent authors have casted doubts on these assignments and concluded that there is no compelling evidence to support a Permian age over an Early Triassic one (Dias-da-Silva, Modesto & Schultz, 2006). Here, we will consider the Buena Vista Formation as Permo-Triassic in age, taking into account recent studies that placed the Colonia Orozco Local Fauna as a transitional assemblage that could contain the Permo-Triassic boundary (see Piñeiro, Ramos & Marsicano, 2012).

Institutional abbreviations. **BP**, Evolutionary Studies Institute (formerly Bernard Price Institute for Palaeontological Research), University of the Witwatersrand, Johannesburg, South Africa; **BSPG**, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; **CPEZ**, Coleção Municipal, São Pedro do Sul; Brazil; **FC-DPV**, Vertebrados Fósiles, Facultad de Ciencias, Montevideo, Uruguay; **GHG**, Geological Survey, Pretoria, South Africa; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; **MCZ**, Museum of Comparative Zoology, Cambridge, USA; **NHMUK**, The Natural History Museum, London, UK; **NM**, National Museum, Bloemfontein, South Africa; **PIMUZ**, Paläontologisches Institut und Museum der Universität Zürich, Zurich, Switzerland; **PIN**, Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia; **PULR**, Paleontología, Universidad Nacional de La Rioja, La Rioja, Argentina; **SAM-PK**, Iziko South African Museum, Cape Town, South Africa; **SMNS**, Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany; **TM**, Ditsong

National Museum of Natural History (formerly Transvaal Museum), Pretoria, South Africa; **UA**, University of Antananarivo, Antananarivo, Madagascar; **UMZC**, University Museum of Zoology, Cambridge, UK; **USNM**, National Museum of Natural History (formerly United States National Museum), Smithsonian Institution, Washington, D.C., USA; **WM~~s~~N**, Westfälisches Museum für Naturkunde, Münster, Germany; **ZAR**, Muséum national d'Histoire naturelle (Zarzaitine collection), Paris, France.

SYSTEMATIC PALAEONTOLOGY

DIAPSIDA Osborn, 1903 sensu Laurin, 1991

SAURIA Gauthier, 1984 sensu Gauthier, Kluge & Rowe, 1988

ARCHOSAUROMORPHA Huene, 1946 sensu Dilkes, 1998

Gen. et sp. indet.

Figures 1, 2D−F, 3A, B, 4, 5

Materials. FC-DPV 2641: ~~co-~~ossified basioccipital and exoccipitals (Figs. 1, 2D−F, 3A, B); FC-DPV 2640: anterior cervical vertebra (Fig. 4A−B); FC-DPV 2637: middle cervical vertebra (Fig. 5); FC-DPV 2639: middle or posterior cervical vertebra (Fig. 4C−G).

Horizon and Locality. Locality close to Colonia Orozco town, intraformational conglomerates of the Buena Vista Formation (Colonia Orozco Local Fauna, Permo-Triassic age, see geological and palaeontological setting), Cerro Largo County, northeastern Uruguay.

Description

Braincase. FC-DPV 2641 (Fig. 1; Table 1) is represented by an almost complete, slightly weathered basioccipital fused to the distal end of both exoccipitals. The presence of exoccipitals

(Fig. 1: exo) is mainly inferred because the ventrolateral borders of the foramen magnum (which are preserved in FC-DPV 2641) are formed by these bones in other amniotans, such as basal synapsids (e.g. Romer & Price, 1940), parareptiles (e.g. *Leptopleuron lacertinum*: Spencer, 2000; *Hypsognathus fenneri*: Sues et al., 2000) and archosauromorphs (e.g. *Azendohsaurus madagaskarensis*: UA 7-20-99-653; '*Chasmatosaurus*' *yuani*: IVPP V2719; *Doswellia kaltenbachi*: USNM 214823; *Chanaresuchus bonapartei*: MCZ 4037). In addition, there is a weak trace of suture between the basioccipital and the right exoccipital. The fusion between the exoccipitals and basioccipital occurs through ontogeny in several groups of amniotans, including basal diapsids (e.g. *Youngina capensis*: TM 3603, Evans, 1987; *Gephyrosaurus bridensis*: Evans, 1980; *Mesosuchus browni*: SAM-PK-6536, Dilkes, 1998) and basal synapsids (e.g. *Secodontosaurus obtusidens*: Romer & Price, 1940; Reisz, Berman & Scott, 1992) (Fig. 2). The presence of this condition in FC-DPV 2641 and the well ossified occipital condyle probably indicate that this specimen did not belong to, at least, an early juvenile.

The occipital condyle of FC-DPV 2641 is poorly posteriorly projected as a result of a reduced occipital neck (Fig. 1: oc), resembling the condition in several basal diapsids (e.g. *Araeoscelis gracilis*: Vaughn, 1955; *Gephyrosaurus bridensis*: Evans, 1980; *Mesosuchus broomi*: SAM-PK-6536; *Proterosuchus alexanderi*: NMQR 1484; *Prolacerta broomi*: BP/1/2675; *Archeopelta arborensis*: CPEZ-239a, Desojo, Ezcurra & Schultz, 2011), parareptiles (e.g. *Hypsognathus fenneri*: Sues et al., 2000) and sphenacodont pelycosaurs (Romer & Price, 1940; Reisz, Berman & Scott, 1992). The occipital condyle is semispherical in overall shape, as occurs in archosauromorphs. Part of the posterior surface of the occipital condyle is flat, resembling the condition in the archosauromorphs *Mesosuchus broomi* (SAM-PK-6536) and *Prolacerta broomi* (BP/1/2675), and some basal synapsids (e.g. *Secodontosaurus obtusidens*: Reisz, Berman & Scott, 1992) (Fig. 2). The occipital condyle possesses a shallow, sub-circular notochordal pit immediately below the ventral border of the foramen magnum (Figs. 1E: np, 3A, B). The shape and position of this pit closely resembles that of *Youngina capensis* (Gardner et al., 2010), *Proterosuchus alexanderi* (NMQR 1484), '*Chasmatosaurus*' *yuani* (IVPP V2719) and some basal synapsids (e.g. *Dimetrodon*: Romer & Price, 1940; *Secodontosaurus obtusidens*: Reisz, Berman & Scott, 1992) (Figs. 2, 3: np). The articular surface of the occipital condyle is delimited laterally by an anteroposteriorly concave recessed surface that forms a slightly constricted occipital neck in ventral view (Fig. 1C, D: rs). This recessed surface is delimited anteriorly by a posteroventrally facing surface that belongs to the lateral flange of the basioccipital body (Figs. 1−3: lf). These lateral flange is well developed, resembling the condition in *Prolacerta broomi* (BP/1/2675), *Proterosuchus* spp. (BSPG 1934 VII 514; NMQR 880, 1484) and '*Chasmatosaurus*' *yuani* (IVPP V2719), and may have overlapped at least partially the ventral ramus of the opisthotic in posterior view (Fig. 3E: lf). The occipital condyle is only differentiated from the ventral surface of the main body of the basioccipital by a gentle, transverse change in slope at the median line, resembling the condition in several amniotans (e.g. *Youngina capensis*: Gardner et al., 2010; *Prolacerta broomi*: BP/1/2675; *Proterosuchus alexanderi*: NMQR 1484; *Secodontosaurus obtusidens*: Reisz, Berman & Scott, 1992).

The ventral surface of the basioccipital, immediately anterior to the occipital condyle, is slightly anteroposteriorly concave and lacks the median tuberosity present in *Garjainia prima* (Gower & Sennikov, 1996). The basioccipital region of the basal tubera is almost completely preserved, but their ventral surfaces are weathered off (Figs. 1−3: bt). These structures are well developed and ventrally directed, resembling the condition in some basal archosauromorphs (e.g. *Proterosuchus* spp.: BSPG 1934 VII 514; NMQR 880, 1484; *Fugusuchus hejiapanensis*: Gower & Sennikov, 1996) and some basal synapsids (e.g. *Dimetrodon*: Romer & Price, 1940; *Haptodus garnettensis*: Laurin, 1993). By contrast, the main axis of the basioccipital portion of the basal tubera is usually lateroventrally directed in most archosauromorphs, such as *Mesosuchus broomi* (SAM-PK-6536), *Azendohsaurus madagaskarensis* (UA 7-20-99-653), *Prolacerta broomi*

