Early evolution of sauropodomorphs: anatomy and phylogenetic relationships of a remarkably wellpreserved dinosaur from the Upper Triassic of southern Brazil

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An exceptional new specimen (CAPPA/UFSM 0035) of *Buriolestes schultzi* was discovered during recent fieldwork at the type locality of the taxon, which is Carnian in age (Late Triassic). This early sauropodomorph is peculiar owing to its faunivorous feeding habits, unusual amongst the members of this large omnivorous/herbivorous clade. The specimen incorporates new data on skeletal portions that have so far been unknown for *B. schultzi*, particularly regarding the skull and axial skeleton. As such, *B. schultzi* is now as complete as the best-known early dinosaurs, such as *Eoraptor lunensis* and *Herrerasaurus ischigualastensis*. A phylogenetic investigation fully supports *B. schultzi* as a sauropodomorph, corroborating the previous assignation. Despite the presence of traits found in Theropoda, distinct skeletal portions of *B. schultzi* do not share its morphospace in a morphological disparity analysis. We also propose an alternative evolutionary scenario for the first members of Sauropodomorpha: some Carnian taxa from South America form a monophyletic group instead of a series of low-diversity lineages paraphyletic with respect to Plateosauria.

ADDITIONAL KEYWORDS: Dinosauria – Gondwana – osteology – phylogenetics – Sauropodomorpha – South America.

INTRODUCTION

There is general agreement that the oldest dinosaurs are those quarried from Carnian strata of southwestern Pangea (e.g. Reig, 1963; Casamiquela, 1967; Colbert, 1970; Sereno *et al.*, 1993; Cabreira *et al.*, 2016), mainly represented by the Santa Maria Supersequence and the Ischigualasto Formation, respectively from Brazil and Argentina (but see Nesbitt *et al.*, 2012; Baron, Norman & Barrett, 2017a). These units yield Saurischian

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dinosaurs, represented by several well-preserved herrerasaurids (Reig, 1963; Colbert, 1970; Alcober & Martínez, 2010), sauropodomorphs (Sereno *et al.*, 1993; Langer *et al.*, 1999; Martínez & Alcober, 2009; Ezcurra, 2010; Cabreira *et al.*, 2011, 2016) and possible theropods (Martínez *et al.*, 2011; Müller *et al.*, 2017). In contrast, ornithischians are poorly known, so far represented only by *Pisanosaurus mertii* (Casamiquela, 1967). In any case, the taxonomic diversity recorded from both Argentina and Brazil suggests that the three main dinosaurian groups were already present in land ecosystems during the Carnian.

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In recent years, however, new findings and diverse/ alternative methodological approaches are challenging and/or complementing those previously proposed evolutionary scenarios. For instance, Nesbitt et al. (2012) described a putative dinosaur from the Anisian of southern Tanzania, implying that dinosaurs arose 15 Myr earlier than previously thought. Langer & Ferigolo (2013) proposed that Silesauridae had ornithischian affinities, increasing their Triassic record. Cabreira et al. (2016) supported this scenario in a recent comprehensive phylogenetic study on Triassic dinosauromorphs, in which several taxa were, for the first time, placed in alternative positions in the dinosaur tree. For instance, Eodromaeus murphi (Martínez et al., 2011) and Tawa hallae (Nesbitt et al., 2009) were originally described as members of Theropoda, being recovered as basal saurischians outside the theropodsauropodomorph dichotomy (Cabreira et al. 2016). In addition, P. mertii has recently been suggested to represent a silesaurid in two independent studies (Agnolín & Rozadilla, 2017; Baron, Norman & Barrett, 2017b). Even more unexpectedly, Baron et al. (2017a) proposed that theropods are closely related to ornithischians instead of sauropodomorphs. At the same time, new data regarding dinosaur relatives came to light, including the description of several new non-dinosaur dinosauromorphs (e.g. Irmis et al., 2007; Cabreira et al., 2016; Martínez et al., 2016) and also the proposal of an entire new clade of early diverging avemetatarsalians (Nesbitt et al., 2017).

Among these new findings, the Carnian Buriolestes schultzi was recovered as the basalmost member of Sauropodomorpha (Cabreira et al., 2016), a group largely known for encompassing giant quadrupedal and herbivorous forms. This new taxon was a small biped and, outstandingly, the only strictly faunivorous sauropodomorph so far described, therefore being a key taxon to understand both biological and ecological trends in sauropodomorph early evolution.

During recent fieldwork at the type locality of *B. schultzi*, we discovered an exceptionally well-preserved new specimen (CAPPA/UFSM 0035), which revealed several skeletal structures so far unknown in *B. schultzi* and even in any other coeval dinosaurs. In the present study, we describe the anatomy of this new specimen in detail and investigate its implications for early dinosaur phylogeny.

MATERIAL AND METHODS

INTITUTIONAL ABBREVIATIONS

CAPPA/UFSM, Centro de Apoio à Pesquisa Paleontológica da Quarta Colônia da Universidade Federal de Santa Maria, São João do Polêsine, Brazil; MCP, Museu de Ciências e Tecnologia Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Brazil; NMT, National Museum of Tanzania, Dar es Salaam, Tanzania; PVSJ, Museo de Ciencias Naturales, Universidad Nacional de San Juan, San Juan Province, Argentina; ULBRA, Universidade Luterana do Brasil, Coleção de Paleovertebrados, Canoas, Brazil; ZPAL, Institute of Paleobiology of the Polish Academy of Sciences, Warsaw, Poland.