(BP/1/2675), *Sarmatosuchus otschevi* (PIN 2865/68), ‘*Chasmatosaurus*’ *yuani* (IVPP V2719), *Erythrosuchus africanus* (NHMUK R3592), *Euparkeria capensis* (SAM-PK-5867), *Archeopelta arborensis* (CPEZ-239a) and *Chanaresuchus bonapartei* (PULR 07, MCZ 4037). The basal tubera are completely separated from each other at their bases, as also occurs in several diapsids (e.g. *Youngina capensis*: Gardner et al., 2010; *Gephyrosaurus bridensis*: Evans, 1980; *Mesosuchus broomi*: SAM-PK-6536; *Prolacerta broomi*: BP/1/2675; *Proterosuchus* spp.: BSPG 1934 VII 514; NMQR 880, 1484; *Euparkeria capensis*: SAM-PK-5867; *Chanaresuchus bonapartei*: PULR 07, MCZ 4037). By contrast, in some other archosauromorphs the basal tubera are connected with each other by a transverse osseous lamina (e.g. *Azendohsaurus madagaskarensis*: UA 7-20-99-653; *Trilophosaurus buettneri*: Spielmann et al., 2008; ‘*Chasmatosaurus*’ *yuani*: IVPP V2719; *Fugusuchus hejiapanensis*: Gower & Sennikov, 1996; *Erythrosuchus africanus*: NHMUK R3592). In ventral view, the basal tubera are parallel to each other and to the sagittal plane of the basioccipital. The ventral surface of the basioccipital, between both basal tubera, is transversely concave and lacks the subcircular foramen present in ‘*Chasmatosaurus*’ *yuani* (IVPP V2719) and some specimens of *Proterosuchus* (NMQR 880).

The lateral surface of the basioccipital is subdivided into dorsolaterally and lateroventrally facing surfaces. Both surfaces meet each other in an obtuse angle in posterior view at the apex of the lateral flange of the bone. The dorsolaterally facing surface is flat and probably participated of the medial wall of the metotic foramen (Fig. 1C, E: wmf). The ventrolaterally facing surface is damaged on the left side of the bone (Fig. 2E: ds), but well preserved on the right side. The ventrolaterally facing surface possesses a complex topology and is subdivided by a diagonal, posteroventrally-to-anterodorsally oriented ridge (Fig. 1: dr). The facet for reception of the ventral ramus of the opisthotic is situated posterodorsally to this ridge (Fig. 1C: fvro). This facet is posterodorsally-to-anteroventrally slightly concave and occupies a large portion of the lateral surface of the basioccipital. The size and shape of this facet suggest the presence of a robust ventral ramus of the opisthotic, probably resembling the condition in basal archosauriforms (e.g. *Proterosuchus* spp.: BSPG 1934 VII 514; NMQR 880, 1484; ‘*Chasmatosaurus*’ *yuani*: IVPP V2719; *Garjainia prima*: PIN 951/60). The surface anteroventral to the diagonal ridge is more deeply anteroposteriorly concave than the facet for the ventral ramus of the opisthotic and is delimited anteriorly by the facet for the parabasisphenoid (Fig. 1: fpbs). The presence of smooth cortical bone on this deeply concave surface indicates that probably it was a non-articulating surface and may have been part of the medial wall of the passage of the pseudolagenar recess (Fig. 1: mwpr). The pseudolagenar recess is present in *Prolacerta broomi*, *Euparkeria capensis*, several proterosuchian-grade archosauriforms and the poposauroid *Xilousuchus sapingensis* (Gower & Sennikov, 1996).

The anterior surface of the basioccipital possesses a slightly transversely convex facet for articulation with the parabasisphenoid (Fig. 1: fpbs). This articular facet extends also onto the anterodorsal surface of the basioccipital, immediately lateral to the floor of the endocranial cavity. The floor of the endocranial cavity is flat and possesses an anteroposteriorly long median longitudinal ridge, which is restricted to the anterior half of the basioccipital (Fig. 1B, E: mlr), resembling the condition in some procolophonids (e.g. *Leptopleuron lacertinum*: Spencer, 2000), synapsids (e.g. *Haptodus garnettensis*: Laurin, 1993) and diapsids (e.g. *Youngina capensis*: Gardner et al., 2010; *Gephyrosaurus bridensis*: Evans, 1980). The floor of the endocranial cavity of *Prolacerta broomi* possesses a pair of longitudinal ridges that delimit a shallow, median groove along most of the dorsal surface of the basioccipital (BP/1/2675).

The trace of suture between the right exoccipital and basioccipital indicates that the exoccipitals did not contact each other, at least, extensively on the floor of the endocranial cavity (Fig. 3A, B). The foramen/foramina for the exit of the hypoglossal and glossopharyngeal cranial nerves (CN XI−XII) are not preserved.

Anterior cervical vertebra. FC-DPV 2640 (Fig. 4 A-B; Table 2) is interpreted as an anterior postaxial cervical vertebra because of its strong anteroposterior elongation and a facet for articulation with the rib (only the base of the left structure is preserved) placed next to the anterior margin of the neural arch. The anterior end of the centrum is damaged. The posterior surface of the centrum is concave and seems to be slightly bevelled, possibly to receive a small intercentrum. The vertebra is possibly not notochordal. The centrum is approximately 3.6 times longer than tall, a ratio that closely resembles the condition in the third and fourth cervical vertebrae of moderately long-necked basal archosauromorphs, such as *Protorosaurus speneri* (BSPG 1995 I 5, cast of WMSN P47361), *Prolacerta broomi* (BP/1/2675) and *Macrocnemus bassanii* (PIMUZ T2472, T4355, T4822). By contrast, the anterior cervical vertebrae of other basal archosauromorphs are proportionally shorter (e.g. *Boreopricea*, PIN 3708/1: 1.92-2.00; *Jesairosaurus lehmani*, ZAR 07: <2.00; *Mesosuchus*, SAM-PK-5882, fourth cervical: 2.01; *Trilophosaurus buettneri*, Spielmann et al. [2008: appendix 10]: 1.84-2.50). The ventral surface of the centrum possesses a low and conspicuous median longitudinal keel. This keel extends along the entire preserved ventral surface of the centrum and becomes lower anteriorly. The centrum is slightly transversely compressed at mid-length and lacks a lateral fossa. The lateral surface of the centrum possesses a thin, longitudinal ridge that extends posteriorly from the base of the diapophysis to its posterior rim (Fig. 4A, B: arrow). A similar ridge is present in *Macrocnemus bassanii* (PIMUZ T4822), *Tanystropheus longobardicus* (PIMUZ T2818) and *Eorasaurus olsoni* (PIN 156/108, 109). A slightly developed longitudinal ridge is also present below the level of the diapophysis in some other basal diapsids (e.g. *Protorosaurus speneri*: Gottmann-Quesada & Sander, 2009). By contrast, the lateral surface of the centrum lacks a ridge in *Petrolacosaurus kansensis* (Reisz, 1981), *Gephyrosaurus bridensis* (Evans, 1981), *Trilophosaurus buettneri* (Spielmann et al., 2008), *Prolacerta broomi* (BP/1/2675) and *Proterosuchus alexanderi* (NMQR 1484). Only the base of the left facet for articulation with the rib is preserved and is restricted to the anterior portion of the neural arch. The neurocentral suture is completely closed, indicating that the animal was not a juvenile at the moment of its death (Brochu, 1996; Irmis, 2007).

The zygapophyses lack their distal ends, but their preserved portions indicate that they were anteroposteriorly long, laterally divergent and sub~~-~~horizontal. As a result, the distal tips of the zygapophyses are well separated from the median line, resembling the condition in the anterior and middle cervicals of other basal archosauromorphs (e.g *Trilophosaurus buettneri*: Spielmann et al., 2008). The neural arch possesses a very shallow depression lateral to the base of the neural spine (Fig. 4A, B: d), as occurs in *Prolacerta broomi* (BP/1/2675) and several other basal archosauromorphs. By contrast, the middle and posterior cervical vertebrae of at least some specimens of *Proterosuchus alexanderi* possess a better defined and deeper, sub~~-~~circular fossa lateral to the base of the neural spine (NMQR 1484). The neural spine is mostly complete, but its dorsal margin is damaged where it becomes very thin transversely (Fig. 4A, B: ns). As a result, it is interpreted that the neural spine should not have been much taller and preserves it general shape. The neural spine is dorsoventrally short and strongly elongated anteroposteriorly, as occurs in *Protorosaurus speneri* (BSPG 1995 I 5, cast of WMSN P47361), *Prolacerta broomi* (BP/1/2675), *Amotosaurus rotfeldens* SMNS 50830) and *Macrocnemus bassanii* (PIMUZ T2472, T4355, T4822), but contrasting with the taller and anteroposteriorly shorter neural spine of *Proterosuchus alexanderi* (NMQR 1484).

Middle cervical vertebra. The degree of anteroposterior elongation and the presence of a parallelogram-shaped centrum indicate that FC-DPV 2637 (Fig. 5; Table 2) belongs to a middle cervical vertebra after comparisons with other basal archosauromorphs (e.g. *Prolacerta broomi*: BP/1/2675; *Proterosuchus alexanderi*: NMQR 1484; *Trilophosaurus buettneri*: Spielmann et al., 2008). The vertebra is moderately elongated anteroposteriorly, in which the length of the centrum is 2.68 times the height of its anterior articular surface. This ratio is slightly lower than that present in the middle cervical vertebrae of moderately long-necked basal archosauromorphs (>3.0, e.g. *Prolacerta broomi*: BP/1/2675; *Macrocnemus be[illegible]nii*: PIMUZ T4822; *Protorosaurus speneri*: BSPG 1995 I 5; *Eorasaurus olsoni*: PIN 156/108, 109). By contrast, the middle cervical vertebrae of *Trilophosaurus buettneri* (Spielmann et al., 2008), rhynchosaurs (e.g. *Mesosuchus browni*: SAM-PK-5882) and several basal archosauriforms (e.g. *Proterosuchus alexanderi*: NMQR 1484, *Erythrosuchus africanus*: NHMUK R3592; *Euparkeria capensis*: SAM-PK-586) are considerably proportionally anteroposteriorly shorter than FC-DPV 2637. The anterior articular facet of the centrum is more dorsally situated than the posterior one, resulting in a parallelogram-shaped centrum in lateral view (Fig. 5E−H), as occurs in basal archosauromorphs (Ezcurra, Scheyer & Butler, 2014). The centrum is amphicoelous and apparently not notochordal (i.e. lacks a continuous canal piercing the centrum), contrasting with the condition present in basal synapsids, parareptiles, early diapsids, basal lepidosauromorphs and the basal archosauromorph *Aenigmastropheus parri[illegible]ni* (Ezcurra, Scheyer & Butler, 2014). The anterior articular facet is subcircular (Fig. 5: afc) and possesses a notochordal pit (Fig. 5: np). The posterior facet is damaged and its overall contour cannot be determined (Fig. 5: pfc), but the preserved portion is congruent in morphology with that of the anterior facet. The ventral surface of the centrum is strongly transversely convex along its entire extension and possesses a subtle median longitudinal edge (Fig. 5K, L). The centrum is incipiently transversely compressed at mid-length. The lateral surface of the centrum is continuously dorsoventrally convex and lacks a lateral fossa. The vertebra possesses a single, anteroposteriorly elongated facet for articulation with the rib (Fig. 5: fr), as occurs in non-archosauromorph diapsids and tanystropheids (e.g. *Tanystropheus longobardicu*[illegible]ild, 1973). This facet is restricted to the anterior half of the vertebra and situated approximately at level with the centrum-neural arch boundary. The neurocentral suture is completely closed.

In the neural arch, a posterior centrodiapophyseal lamina delimits a central infradiapophyseal fossa below the base of the transverse process (Fig. 5: pcdl). In addition, a tuberosity runs from the base of the transverse process towards the base of the postzygapophysis, but it does not reach the latter structure. This tuberosity and the posterior centrodiapophyseal lamina delimit a shallow subtriangular depression that is topologically equivalent to a postzygapophyseal centrodiapophyseal fossa. There are no anterior centrodiapophyseal and prezygodiapophyseal laminae in the neural arch, which may be a result of the relatively anterior position of the vertebra in the cervical series. The zygapophyses are horizontal and anteroposteriorly short, but extend slightly beyond the margins of the anterior and posterior articular facets of the centrum, respectively. The prezygapophyses are anterolaterally directed and, as a result, their distal tips are well separated from the median line (Fig. 5: prz), as occurs in the cervico-dorsal vertebrae of *Macrocnemus bessanii* (PIMUZ T482), *Tanystropheus longobardicus* (Wild, 1973) and *Trilophosaurus buettneri* (Spielmann et al., 2008). The articular surfaces of the zygapophyses are damaged and it is not possible to determine their morphology. A shallow and poorly defined, circular depression is present laterally to the base of the neural spine (Fig. 5: d), as occurs in at least some specimens of *Proterosuchus alexanderi* (NMQR 1484). The neural spine is moderately low and strongly anteroposteriorly elongated, being considerably anteroposteriorly longer than tall (Fig. 5: ns), closely resembling the condition in *Protorosaurus speneri* (BSPG 1995 I 5), *Macrocnemus bessanii* (PIMUZ T4822) and *Prolacerta broomi* (BP/1/2675). By contrast, in *Mesosuchus browni* (SAM-PK-5882), *Trilophosaurus buettneri* (Spielmann et al., 2008), *Proterosuchus fergusi* (BSPG 1934-VIII-514; GHG 231), *Sarmatosuchus otschevi* (PIN 2865/13-19), *Erythrosuchus africanus* (NHMUK R3592), *Garjainia prima* (PIN 2394/5-13, 5-16) and *Euparkeria capensis* (SAM-PK-586) the neural spines are taller than long. The neural spine possesses an anterior overhang that extends anteriorly beyond the base of the spine (Fig. 5: ao), as occurs in *Protorosaurus speneri* (BSPG

1995 I 5), *Macrocnemus bessanii* (PIMUZ T4822), *Trilophosaurus buettneri* (Spielmann et al., 2008) and *Prolacerta broomi* (BP/1/2675). The distal margin of the neural spine possesses a low transverse thickening (Fig. 5: dt), but it does not form a spine table or a mammillary process. The same thickening on the distal margin of the neural spine is present in several other long-necked archosauromorphs (e.g. *Macrocnemus bessanii*: PIMUZ T4822; *Prolacerta broomi*: BP/1/2675). The pre- and postspinal fossae are deep and transversely wide (Fig. 5: posf, prsf). The prespinal fossa is restricted to the base of the neural spine and the postspinal fossa extends onto most of the posterior surface of the spine, as usually occurs in other basal archsoauromorphs (e.g. *Prolacerta broomi*: BP/1/2675).

Middle−posterior cervical vertebra. FC-DPV 2639 (Fig. 4C−G; Table 2) belongs to a middle or posterior cervical vertebra because the parapophyses are situated slightly above the mid-height of the centrum, adjacent to its anterior margin (Fig. 4D: pa), and the neural spine is anteroposteriorly short (Fig. 4D, E: ns). This vertebra is well-preserved, but moderately squeezed posteroventrally to the right side (Fig. 4G), the posterior articular facet of the centrum is damaged and most of the prezygapophyses, right diapophysis and neural spine are missing. The centrum is amphicoelous and apparently not notochordal. The centrum length represents 1.7 times the height of its anterior articular facet, being proportionally shorter than FC-DPV 2637 and resembling the ratio present in the middle-posterior cervical vertebrae of several basal archosauromorphs (e.g. *Aenigmastropheus parringtoni*: UMZC T836; *Eorasaurus olsoni*: PIN 156/109; *Trilophosaurus buettneri*: Spielmann et al., 2008; *Proterosuchus alexanderi*: NMQR 1484). The ventral surface of the centrum is transversely convex and lacks a median ventral keel. The centrum is slightly transversely compressed at mid-length. The anterior articular facet of the centrum is transversely broader than tall. The contour of the posterior facet cannot be determined because of damaging (Fig. 4G: pfc). The parapophyses are situated on laterally projected peduncles (Fig. 4C, D, F, G:

pa). The peduncle of the parapophysis possesses a moderately deep depression on its ventral surface. The facet of the parapophysis is semi-circular, with a mostly straight anterior margin, and mainly laterally facing, with a low anteroventral component. A su~~b-h~~orizontal ridge extends posteriorly from the base of the parapophysis to the lateral surface of the centrum, but it does not reach the level of mid-length of the centrum (Fig. 4C, D: arrow). A similar ridge is also present in FC-DPV 2640 (Fig. 4A, B) and other basal archosauromorphs, such as *Macrocnemus bassanii* (PIMUZ T4822), *Tanystropheus longobardicus* (PIMUZ T2818), *Eorasaurus olsoni* (PIN 156/108, 109) and *Garjainia prima* (PIN 2394/5-11, 5-13). The lateral surface of the centrum lacks a lateral fossa and the neurocentral suture is completely closed.