PHYLOGENETIC ANALYSIS

Owing to its completeness, CAPPA/UFSM 0035 allowed the inclusion of many additional scores for *B. schultzi*, as several features are unavailable in the holotype. Accordingly, we performed a series of analyses to assess the relationships of CAPPA/UFSM 0035 and its possible implications for early dinosaurian evolution.

Firstly, it was simply scored in the data matrix by Cabreira et al. (2016), in order to test its taxonomic assignment to B. schultzi. In order to do so, CAPPA/ UFSM 0035 and ULBRA-PVT280 (the holotype of B. schultzi) were coded as two distinct operational taxonomic units (OTUs). All parameters of the original analysis were replicated, and the data matrix was processed with the software TNT v1.1 (Goloboff, Farris & Nixon, 2008), with the most parsimonious trees (MPTs) recovered via 'traditional search' [random addition sequence + tree bisection reconnection (TBR)] with 1000 replicates of Wagner trees (with random seed = 0), TBR and branch swapping (holding 20 trees saved per replicate). Decay indices (Bremer support values) and bootstrap values (1000 replicates) were also obtained with TNT v1.1.

In the second analysis, CAPPA/UFSM 0035 and ULBRA-PVT280 were merged into a single OTU, keeping the computational parameters unchanged.

The third and fourth analyses used a modified version of the data matrix of Cabreira et al. (2016), in which B. schultzi was scored by combining its original entries with CAPPA/UFSM 0035, as follows. Character 36, originally with three states related to the median recess in the parabasisphenoid, had one deleted, and now reads: '0' shallow depression; '1' fossa or deep depression. Character 37, regarding the outline of the caudal margin of the parabasisphenoid in ventral view, was rescored for several taxa. Character 41, which describes the presence of a rugose ridge on the craniolateral edge of the supraoccipital (Nesbitt, 2011), was redefined as 'supraoccipital, dorsal surface: rugose ridge along exoccipital contact', with two states: '0' absent; '1' present. Several OTUs were rescored for character 42, which is related to the foramen for the trigeminal nerve and middle cerebral vein. Panphagia protos was rescored from '1' to '0/1' in character 63, which is associated with the shape of the caudal edge of the caudal half of the maxilla/dentary teeth. Dentition of this dinosaur shows both proposed morphologies: 'concave or straight' and 'convex'. For character 246, which describes the presence of serrations in the mesial margin of the premaxillary teeth, P. protos was changed from '1' to '?', because there are no premaxillary teeth preserved for this dinosaur. Three additional characters were included in the data matrix. The first one (257) is modified from Nesbitt (2011) and defined as 'blind pit in the basioccipital'. Three states are proposed: '0' absent; '1' one pit; '2' two pits. The second character (258) is based upon the observations by Cabreira et al. (2011) on the prefrontal shape in early dinosaurs and defined as 'bone sheet between the rostral and ventral processes of the prefrontal'. Two states are proposed: '0' present; '1' absent. The third character (259) was proposed by Ezcurra (2006) as 'angle between ascending process and caudal process of jugal', with two states: '0' right or obtuse; '1' acute, with an ascending process strongly dorsocaudally oriented. This modified data matrix (which comprises 259 characters and 43 OTUs) was analysed following the same parameters as the first two analyses, with the three new characters treated as non-additive. The scores for all OTUs are included in the Appendix.

In the fourth analysis, the dataset was run using implied character weighting, with the value of the concavity constant (k) ranging between three and nine. According to Legg, Sutton & Edgecombe (2013), equal character weighting is only appropriate in analyses with no potential homoplasy, which is not the case for early dinosaurs (Langer, 2014). In addition, Goloboff *et al.* (2008) concluded that implied character weighting against homoplasy could improve phylogenetic analysis of morphological data matrices. Therefore, in this last analysis, we used implied character weighting in an attempt to minimize the effect of homoplasy. Nodal support was measured using symmetric resampling (Goloboff *et al.*, 2003), performed with 1000 replicates, each with a 33% of change probability.

In addition, a fifth analysis was carried out using the data matrix of Langer *et al.* (2017), which is a modified version of that of Baron *et al.* (2017a). In this analysis, the new information gathered from CAPPA/UFSM 0035 was added to *B. schultzi*. All the characters received the same weight, and the same parameters as for the previous analysis were used to recover the MPTs.

MORPHOLOGICAL DISPARITY ANALYSIS

In spite of its sauropodomorph affinity, *B. schultzi* shares several morphological features with theropods. Therefore, in order to explore both phylogenetic signals and putative convergences within distinct skeletal portions of this dinosaur, we conducted a morphological disparity analysis. Our analysis follows that of

Novas et al. (2015), which aimed to investigate different homoplastic signals in distinct body parts of Chilesaurus diegosuarezi. We used a modified version of the dataset from the third and fourth phylogenetic analyses, with the polymorphic scores changed to 'missing entries' (Novas et al., 2015). Then, six skeletal parts were isolated in the data matrix: skull; skull excluding dentition; postcranium; axial skeleton; pectoral girdle/ forelimb; and pelvic girdle/hindlimb. Taxa with missing entries for a given skeletal part were excluded from the partitioned matrices. Next, seven Euclidian distance matrices (EDMA) were calculated using the software MATRIX (Will, 1998). The matrices were calculated from the six partitioned and one data matrix with all the characters. A principal coordinate analysis (PCoA) was then performed for each EDMA with the multivariate package GINKGO (Bouxin, 2005). At this point, we followed the parameters applied by Butler et al. (2012), in which the centroid of all OTUs is taken as the origin of multivariate axes, also using the Calliez method of negative eigenvalue correction. Finally, a bivariate graph with axes 1 and 2 of each PCoA was constructed using the software PAST (Hammer, Haper & Ryan, 2001). Convex hulls were drawn from the results of the third phylogenetic analysis performed here.

SYSTEMATIC PALAEONTOLOGY

DINOSAURIA OWEN, 1842 SAURISCHIA SEELEY, 1887 SAUROPODOMORPHA HUENE, 1932 BURIOLESTES SCHULTZI CABREIRA ET AL., 2016

Holotype

ULBRA-PVT280, articulated partial skeleton, including partial skull with both lower jaws; few presacral, three sacral and 42 tail vertebrae; left scapula and forelimb lacking most of the manus; paired ilia and ischia; partial left pubis; and a nearly complete left hindlimb (Cabreira *et al.*, 2016).

Referred specimen

CAPPA/UFSM 0035, a nearly complete and articulated skeleton (Fig. 1A, C). The skull is almost entirely preserved, including both lower jaws. The axial skeleton includes the complete cervical and trunk series but lacks the last sacral vertebra and the caudal series. Pectoral elements include a partial left scapula and coracoid and a fragmentary left humerus. Pelvic elements include both ilia, the proximal portion of both pubes, the proximal portion of the right ischium, an almost complete right femur, a fragmentary left femur and partial right tibia and fibula. There are also some phalanges from the right pedal digits III and IV.



Figure 1. CAPPA/UFSM 0035 and the location of the study area. A, CAPPA/UFSM 0035 in the rock block before the final preparation. B, map of the São João do Polêsine area, Rio Grande do Sul, Brazil, showing the location of the Buriol outcrop (modified from Müller *et al.*, 2017). C, reconstruction of the preserved portions of the skeleton of CAPPA/UFSM 0035.

Locality and horizon

The new specimen was excavated from the Buriol outcrop (29°39′34.2″S; 53°25′47.4″W), in São João do Polêsine, Rio Grande do Sul, Brazil (Fig. 1B). This outcrop corresponds to the type locality of *B. schultzi* (Cabreira *et al.*, 2016). CAPPA/UFSM 0035 comes from the same layer that yielded the holotype (ULBRA-PVT280). Site strata belong to the lower portion of the Candelária Sequence (Horn *et al.*, 2014), which is part of the Santa Maria Suspersequence of Zerfass *et al.* (2003) (Fig. 2). The presence of specimens ascribed to the rhynchosaur *Hyperodapedon* (Dias-da-Silva, Cabreira & Roberto-da-Silva, 2011; Roberto-da-Silva

et al., 2014; Müller et al., 2017) allows the correlation with the Ischigualasto Formation, in northwest Argentina, radioisotopically dated as 231.4 ± 0.3 Mya (Martínez et al., 2011). In addition to *B. schultzi* and *Hyperodapedon* sp., the Buriol outcrop has also yielded the lagepetid *Ixalerpeton polesinensis* (Cabreira et al., 2016), whereas fishes (dipnoi plate, hybodontiform shark spine and actinopterygian remains), aetosaurs, temnospondyls and cynodonts were found in close surrounding outcrops (Perez & Malabarba, 2002; Toledo & Bertini, 2005; Richter & Toledo, 2008; Dias-da-Silva et al., 2011, 2012; Roberto-da-Silva et al., 2014; Pacheco et al., 2017).



Figure 2. Chrono- and biostratigraphy of the Triassic units from southern Brazil, showing the level of CAPPA/UFSM 0035. Scheme based on Zerfass *et al.* (2003) and Horn *et al.* (2014). Geological time scale follows Gradstein *et al.* (2012). The radiometric dating of 236.1, 231.4 and 225.9 Mya corresponds to the first half of the Chañares Formation (Marsicano *et al.*, 2016) and the base of the Ischigualasto Formation (Martínez *et al.*, 2011), respectively.

DESCRIPTION

CRANIAL SKELETON

The skull preserves most bones in articulation (Figs 3-5), but some of them are almost entirely covered by matrix or other bones, for instance, the prootic, coronoid and intercoronoid. In addition, a few elements

were displaced from their original position. Indeed, part of the skull roof suffered dorsoventral compression during fossil diagenesis. Hence, despite the excellent preservation, its height does not reflect the original condition. The skull length, from the preserved rostral tip of the premaxilla to the caudal margin of the occipital condyle, is 108.5 mm, but only the caudal



Figure 3. Skull of CAPPA/UFSM 0035 in left lateral view. A, photograph and interpretative drawing. B, reconstruction of the skull of *Buriolestes schultzi* (ULBRA-PVT280 plus CAPPA/UFSM 0035). Abbreviations: a, angular; af, antorbital fenestra; anf, antorbital fossa; ar, articular; ec, ectopterygoid; emf, external mandibular fenestra; f, frontal; j, jugal; l, lacrimal; ls, laterosphenoid; ltf, laterotemporal fenestra; m, maxilla; n, nasal; nf, narial fossa; oc, occipital condyle; p, parietal; pl, palatine; pm, premaxilla; po, postorbital; popr, paraoccipital process; prf, prefrontal; q, quadrate; qj, quadratojugal; sa, surangular; sp, splenial; sq, squamosal.

half of the premaxilla is preserved. This corresponds to ~80% of the femoral length. In contrast, the right lower jaw is entirely preserved, with a total length of 111.75 mm from the rostral tip of the dentary to the caudal extremity of the retroarticular process. The rostrocaudal length of the orbit is 25 mm; the internal antorbital fenestra is 24 mm long and has a maximal height of 10 mm. The external naris was probably low, given the dorsoventral space (3.5 mm) between the dorsal surface of the premaxilla and the ventral margin of the nasal (on the right side).