The diapophysis is mostly restricted to the anterior half of the neural arch (Fig. 4E: dp) and situated well above the centrum-neural arch boundary (Fig. 4C, D: dp). The diapophysis is moderately long and laterally developed, resembling the condition in other basal archosauromorphs (e.g. *Prolacerta broomi*: BP/1/2676). By contrast, in *Eorasaurus olsoni* and basal archosauriforms (e.g. *Proterosuchus alexanderi*: NMQR 1484) the diapophyses are better laterally developed than in FC-DPV 2639 (Ezcurra, Scheyer & Butler, 2014). The articular facet of the diapophysis is anteroposteriorly long, being considerably longer than tall. The neural arch possesses paradiapophyseal (Fig. 4C, D: pdl), posterior centrodiapophyseal (Fig. 4C, D: pcdl), prezygodiapophyseal (Fig. 4C−E: prdl) and postzygodiapophyseal laminae (Fig. 4C, D, G: podl), as also occurs in the posterior cervical and anterior dorsal vertebrae of some basal archosauromorphs (e.g. *Protorosaurus speneri*: BSPG 1995 I 5; *Tanystropheus longobardicus*: PIMUZ T2817; *Spinosuchus caseanus*: Spielmann et al., 2009) and several crown-archosaurs (Butler, Barrett & Gower, 2012). By contrast, *Prolacerta broomi* possesses only anterior centrodiapophyseal/paradiapophyseal and prezygodiapophyseal laminae (BP/1/2675), and *Proterosuchus* spp. possesses anterior centrodiapophyseal/paradiapophyseal (NMQR 1484) and, in some specimens, postzygodiapophyseal laminae (SAM-PK-11208). The four laminae of FC-

DPV 2639 delimit prezygapophyseal centrodiapophyseal, postzygapophyseal centrodiapophyseal, and centrodiapophyseal fossae. The zygapophyses are sub-horizontal and diverge slightly from the median line, resembling the condition in FC-DPV 2637 and FC-DPV 2640. The postzygapophysis (Fig. 4C−E, G: poz) lacks epipophysis and its articular facet faces lateroventrally. There is a shallow fossa immediately lateral to the base of the neural spine (Fig. 4E: d), as occurs in FC-DPV 2637, *Protorosaurus speneri* and *Proterosuchus alexanderi* (NMQR 1484). The base of the neural spine is posteriorly displaced from the point of mid-length between the zygapophyses and subtriangular in cross-section, with an anteriorly oriented apex (Fig. 4C−E: ns). The postspinal fossa is transversely broad and deep, and extends dorsally onto the entire preserved posterior surface of the neural spine (Fig. 4G: posf).

Taxonomic affinities

The partial braincase FC-DPV 2641 differs from those of parareptiles (e.g. *Procolophon trigoniceps*: Watson, 1914; *Leptopleuron lacertinum*: Spencer, 2000; *Owenetta kitchingorum*: Reisz & Scott, 2002; *Hypsognathus fenneri*: Sues et al., 2000) in the combination of a proportionally anteroposteriorly long basioccipital body (anteroposterior length of the body [excluding occipital condyle and anterior projection between posterolateral processes of the basisphenoid] versus maximum transverse width = 0.64; whereas the same ratio is 0.29 in *Leptopleuron lacertinum* [Spencer, 2000], 0.40 in *Owenetta kitchingorum* [Reisz & Scott, 2002], and 0.23 in *Hypsognathus fenneri* [Sues et al., 2000]), transversely narrow exoccipitals, vertical basal tubera and a semi-spherical occipital condyle. In addition, FC-DPV 2641 differs from basal synapsids in the presence of anteroposteriorly long basal tubera, being considerably longer than broad, and a sub-spherical occipital condyle (Fig. 2). By contrast, the occipital condyle of most pelycosaurs possesses an extensive planar posterior surface, resulting in a sub-quadrangular structure in ventral or lateral view (Fig. 2B; but a sub-spherical occipital condyle is also present in *Varanops brevirostris*: Campione & Reisz, 2010), the basioccipital component of the basal tubera are strongly restricted posteriorly, being approximately as long as broad (Fig. 2C), and lacks an embayment to receive the massive footplate of the stape (e.g. *Dimetrodon limbatus*: Romer & Price, 1940; *Edaphosaurus pogonias*: Romer & Price, 1940; *Ophiacodon uniformis*: Romer & Price, 1940; *Aerosaurus wellesi*: Langston & Reisz, 1981; *Secodontosaurus obtusidens*: Reisz, Berman & Scott, 1992; *Haptodus garnettensis*: Laurin, 1993; *Varanops brevirostris*: Campione & Reisz, 2010). Furthermore, the Uruguayan partial braincase differs from Permo-Triassic cynodont synapsids (e.g. *Platycraniellus elegans*: Abdala, 2007) in the presence of a single occipital condyle. Within Diapsida, FC-DPV 2641 differs from non-archosauromorph taxa (e.g. *Araeoscelis gracilis*: Vaughn, 1955; *Gephyrosaurus bridensis*: Evans, 1980; *Planocephalosaurus robinsonae*: Fraser, 1982; *Youngina capensis*: Evans, 1987; Gardner et al., 2010) in the presence of a semi-spherical occipital condyle and vertical basal tubera.

The presence of a semi-spherical occipital condyle, considerably anteroposteriorly longer than broad and vertical basal tubera, and possibly a robust ventral ramus of the opisthotic is a combination of characters present only in Archosauromorpha, and allow the assignment of FC-DPV 2641 to this clade. No archosauromorph cranial remains have been described from other Permo-Triassic beds of South America (Dias-da-Silva, 1998; Da-Rosa et al., 2009; Dias-da-Silva & Da-Rosa, 2011), hampering comparisons with FC-DPV 2641. Similarly, we could not make comparisons with Late Permian archosauromorphs, such as *Archosaurus rossicus* and *Protorosaurus speneri*, because the knowledge of the braincase anatomy in these taxa is null or very limited (Sennikov, 1988; Gottmann-Quesada & Sander, 2009; Ezcurra, Scheyer & Butler, 2014). Indeed, in only one specimen assigned to *Protorosaurus speneri* the occipital region is exposed but it is badly preserved and does not allow making proper comparisons (Fig. 3C). In particular, among archosauromorphs, FC-DPV 2641 shares with the South African species of *Proterosuchus* (~~i.e.~~ *Proterosuchus fergusi*: BSPG 1934 VIII 514; *Proterosuchus alexanderi*:

NMQR 1484; *Proterosuchus goweri*: NMQR 880) and *Fugusuchus hejiapanensis* (Gower & Sennikov, 1996) the presence of vertical basal tubera (Fig. 3A, B, D, E). By contrast, in other basal archosauromorphs the basal tubera are lateroventrally oriented, being divergent from each other in posterior view (e.g. *Azendohsaurus madagaskarensis*: UA-7-20-99-653; *Trilophosaurus buettneri*: Spielmann et al., 2008; *Mesosuchus browni*: SAM-PK-6536; *Howesia browni*: SAM-PK-5885; *Prolacerta broomi*: BP/1/2675; '*Chasmatosaurus*' *yuani*: IVPP V2719; *Sarmatosuchus otschevi*: PIN 2865/68; *Garjainia prima*: PIN 951/60; *Erythrosuchus africanus*: NHMUK R3592). In addition, FC-DPV 2641 and the South African species of *Proterosuchus* differ from *Fugusuchus hejiapanensis* in the presence of basal tubera not connected to each other at their base. FC-DPV 2641 seems to differ from *Proterosuchus* (e.g. *Proterosuchus alexanderi*: NMQR 1484) in the presence of a broader contribution of the basioccipital to the floor of the endocranial cavity (Fig. 3). However, this possible difference should be taken with caution because of the strong degree of fusion between the exoccipitals and basioccipital in the Uruguayan specimen. In conclusion, the combination of features present in FC-DPV 2641 are consistent with those present in *Proterosuchus* and the presence of the vertical basal tubera is probably an apomorphy of a grade of basal archosauriforms, because *Fugusuchus hejiapanensis* has been recovered as a more crownward archosauriform than proterosuchids in a recent phylogenetic analysis (Ezcurra, Lecuona & Martinelli, 2010). Therefore, FC-DPV 2641 is interpreted as an indeterminate archosauromorph, possibly archosauriform (depending on the phylogenetic relationships of basal members of the clade that are currently in state of flux; Ezcurra, Butler & Gower, 2013), *cf.* Proterosuchidae.