Premaxilla

Only the caudal portions of both premaxillae are preserved (Fig. 6). The left element, measuring 9 mm long and 4.75 mm wide (at the transversely wider portion) is more complete. Despite the poor preservation of the rostral region, it is clear that the premaxilla is slightly sloped, with its rostral portion projecting more ventrally than the caudal portio. Based on the preserved portion, it is possible to observe a shallow narial fossa. The rostral edge of the bone, as preserved, bears the caudal half of a foramen located at the rostrocaudal



Figure 4. Photograph and interpretative drawing of the skull of CAPPA/UFSM 0035 in right lateral view. Abbreviations: a, angular; ar, articular; f, frontal; j, jugal; l, lacrimal; m, maxilla; n, nasal; p, parietal; pl, palatine; pm, premaxilla; po, postorbital; popr, paraoccipital process; prf, prefrontal; q, quadrate; qj, quadratojugal; sa, surangular; sq, squamosal; v, vomer.

level of the last premaxillary tooth. The caudolateral process tapers to a point caudally and does not project dorsally, although it contacts the rostroventral process of the nasal, excluding the maxilla from the caudal portion of the narial fenestra. In dorsal view, the caudomedial premaxillary margin is rounded in response to the lateral direction of the caudolateral process. The caudal margin of this process rests on the rostral process of the maxilla. Below it, a 3.5-mm-long subnarial gap marks the contact between the premaxillary and maxillary alveolar margins (Fig. 6A). The premaxilla contributes to the convex rostrodorsal margin of the gap, resulting in a semicircular gap.

Maxilla

Both maxillae are almost entirely preserved (Fig. 7). The bone is ~60 mm long, corresponding to ~55% of the total skull length. The rostral process is short (~12% of the total rostrocaudal length of the bone), with the dorsal margin (which receives the premaxilla) oblique to the main axis of the maxilla. Its ventral/alveolar margin is slightly upturned at the rostral half but aligned to that of the rest of the maxilla in the caudal half. The rostral margin of the rostral process is excavated (Fig. 7A, B), forming the caudal border of the subnarial foramen, as in the holotype (ULBRA-PVT280) of *B. schultzi*. This condition is unique among

early dinosaurs, with the subnarial foramen totally confluent with the subnarial gap. In addition, several other foramina pierce the lateral surface of the rostral process. The dorsal process of the maxilla is not well expanded, and its dorsal margin is almost parallel to that of the caudal process of the maxilla, resulting in a dorsoventrally low rostrum. The caudal tip of the dorsal process reaches the middle of the antorbital fenestra, and its dorsal surface receives the ventral surface of the nasal. The height of the facial maxillary surface, between the alveolar margin and the ventral limit of the dorsal process, corresponds to about onethird of the height of the dorsal process.

The caudal process of the maxilla is elongated (~90% of the total craniocaudal length of the bone) and tapers caudally along its distal tenth. A longitudinal ridge divides the lateral and dorsal surfaces of the caudal process, bordered ventrally by a row of neurovascular foramina, the caudalmost of which is associated with a 4-mm-long caudal fossa. The alveolar margin of the caudal process is straight along its entire length. The process extends until the midhalf of the ventral border of the orbit, where the jugal articulates to the dorsal surface of the bone. The ventral portion of the medial surface of the maxilla is dorsoventrally convex, where the maxillary dentition is separated by lanceolate interdental plates (Fig. 7C). The palatine is



Figure 5. Skull of CAPPA/UFSM 0035. A, photograph and interpretative drawing in dorsal view. B, photograph and interpretative drawing in ventral view. Abbreviations: a, angular; ar, articular; bo, basicoccipital; c, coronoid; cpr, cultriform process; d, dentary; ec, ectopterygoid; f, frontal; hy, hyoid; j, jugal; l, lacrimal; n, nasal; p, parietal; pbs, parabasisphenoid; pl, palatine; pm, premaxilla; po, postorbital; popr, paraoccipital process; pra, prearticular; prf, prefrontal; pt, pterygoid; q, quadrate; sa, surangular; so, supraoccipital; sq, squamosal; v, vomer.

disarticulated from the maxilla, but it probably contacted the medial surface of the main body of the bone on the caudal half of the antorbital fenestra.

The maxillary antorbital fossa is slightly longer rostrocaudally than dorsoventrally deep and restricted to the rostral portion of the antorbital fenestra. There is no promaxillary fossa at the rostral extremity of the antorbital fossa. The ventral portion of the antorbital fossa extends caudally for half the total craniocaudal length of the caudal process of the maxilla.