The anterior cervical vertebra FC-DPV 2640 and middle cervical vertebra FC-DPV 2637 are assigned to an archosauromorph diapsid because of the following combination of characters: probable non-notochordal and anteroposteriorly elongated centra, a sub-horizontal ridge on the lateral surface of the centra, a shallow fossa immediately lateral to the base of the neural spines, and neural spines considerably anteroposteriorly longer than tall (Fig. 4). In addition, the centrum of FC-DPV 2637 is parallelogram-shaped in lateral view, a character that was found as a synapomorphy of Archosauromorpha (Ezcurra, Scheyer & Butler, 2014), and has an anterior overhang and a transversely thickened distal margin on the neural spine, features that occur together in the basal archosauromorphs *Macrocnemus bessanii* (PIMUZ T4822) and *Prolacerta broomi* (BP/1/2675). These anterior and middle cervical vertebrae differ from those of "pelycosaur" synapsids and araeoscelidian diapsids in the presence of a probable non-notochordal centrum and a lower and longer neural spine (Ezcurra, Scheyer & Butler, 2014). Among long-necked basal archosauromorphs, FC-DPV 2637 and FC-DPV 2640 differ from *Prolacerta broomi* and *Trilophosaurus buettneri* in the presence of a low longitudinal lateral crest that runs posteriorly from the base of the facet for articulation with the rib, from *Macrocnemus bessanii* in the absence of epipophyses (PIMUZ T4822), and from other tanystropheids in the presence of a proportionally anteroposteriorly shorter centrum (e.g. *Amotosaurus rotfeldensis*: SMNS 50830). Although the neural spines possess damaged distal margins, they seem to have been dorsoventrally short. As a result, they differ from *Protorosaurus speneri* (BSPG 1995 I 5), which possesses tall neural spines. The combination of characters observed in FC-DPV 2640 is consistent with that present in basal archosauromorphs, such as *Prolacerta broomi* (BP/1/2675), but FC-DPV 2637 differs from this species in the presence of proportionally anteroposteriorly shorter centrum, and a less developed anterior overhang on the neural spine. FC-DPV 2637 and FC-DPV 2640 differ from the protorosaur cervical vertebra described by Dias-da-Silva (1998) from the Sanga do Cabral Formation in being considerably anteroposteriorly shorter. However, these differences could be due to the position of the vertebrae in the cervical series and the possibility that they belong to closely related species cannot be ruled out. Finally, the probable presence of a single facet for articulation with the cervical rib in FC-DPV 2637 is a feature shared with non-archosauromorph diapsids (e.g. *Gephyrosaurus bridensis*, Evans, 1981;

Planocephalosaurus robinsonae: Fraser & Walkden, 1984) and tanystropheids (e.g. *Amotosaurus rotfeldensis*: SMNS 50830; *Tanystropheus longobardicus*: Wild, 1973; Nosotti, 2007). By contrast, more derived archosauromorphs possess distinct parapophyses and diapophyses in the postaxial cervicals (e.g. *Mesosuchus*: Dilkes, 1998; *Trilophosaurus buettneri*: Spielmann et al., 2008; *Prolacerta*: BP/1/2675). Accordingly, FC-DPV 2637 and FC-DPV 2640 are interpreted as indeterminate basal archosauromorphs, but at least FC-DPV 2637 might belong to a very basal member of the clade because of the presence of a single facet for the rib.

The middle-posterior cervical vertebra FC-DPV 2639 possesses a series of characters that were found as synapomorphies of Archosauromorpha or less inclusive clades within the group by Ezcurra, Scheyer & Butler (2014): a trapezoidal and probable non-notochordal centrum, and anterior centrodiapophyseal, posterior centrodiapophyseal, prezygodiapophyseal and postzygodiapophyseal laminae on the neural arch (Fig. 4C, D). The combination of characters observed in FC-DPV 2639 resembles that present in several disparate basal archosauromorphs (e.g. *Protorosaurus speneri*: BSPG 1995 I 5; *Tanystropheus longobardicus*: PIMUZ T2817; *Spinosuchus caseanus*: Spielmann et al., 2009). Nevertheless, FC-DPV 2639 differs from *Prolacerta broomi* and *Proterosuchus fergusi* in the presence of a posterior centrodiapophyseal lamina. FC-DPV 2639 cannot be properly compared with the protorosaur cervical vertebra from the Sanga do Cabral Formation (Dias-da-Silva, 1998) because the latter belongs to a more anterior element in the axial series. As a result, FC-DPV 2639 is interpreted as an indeterminate basal archosauromorph, but distinct from *Prolacerta* and proterosuchids.

Discussion

The presence of archosauromorphs in the Permo-Triassic Buena Vista Formation was previously reported by Piñeiro (2002) and Piñeiro & Ubilla (2003), but no detailed description or taxonomic discussion have been provided so far. The cranial and postcranial remains described here increase the meagre archosauromorph record in Permo-Triassic rocks of South America.

The partial braincase with resemblances to *Proterosuchus* is particularly interesting because it probably reinforces the broad palaeobiogeographic distribution of proterosuchids during Permo-Triassic times (i.e. European Russia, China, South Africa, possibly Australia) (Ezcurra, Butler & Gower, 2013). However, we need to be cautious about this hypothesis because the specimen shows some differences that could not be properly compared with the Permian representatives of the group, such as the possible broad contribution of the basioccipital to the ventral margin of the foramen magnum (Fig. 3). The complete skull length of FC-DPV 2641 is estimated between 200–250 mm based on linear regressions of the total length of the skull versus the width and height of the occipital condyle, respectively, of a series of proterosuchid skulls from the *Lystrosaurus* Assemblage Zone of South Africa (N = 4: NMQR 880, 1484, BSPG 1934 VIII 514, GHG 231; occipital condyle width: $y = 0.0514x – 0.02115$, $R^2=0.96$; occipital condyle height: $y = 0.0295x + 2.8892$, $R^2=0.80$). The skull length range recovered for FC-DPV 2641 falls in the 4th to 18th percentile of the South African proterosuchid sample (N = 14, total skull length ranges from 177 to 477 mm; Ezcurra and Butler, 2014). The presence of a medium-sized basal archosauromorph in the Permo-Triassic of South America is not unexpected because of the presence of relatively large proterosuchids in the latest Permian of Russia (*Archosaurus rossicus*) and relatively large basal archosauromorphs in the earliest Triassic of Antarctica (Smith et al., 2011), South Africa (*Proterosuchus fergusi*) and China (‘*Chasmatosaurus*’ *yuani*).

The archosauromorph partial braincase described here belongs to an individual considerably larger than those of the cervical vertebrae. Among the postcranial bones, the middle-posterior cervical vertebra (FC-DPV 2639) pertained to an animal larger than those of the anterior and middle-posterior cervical vertebrae (FC-DPV 2637, 2640), and the latter two vertebrae are similar in size to each other (Table 2: compare transverse width of the centra). We could not find any autapomorphy or combination of features that might allow refer the cervical vertebrae to a single species. Conversely, the simultaneous occurrence of a proterosuchid-like partial braincase and a middle-posterior cervical vertebra with clear differences with proterosuchids support the hypothesis of a multi-taxonomic archosauromorph assemblage. The archosauromorph record of the Buena Vista Formation seems to bolster a Permo-Triassic age for the unit, as previously concluded by Piñeiro, Ramos & Marsicano (2012). Unfortunately, this archosauromorph assemblage does not help in the debate of a Permian or Triassic age for this unit because both basal archosauromorphs and early archosauriforms (e.g. proterosuchids) are present across the Permo−Triassic boundary (Ezcurra, Scheyer & Butler, 2014).

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FIGURE CAPTIONS

Figure 1. Partial braincase (FC-DPV 2641) from the Late Permian−Early Triassic Buena Vista Formation (Uruguay) in (A) posterior; (B) anterior; (C) right lateral; (D) left lateral; (E) dorsal; and (F) ventral views. Abbreviations: bt, basal tubera; dr, diagonal ridge; ecf, endocranial floor; eo, exoccipital; fpbs, facet for the parabasisphenoid; fvro, facet for the ventral ramus of the opisthotic; lf, lateral flange of the basioccipital; mlr, median longitudinal ridge; mwpr, medial wall of the pseudolagenar recess; np, notochordal pit; oc, occipital condyle; rs, recessed surface; wmf, wall of the metotic foramen. Scale bar equals 5 mm.

Figure 2. Anatomical comparison between (A−C) the pelycosaur *Secodontosaurus obtusidens* (modified from Reisz, Berman & Scott, 1992) and (D−F) FC-DPV 2641 in (A, D) posterior, (B, E) left lateral, and (C, F) ventral views. Abbreviations: bo, basioccipital; bt, basal tubera; ds, damaged surface; eo, exoccipital; lf, lateral flange of the basioccipital; mwpr, medial wall of the pseudolagenar recess; np, notochordal pit; oc, occipital condyle; op, opisthotic; ps, parasphenoid; so, supraoccipital. Scale bars equal 10 mm.