Nasal

The rostral portion of both nasals is not preserved (Fig. 7). Yet, based on premaxillary and maxillary morphology, it is reasonable to assume that the original nasal length is ~0.35 of the total skull length. The



Figure 6. Cranial end of the skull of CAPPA/UFSM 0035. A, left lateral view. B, dorsal view. Abbreviations: clppm, caudolateral process of the premaxilla; m, maxilla; mt, maxillar tooth; n, nasal; pm, premaxilla; pmt, premaxillar tooth; rvpn, rostroventral process of the nasal; sng, subnarial gap.

nasal is dorsoventrally flat and 16 mm broad at the point of maximal transverse extension. Its rostral portion slopes ventrally, so that the bone is gently inclined. Its dorsal surface is mostly smooth, but slightly excavated along the internasal suture. The nasal rests on the dorsal surface of the dorsal process of the maxilla, forming a laterally expanded bone shelf and the dorsal roof of the antorbital fenestra (Fig. 8A). The ventral edge of the shelf is lateromedially concave and projects further laterally than the maxilla, so that the nasal is also observed in palatal view. The caudolateral process envelops the rostral process of the lacrimal, covering a small portion of the latter in lateral view. The nasal contact with the prefrontal and frontal is obscured by the fragmentary condition of the caudal portion of the nasals. The tip of the rostroventral process of the right nasal is preserved, being laterally covered by the maxilla and resting on the dorsal surface of the caudolateral process of the premaxilla, forming the caudal margin of the external naris (Fig. 8).

Lacrimal

The right lacrimal is completely preserved (Fig. 8A), whereas part of the rostral process is missing in the left one. The ventral and dorsal portions of the lacrimal are strongly offset, with the dorsal portion projecting laterally. The lacrimal separates the antorbital fenestra from the orbit, its height corresponding to twothirds that of the fenestra. Its caudal margin forms an angle of ~45° with the caudal process of the maxilla. The rostral process is rostrocaudally longer (16 mm) than the ventral process (14 mm), folding over the caudodorsal part of the antorbital fenestra and forming a rostral notch that fits the nasal. At the point of its maximal transverse extension, the rostral process is 9.5 mm broad. This portion also corresponds to the broadest part of the preorbital portion of the skull. The lateral and medial edges of the rostral process expand ventrally, forming a slightly concave ventral surface or invagination. Part of the rostral and medial edges of the rostral process articulates with the nasal. The caudally concave caudomedial margin of the lacrimal receives the prefrontal, which extends ventrally along its medial margin.

The rostral and ventral processes of the lacrimal form a right angle. A lateral flange extends over the dorsal half of the ventral process (Fig. 8A). The dorsal portion of this flange merges rostrally with the ventral ridge of the rostral process. On the medial portion of the lacrimal, a marked ridge forms the caudal part of the antorbital fossa, corresponding to the rostral portion of the ventral process of the lacrimal. On the caudal surface of that process, the lacrimal foramen is visible (Fig. 9B), caudoventrally bordered by a shallow excavation. The contact with the jugal occurs at the level of the ventral margin of the orbit, where the ventral surface of the lacrimal overlaps the dorsal surface of the rostral tip of the jugal. The displaced condition of both lacrimals precludes the observation of a putative contact with the maxilla.

Prefrontal

The left prefrontal is nearly complete (Fig. 9), whereas the right one lacks the ventral process (Fig. 8A). This



Figure 7. Snout of the skull of CAPPA/UFSM 0035. A, right lateral view. B, left lateral view. C, medial view of the right maxilla. Abbreviations: af, antorbital fenestra; anf, antorbital fossa; cpm, caudal process of the maxilla; d, dentary; dpm, dorsal process of the maxilla; idp, interdental plate; j, jugal; l, lacrimal; mt, maxillary tooth; n, nasal; pl, palatine; pm, premaxilla; rdg, ridge; rpm, rostral process of the maxilla; sng, subnarial gap; sp, splenial.

bone has a concave caudal margin that forms the rostrodorsal part of the orbital rim. The prefrontal articulates with the nasal rostrally, the lacrimal rostrolaterally, and the caudal process expands somewhat to fit medially an excavation on the frontal. In dorsal view, the caudal process is leaf shaped, with its tip tapering to a point (Fig. 9A). The process is 20 mm long and restricted to the rostral half of the orbit. Its medial



Figure 8. Right antorbital region of the skull of CAPPA/UFSM 0035. A, lateral view. B, dorsal view. Abbreviations: af, antorbital fenestra; clpn, caudolateral process of the nasal; cpprf, caudal process of the prefrontal; en, external nares; f, frontal; j, jugal; l, lacrimal; m, maxilla; m, nasal; prf, prefrontal; prf, rpl, rostral process of the lacrimal; rvpn, rostroventral process of the nasal; vpl, ventral process of the lacrimal.

margin is straight, becoming gently convex rostrocaudally. In the caudolateral margin, a bony sheet connects the dorsal process to the ventral one (Fig. 9B). In addition, it covers the caudodorsal portion of the main body of the lacrimal. The ventral process of the prefrontal is narrow (~1.5 mm in width) and articulates with the lacrimal laterally.