Figure 3. Anatomical comparison between (A, B) FC-DPV 2641, (C) *Protorosaurus speneri* (modified from Gottmann-Quesada & Sander, 2009), and (D, E) a su[illegible]ult specimen of *Proterosuchus alexanderi* (NMQR 1484) in occipital views. Abbreviations: XII?, possible exit of the hypoglossal cranial nerve; bo, basioccipital; bo?, possible basioccipital; bt, basal tubera; eo, exoccipital; eo?, possible exoccipital; fm, foramen magnum; fo, fenestra ovalis; lf, lateral flange of the basioccipital; mf, metotic foramen; mf?, possible metotic foramen; np, notochordal pit; p, parietal; plr, pseudolagenar recess; pp, paraoccipital process; so, supraoccipital; vrop, ventral ramus of the opisthotic. Scale bars equal 10 mm.

Figure 4. Photographs and interpretive drawings of (A−B) an anterior cervical vertebra (FC-DPV 2640) and (C−G) a middle-posterior cervical vertebra (FC-DPV 2639) from the Late Permian−Early Triassic Buena Vista Formation (Uruguay) in (A−D) right lateral, (E) dorsal, (F) ventral, and (G) posterior views. The arrows indicate the longitudinal ridge on the lateral surface of the centrum. Abbreviations: d, depression; dp, diapophysis; ns, neural spine; pa, parapophysis; pcdl, posterior centrodiapophyseal lamina; pdl, paradiapophyseal lamina; pfc, posterior facet of the centrum; podl, postzygodiapophyseal lamina; posf, postspinal fossa; prdl, prezygodiapophyseal lamina; prz, prezygapophysis; poz, postzygapophysis. Scale bars equal 5 mm.

Figure 5. Photographs and interpretive drawings of a middle cervical vertebra (FC-DPV 2637) from the Late Permian−Early Triassic Buena Vista Formation (Uruguay) in (A, B) anterior; (C, D) posterior; (E, F) right lateral; (G, H) left lateral; (I, J) dorsal; and (K, L) ventral views. Abbreviations: afc, anterior facet of the centrum; ao, anterior overhanging; d, depression; dt, distal thickening; fr, facet for the rib; nc, neural canal; np, notochordal pit; ns, neural spine; pcdl, posterior centrodiapophyseal lamina; pfc, posterior facet of the centrum; posf, postspinal fossa; poz, postzygapophysis; prsf, prespinal fossa; prz, prezygapophysis. Scale bars equal 5 mm.

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Figure 1

Partial braincase (FC-DPV 2641) from the Late Permian−Early Triassic Buena Vista Formation (Uruguay) in (A) posterior; (B) anterior; (C) right lateral; (D) left lateral; (E) dorsal; and (F) ventral views. Abbreviations: bt, basal tubera; dr, diagonal ridge; ecf, endocranial floor; eo, exoccipital; fpbs, facet for the parabasisphenoid; fvro, facet for the ventral ramus of the opisthotic; lf, lateral flange of the basioccipital; mlr, median longitudinal ridge; mwpr, medial wall of the pseudolagenar recess; np, notochordal pit; oc, occipital condyle; rs, recessed surface; wmf, wall of the metotic foramen. Scale bar equals 5 mm.

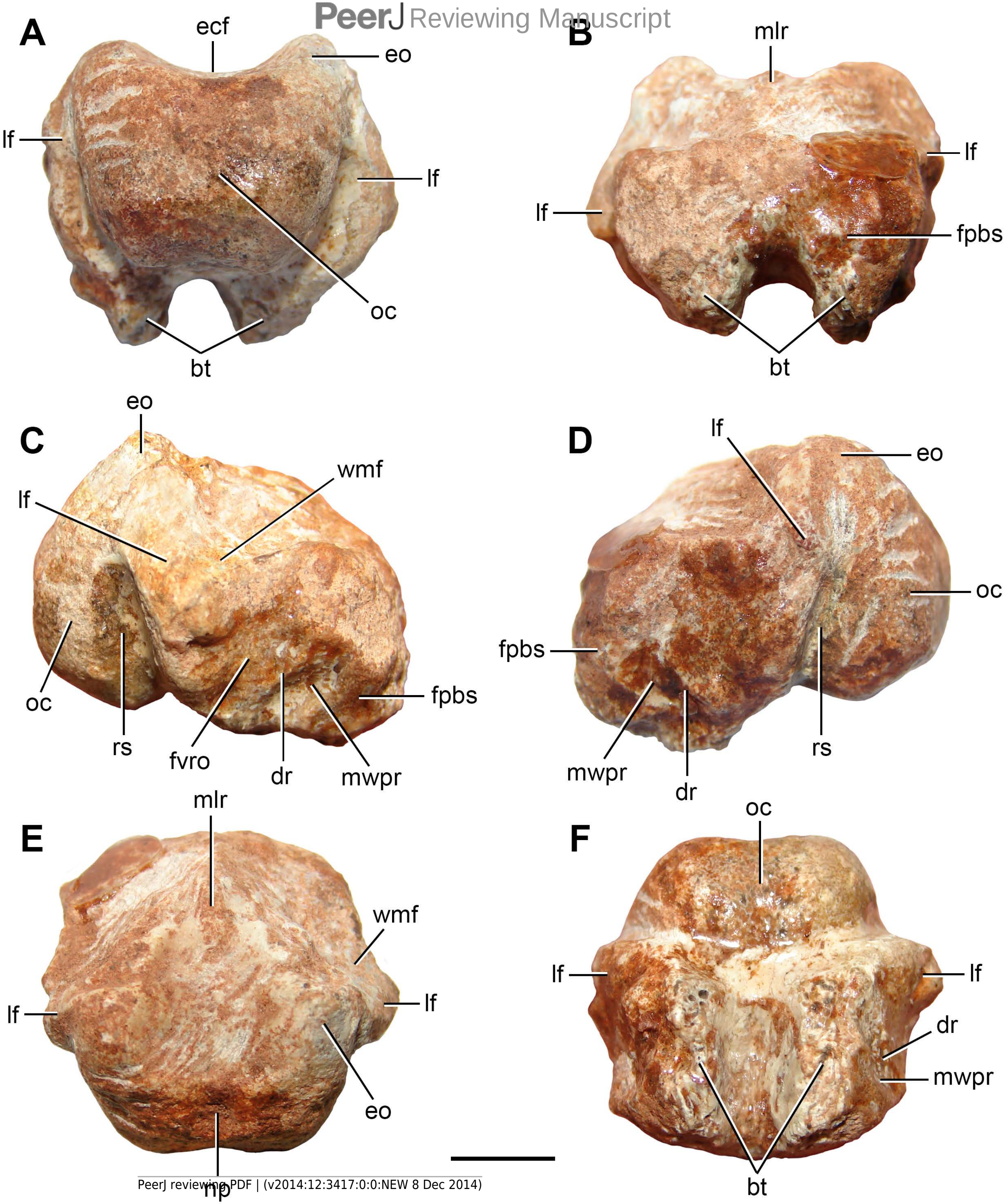
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Figure 2

Anatomical comparison between (A−C) the pelycosaur *Secodontosaurus obtusidens* (modified from Reisz, Berman & Scott, 1992) and (D−F) FC-DPV 2641 in (A, D) posterior, (B, E) left lateral, and (C, F) ventral views. Abbreviations: bo, basioccipital; bt, basal tubera; ds, damaged surface; eo, exoccipital; lf, lateral flange of the basioccipital; mwpr, medial wall of the pseudolagenar recess; np, notochordal pit; oc, occipital condyle; op, opisthotic; ps, parasphenoid; so, supraoccipital. Scale bars equal 10 mm.