Frontal

In this paired element, the rostral margin is fractured (Fig. 9A). The bone is longer (38 mm) than wide (17 mm in the caudal portion), and the caudal margin is slightly wider than the rostral one (10.5 mm). Their respective lateral projections give a concave aspect to the lateral margin of the frontal in dorsal/ventral view, where it forms the entire dorsal margin of the orbital rim. At the middle of the orbital rim, the lateral and the medial edges are slightly elevated in comparison with the surface between them. The lateral margin of the frontal is as not as dorsoventrally deep (i.e. 1 mm in height) as the medial margin (5.5 mm in height). The interfrontal suture is straight and occupies the entire medial margin of the bones (Fig. 8A). Rostrally, the frontal articulates with the nasal, and a V-shaped notch on the lateral region corresponds to the articulation with the prefrontal. On the dorsal surface of the caudolateral process, there is a sigmoid excavation for the articulation with the postorbital, which tapers medially. Mediocaudally, the frontal contacts the parietal via a well-marked interdigitating suture. On the lateral portion of the caudal part of the frontal, an 8-mm-broad depression corresponds to the rostral extension of the supratemporal fossa. This surface probably received the m. pseudotemporalis



Figure 9. Left orbital region of the skull of CAPPA/UFSM 0035. A, dorsal view. B, lateral view. Abbreviations: c, coronoid; cppo, caudal process of the postorbital; cpprf, caudal process of the prefrontal; cpsq, caudal process of the squamosal; dpqj, dorsal process of the quadratojugal; ec, ectopterygoid; f, frontal; j, jugal; l, lacrimal; lf, lacrimal foramen; ls, laterosphenoid; mpsq, medial process of the squamosal; p, parietal; popr, paraoccipital process; ppf, postparietal fenestra; prf, prefrontal; pw, parietal wing; q, quadrate; rlpp; rostrolateral process of the squamosal; so, supraoccipital; stf, supratemporal fossa; vpl, ventral process of the lacrimal; vppo, ventral process of the postorbital; vpprf, ventral process of the prefrontal; vpsq, ventral process of the squamosal.

superficialis (Button, Barrett & Rayfield, 2016), and its rostral margin forms a shallow rostral invagination. Although the frontal has an extensive participation in the supratemporal fossa, it is excluded from the internal supratemporal fenestra by the parietal-laterosphenoid contact.

Parietal

The specimen preserves both parietals, with the left one being better preserved (Fig. 9). The bone is 20 mm long, 14 mm wide at the rostral edge and 13 mm wide at the caudal edge. In dorsal/ventral view, the lateral margin of the parietal is concave and the medial is

straight. The interparietal suture indicates that the parietals are not fused, but there is no clear evidence of a foramen between them. The rostral margin of the parietal contacts the frontal via a serrated suture. The rostrolateral process articulates with the postorbital dorsally and with the laterosphenoid ventrally. The dorsal surface of the parietal possesses a medial depression bounded laterally by a low longitudinal ridge (Fig. 9A). This ridge delimits the medial margin of the supratemporal fossa, which housed the m. adductor mandibulae externus profundus (see Dilkes et al., 2012; Sereno, 2012). The parietal wings diverge from one another caudolaterally, forming an angle of ~60° with the caudomedial border of the supratemporal fossa. In this region, the parietal contacts the squamosal laterally, the supraoccipital rostromedially and the paroccipital process of the opisthotic caudomedially. In dorsal/ventral view, the rostral surface of the parietal wing is convex, whereas the caudal is concave; the latter probably related to the m. transversospinalis capitis (Snively & Russell, 2007). A large triangular-shaped postparietal fenestra occurs between the caudal margin of these wings and the rostral end of the supraoccipital (Fig. 9A).

Postorbital

The postorbital comprises a triradiate bone with rostromedial, ventral and caudal processes. The left postorbital is complete (Fig. 9B), whereas the right one lacks the caudal process. The rostromedial process articulates with the frontal medially, forming the caudodorsal portion of the orbital rim. The caudal half of the rostromedial process contacts the parietal and the laterosphenoid medially. In dorsal view, the process is sigmoid, with its tip tapering to a point. The caudal surface of the process forms the rostrolateral margin of the supratemporal fenestra. The ventral process is slightly displaced, but in vivo it would have been articulated with the jugal, forming part of the caudal margin of the orbital rim. The tip of the ventral process is pointed and directed rostroventrally. Part of the caudal margin of the ventral process forms the dorsalmost portion of the rostral margin of the laterotemporal fenestra. The rostral margin of the bone, between the rostromedial and ventral processes, bears a rostrally oriented orbital flange (Fig. 9B). It invades the caudal rim of the orbit and has a rough rostral edge. The caudal process is 11.5 mm long and slender in comparison with the other two processes of the bone. It becomes dorsoventrally narrower rostrocaudally, where it tapers to a point. The process fits into the lateral surface of the rostral process of the squamosal, almost reaching the caudodorsal corner of the laterotemporal fenestra. A faint longitudinal ridge extends on the lateral surface of the caudal process, and it could be related to the attachment of m. adductor mandibulae externus superficialis.

Squamosal

Only the ventral process of the right squamosal is preserved, whereas the left element is complete (Fig. 9B). The squamosal is composed of four distinct processes: rostral, medial, ventral and caudal. The rostral process is ~12 mm long, with a gently rostrocaudally convex medial surface that delimits the lateral margin of the supratemporal fenestra. Its ventral surface is straight and forms the dorsal margin of the laterotemporal fenestra. The lateral surface accommodates the caudal process of the postorbital in a V-shaped notch. A thin ridge rises from the caudal portion of the dorsal surface of the rostral process, folding medially. This leads to the medial process, which is 5 mm wide. The dorsal surface of this process receives the parietal wing.

The ventral process forms an angle of $\sim 45^{\circ}$ with the rostral process. It extends rostroventrally and tapers to a point. The caudal surface is concave in lateral view and articulates with the rostral surface of the quadrate. Its ventral tip contacts the dorsal tip of the quadratojugal, extending until the rostralmost portion of the lateral quadrate flange. The ventral process is rostrocaudally short and does not wrap the quadrate shaft medially. The caudal process is 6.75 mm long. It articulates against the quadrate ventrally and with the paroccipital process caudally. The process bears a caudal projection that extends 5 mm over the articulation with the quadrate. It is plate like and slightly laterally oriented, following the orientation of the paroccipital process. Together with the paroccipital process, this projection might have supported m. depressor mandibulae (Sereno, 2012).

Jugal

The left jugal is better preserved than the right one (Fig. 10), but both elements are fractured and displaced from their original position, as their ventral surfaces are visible in lateral view. The jugal is Y shaped, including three main processes. The rostral process is 22 mm long, contributes to the ventral margin of the orbit, and is subparalel to the caudal ramus of the maxilla. Both ventral and dorsal margins of the rostral process are parallel along almost their entire length, but it tapers rostrally. Its tip rests in a slot on the caudal portion of the maxilla and receives the ventral margin of the lacrimal dorsally. On the right side, the tip of the process contributes minimally to the caudoventral corner of the external antorbital fenestra. On the lateroventral surface of the rostral process, a longitudinal ridge marks the lateral margin of a longitudinal fossa. Sereno (2012) speculated that a putative homologous surface in Heterodontosaurus tucki could support the origin of the m. adductor mandibulae externus ventralis.

The dorsal process of the jugal extends dorsocaudally, forming an angle of 45° with the caudal process.



Figure 10. Jugal of CAPPA/UFSM 0035 in lateral view. Abbreviations: c, coronoid; cpj, caudal process of the jugal; dpj, dorsal process of the jugal; ec, ectopterygoid; l, lacrimal; rpj, rostral process of the jugal.

Its tip tapers to a point. The rostral margin articulates against the ventral process of the postorbital, whereas the caudal surface forms the ventral half of the rostral margin of the laterotemporal fenestra. The caudal process is poorly preserved in both elements. Nonetheless, it is possible to observe that they do not fork close to their rostral portion (Fig. 10), but a pedicel is present between the base and the caudal bifurcation of the caudal process.

Quadratojugal

Only the caudal portion of the right quadratojugal is preserved (Fig. 4), whereas for the left one part of the dorsal and cranial processes is preserved (Fig. 9B). The bone would exhibit the typical inverted L shape, but as the length of the processes is uncertain, this cannot be stated with certainty. The dorsal process articulates with the ventral part of the rostral surface of the quadrate, forming the ventrocaudal margin of the laterotemporal fenestra. The dorsal portion of the dorsal process is caudally concave in lateral view, and its tip contacts the ventral tip of the squamosal.

The rostral process seems to be longer (or at least subequal in length) and more robust than the dorsal process. Both processes form an almost right angle, tapering to a point at their tips. The articulation with the jugal is not well preserved, but the caudal portion of the quadratojugal is triangular in lateral view. Its lateral surface is convex, and the ventral margin is straight (Fig. 4). Indeed, the notch on the ventral margin of the caudalmost portion of the bone, present in *Eoraptor lunensis* (Sereno, Martínez & Alcober, 2013), is absent in CAPPA/UFSM 0035, as well as in the holotype of *B. schultzi*. The quadratojugal has a limited contribution to the craniomandibular joint, contacting only a restricted portion of the dorsolateral surface of the surangular.

Quadrate

Both guadrates are preserved in the specimen. The right element is broken into two pieces (Fig. 11), dorsal and ventral, whereas the left one lacks the condyles (Fig. 11A). In lateral view, the quadrate is arched (e.g. with convex cranial and concave caudal margins). The quadrate head is rounded, and it rests in a socket on the ventral surface of the squamosal (Fig. 9B). Ventral to that, the quadrate shaft bears two longitudinal bone flanges (Fig. 11A). The lateral one is rostrolaterally oriented, articulating dorsally with the ventral process of the squamosal and ventrally with the dorsal process of the quadratojugal. The ventral margin of the lateral flange connects smoothly onto the shaft, whereas that contact is more abrupt at the dorsal margin. There is no clear evidence of a quadrate foramen in the specimen. The other flange rises from the quadrate shaft (i.e. the pterygoid ramus). It is rostromedially directed, and its lateral surface has been considered the origin of the m. adductor mandibulae posterior (Button et al., 2016). There is a dorsoventrally oriented groove on the medial surface of the bone, between its shaft and the pterygoid ramus. Ventral to that, a horizontal shelf is visible, but fractured and incomplete in both elements.

The quadrate shaft is transversely expanded (9 mm in width) in its ventral portion, where both mandibular



Figure 11. Caudal portion of the skull of CAPPA/UFSM 0035. A, occipital view. B, dorsal view. Abbreviations: ar, articular; bo, basioccipital; bt, basal tubera; ex, exoccipital; fm, foramen magnum; frm, foramen; j, jugal; lcp, lateral condyle of the quadrate; mcq, medial condyle of the quadrate; nc, nuchal crest; neov, notch for the external occipital vein; p, parietal; po, postorbital; popr, paraocciptal process; ppf, postparietal fenestra; q, quadrate; qj, quadratojugal; rdg, ridge; sq, squamosal; stf, supratemporal fenestra; XII, foramen for hypoglossal nerve.

condyles are located (Fig. 11). The medial condyle exceeds the caudal expansion of the lateral and articulates with both articular and prearticular. Close to the contact with the lower jaw, the caudal surface of the bone bears a transverse protuberance, and a shallow groove divides the medial and lateral condyles. The latter is laterally covered by the quadratojugal and articulates ventrally with the articular and surangular.