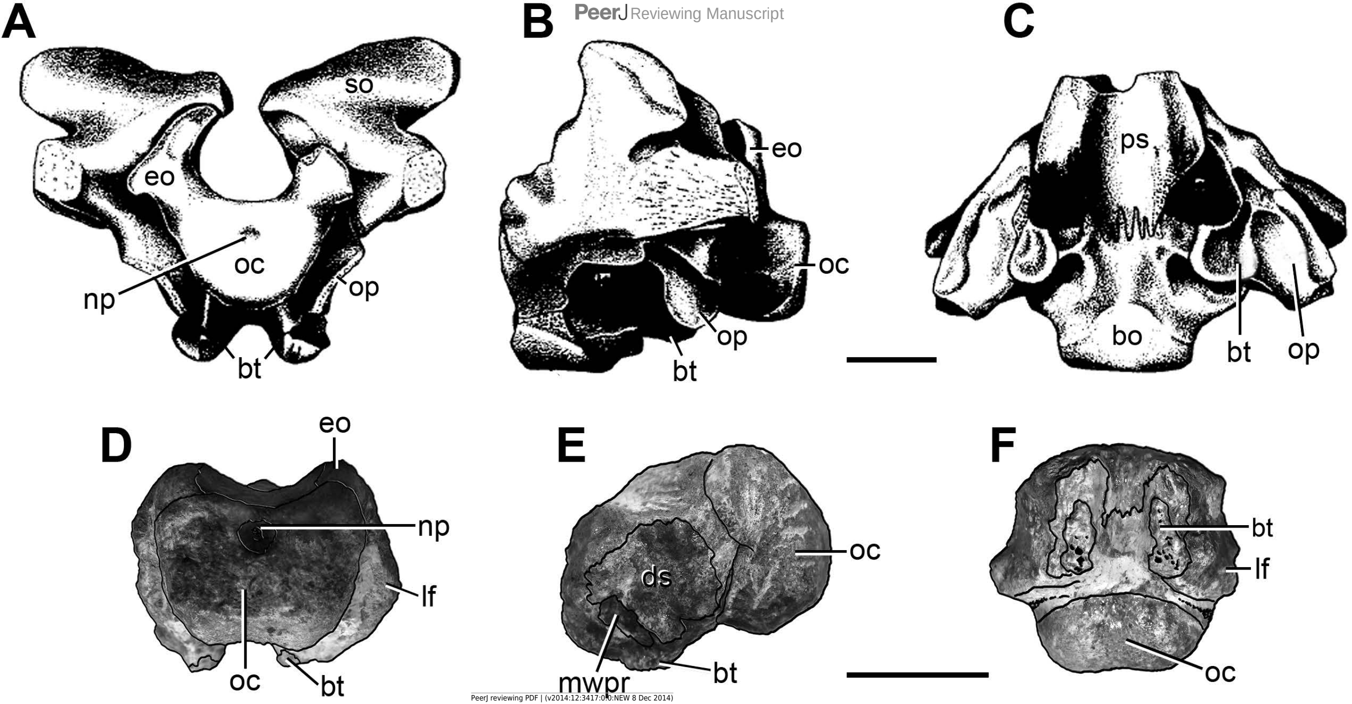
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Figure 3

Anatomical comparison between (A, B) FC-DPV 2641, (C) *Protorosaurus speneri* (modified from Gottmann-Quesada & Sander, 2009), and (D, E) a subadult specimen of *Proterosuchus alexanderi* (NMQR 1484) in occipital views. Abbreviations: XII?, possible exit of the hypoglossal cranial nerve; bo, basioccipital; bo?, possible basioccipital; bt, basal tubera; eo, exoccipital; eo?, possible exoccipital; fm, foramen magnum; fo, fenestra ovalis; lf, lateral flange of the basioccipital; mf, metotic foramen; mf?, possible metotic foramen; np, notochordal pit; p, parietal; plr, pseudolagenar recess; pp, paraoccipital process; so, supraoccipital; vrop, ventral ramus of the opisthotic. Scale bars equal 10 mm.

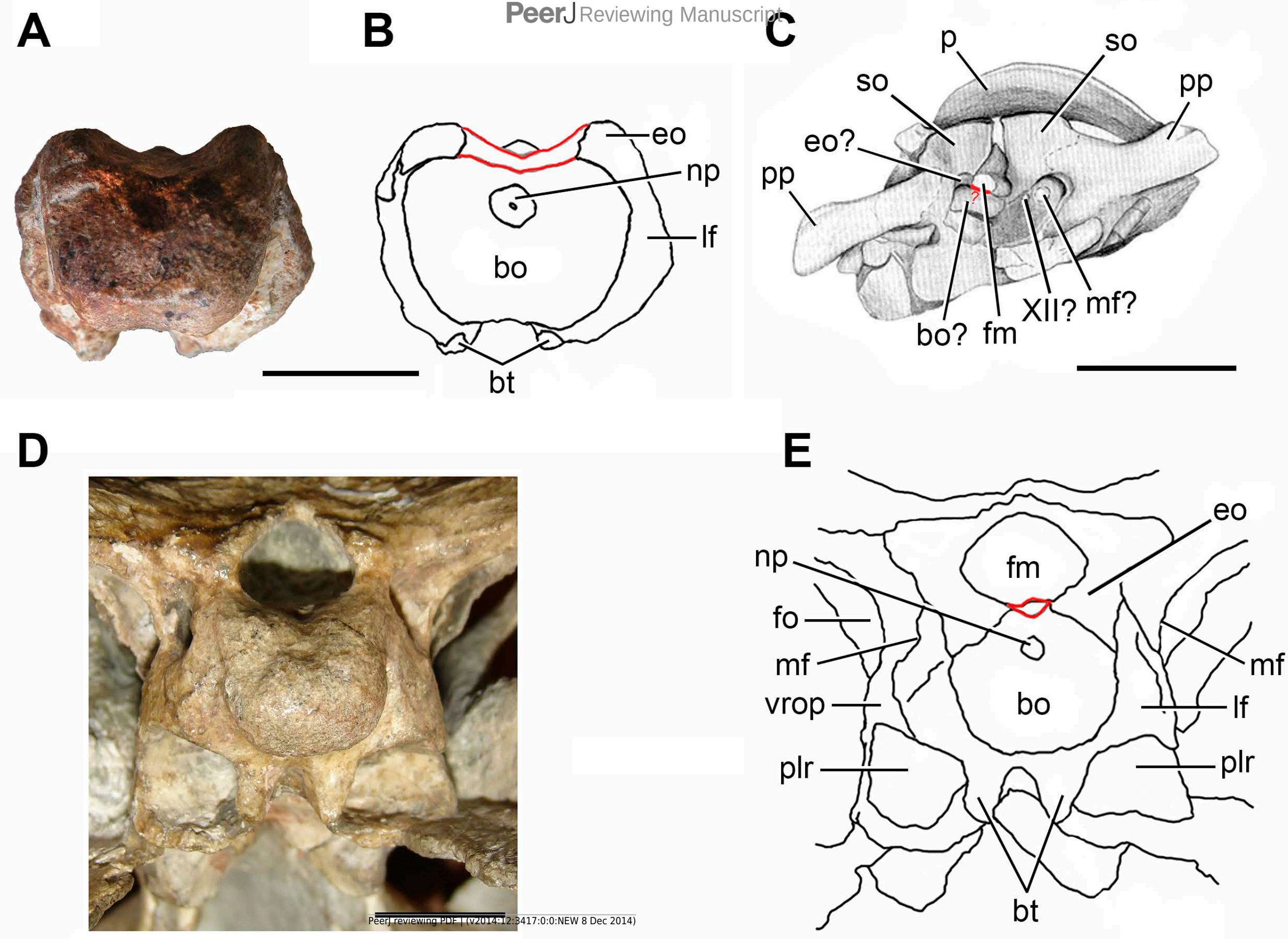
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Figure 4

Photographs and interpretive drawings of (A−B) an anterior cervical vertebra (FC-DPV 2640) and (C−G) a middle-posterior cervical vertebra (FC-DPV 2639) from the Late Permian−Early Triassic Buena Vista Formation (Uruguay) in (A−D) right lateral, (E) dorsal, (F) ventral, and (G) posterior views. The arrows indicate the longitudinal ridge on the lateral surface of the centrum. Abbreviations: d, depression; dp, diapophysis; ns, neural spine; pa, parapophysis; pcdl, posterior centrodiapophyseal lamina; pdl, paradiapophyseal lamina; pfc, posterior facet of the centrum; podl, postzygodiapophyseal lamina; posf, postspinal fossa; prdl, prezygodiapophyseal lamina; prz, prezygapophysis; poz, postzygapophysis. Scale bars equal 5 mm.

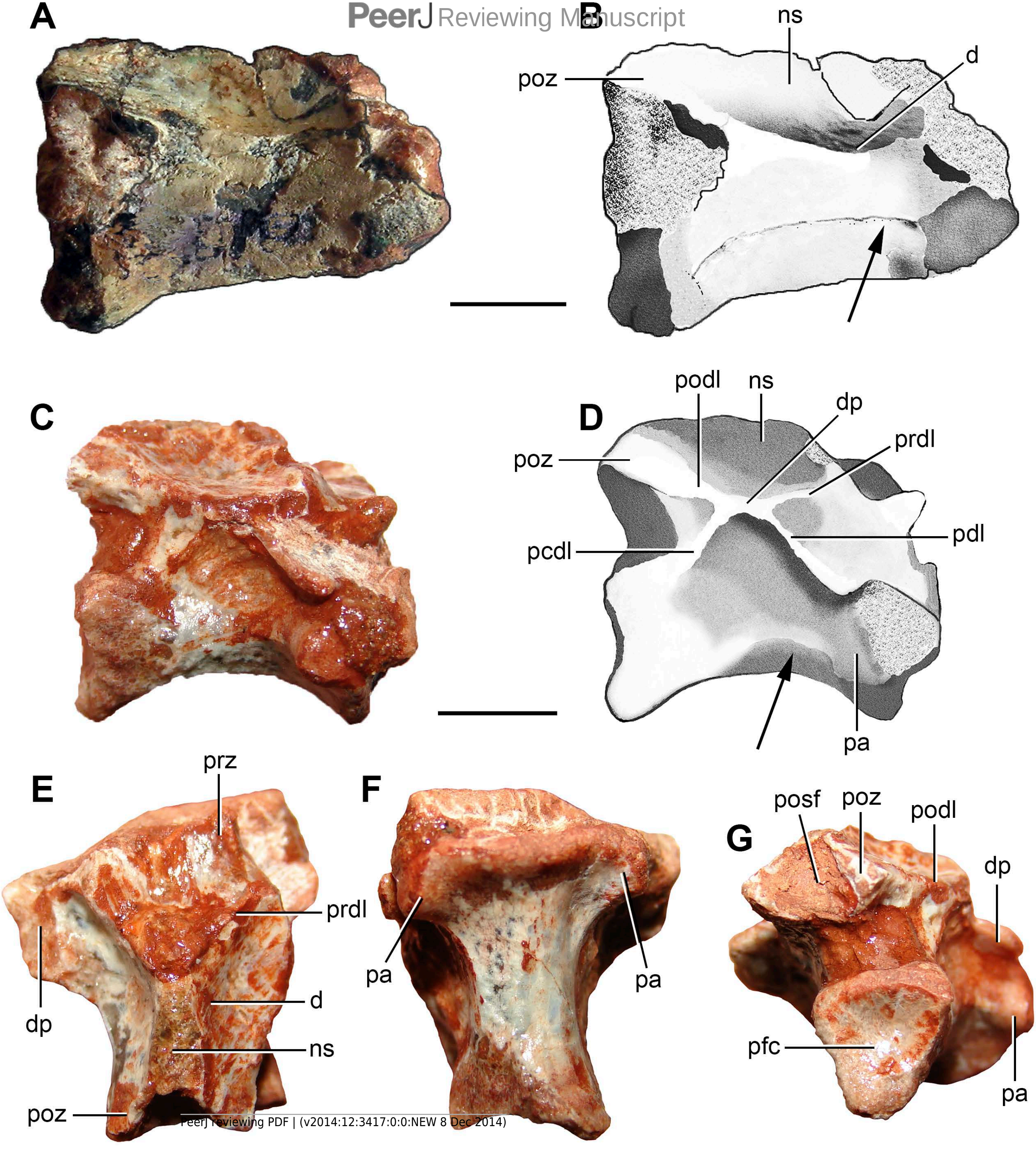
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Figure 5

Photographs and interpretive drawings of a middle cervical vertebra (FC-DPV 2637) from the Late Permian−Early Triassic Buena Vista Formation (Uruguay) in (A, B) anterior; (C, D) posterior; (E, F) right lateral; (G, H) left lateral; (I, J) dorsal; and (K, L) ventral views. Abbreviations: afc, anterior facet of the centrum; ao, anterior overhanging; d, depression; dt, distal thickening; fr, facet for the rib; nc, neural canal; np, notochordal pit; ns, neural spine; pcdl, posterior centrodiapophyseal lamina; pfc, posterior facet of the centrum; posf, postspinal fossa; poz, postzygapophysis; prsf, prespinal fossa; prz, prezygapophysis. Scale bars equal 5 mm.

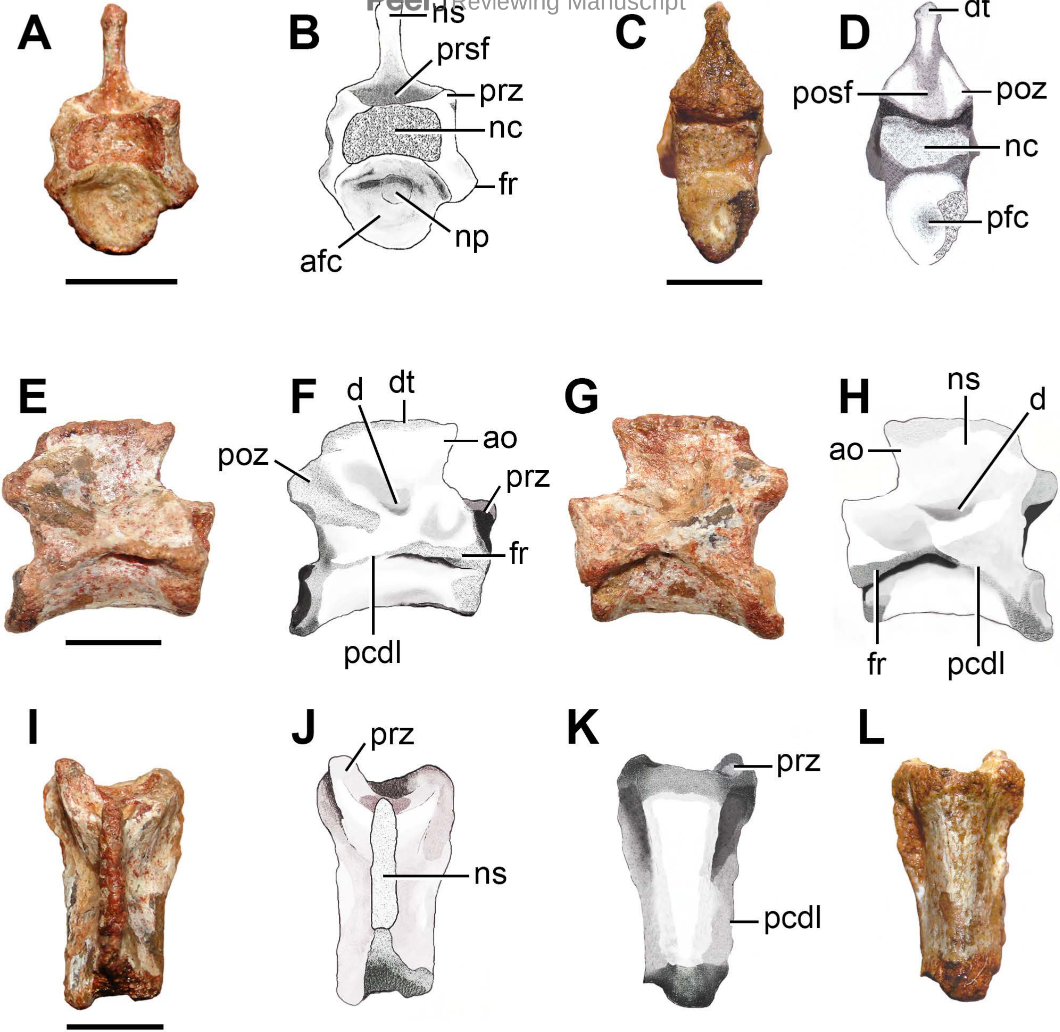
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Table 1(on next page)

Table 1

Table 1. Measurements of the basioccipital+exoccipitals (FC-DPV 2641) in millimeters. Values between brackets indicate incomplete measurements. Maximum deviation of the digital caliper is 0.02 mm but measurements were rounded to the nearest 0.1 millimeter.

Length of basioccpital	16.6
Width of basioccipital	(17.1)
Height of basioccipital	(13.6)
Occipital condyle height	9.0
Occipital condyle width	12.6
Occipital condyle length	5.3
Notochordal pit height	2.0
Notochordal pit width	2.3
Basal tuber length	8.5
Basal tuber width	4.2

Table 2(on next page)

Table 2

Table 2. Measurements of the anterior (FC-DPV 2640), middle (FC-DPV 2639), and middle−posterior (FC-DPV 2637) cervical vertebrae in millimeters. Values between brackets indicate incomplete measurements and between squared brackets indicate estimated measurements. The length along the zygapophyses is the maximum anteroposterior length between the anterior tips of the prezygapophyses and the posterior tips of the postzygapophyses. Maximum deviation of the digital caliper is 0.02 mm but measurements were rounded to the nearest 0.1 millimeter.

	FC-DPV2640	FC-DPV 2637	FC-DPV 2639
Centrum length	(17.8)	12.6	12.1
Anterior facet of centrum width	-	4.4	[7.8]
Anterior facet of centrum height	-	4.7	[7.1]
Posterior facet of centrum width	4.8	(4.2)	(5.9)
Posterior facet of centrum height	(4.9)	4.7	(6.5)
Length along zygapophyses	(19,8)	(13.5)	(11.8)
Height of neural spine	(3.1)	5.8	-
Length of neural spine	(9.4)	8.9	4.7
Maximum height of vertebra	(13.2)	14.0	(12.2)