Pterygoid

Both pterygoids are preserved, but only their palatal view is exposed (Fig. 12). The left pterygoid is almost complete. It is \sim 70 mm long, comprising more than one-half of the total skull length. Each element contacts its opposite medially via a caudomedial process in the caudal portion. Along the rostral length, the pterygoids are separated from one another by the

interperygoid vacuity, in which the caudal half of the parasphenoid is observable.

The rostral ramus of the pterygoid is long, reaching the rostral half of the antorbital fenestra. Laterally, the rostral ramus articulates with the palatine, but a small part of its lateral edge participates in the caudomedial margin of the postpalatine fenestra, precluding the contact between the palatine and ectopterygoid. The caudal portion of the rostral ramus forms a subtriangular lamina, whereas the rostral part becomes transversely narrower, with a marked ventral ridge forming its medial edge. This ridge extends along the entire



Figure 12. Ventral view of the palate of CAPPA/UFSM 0035. Abbreviations: bo, basioccipital; cmppt, caudomedial process of the pterygoid; cpr, cultriform process; d, dentary; ec, ectopterygoid; hy, hyoid; iptv, interpterygoid vacuity; lrpt, lateral ramus of the pterygoid; pbs, parabasisphenoid; pl, palatine; ppf, postpalatine fenestra; pra, prearticular; qrpt, quadrate ramus of the pterygoid; rdg, ridge; rrpt, rostral ramus of the pterygoid; t, tooth; v, vomer.

length of the rostral ramus. It is more conspicuous on the rostral half, where it meets the caudal part of the vomer. The ridge is wider in its caudal half, supporting a row of small palatal teeth. The ridge then turns laterally at its caudal part, extending along the lateral ramus, which forms a right angle with the rostral ramus. The lateral ramus is thicker dorsoventrally and extends laterally in the direction of the adductor fossa of the lower jaw. The quadrate ramus of the pterygoid projects caudally, forming a thin bony sheet with a concave lateral margin in palatal view. This structure articulates to the shelf on the medial surface of the quadrate. In palatal view, the basipterygoid process of the basisphenoid overlaps the quadrate ramus of the pterygoid, being overlapped by its caudal process, the latter simply corresponding to a caudal projection with a rounded margin.

Palatine

Both palatines are preserved in the specimen, with the right exposed in lateral (Fig. 4) and palatal views (Fig. 12), whereas the left is visible only in lateral view (Fig. 3A). The palatine is longer (31 mm) than wide (10 mm), with the medial margin of the rostral process, which is thin transversely, articulating against the caudal part of the vomer. In lateral view, the rostral portion of the palatine becomes shallower from the caudal to the rostral pointed tip. Its dorsal margin is straight, whereas the ventral is comparatively oblique. The caudal half of the palatine is dorsoventrally compressed and transversely broader than the rostral half. Its medial margin is longer than the lateral and lacks projections (i.e. peg-like structures). In palatal view, the pterygoid overlaps the thin medial lamina medially along its entire length. The lateral margin of the palatine is transversely flat, with a ventral lamina that articulates against the medial surfaces of the maxilla and the lacrimal. The caudolateral edge of the palatine forms the rostromedial margin of the postpalatine fenestra (Fig. 12), which is slightly shorter (19 mm in length) than the orbit.

Ectopterygoid

Both ectopterygoids are preserved (Figs 9, 12), but some parts are fractured and/or covered by rock matrix. The ectopterygoid rests on the dorsal surface of the transverse flange of pterygoid (Fig. 12) and connects the medial surface of the jugal to the palatal complex. The main body of the ectopterygoid is dorsoventrally compressed and longitudinally short, as observed in the preserved portion of the left element, which is 8 mm long. The lateral process is elongated, with the lateral extremity expanding caudally to contact the jugal. In ventral/dorsal view, the rostral margin of this process is convex and the caudal is concave. The bone lacks any ventral pneumatic recess, but a 9 mm dorsoventrally deep flange projects ventrally from the shaft of the lateral process. The flange is arched, with the concave margin facing medially. In addition, its rostral margin is convex, whereas the caudal is straight. The flange may articulate along the lateral margin of the pterygoid flange, as described by Sereno *et al.* (2013) for *E. lunensis* (PVSJ 512). However, both ectopterygoids are displaced from their original position, so the pterygoid–ectopterygoid suture is unclear.

Vomer

Only the caudal part of the right vomer is exposed (Figs 4, 12). It includes a transversely compressed lamina (~1 mm in width), which is longer than deep. The caudal end of that lamina rests in a groove bounded medially by the pterygoid and laterally by the palatine (Fig. 12). The caudal end of the bone extends until the middle of the antorbital fenestra and is caudodorsally oriented. Its caudal tip is slightly laterally oriented.

Supraoccipital

The supraoccipital is completely preserved (Fig. 11), with the following measurements: 12 mm long, 16 mm wide and 9 mm high. It contacts the parietal rostrally, the exoccipital-opisthotic ventrolaterally and, probably, the prootic rostroventrally. A low broad ridge on the medial portion of the cranial half of the bone corresponds to the nuchal crest. This structure seems to be related to the nuchal ligaments (Sereno & Novas, 1994). The tip of the rostral margin of the supraoccipital is almost straight.

The notch for the external occipital vein (= midcerebral vein; Sampson & Witmer, 2007) is visible on the dorsal surface of the supraoccipital, lateral to the nuchal crest, forming an angle of 45° with the longitudinal axis of the bone (Fig. 11). This indicates that the vein would exit the skull between the parietal and the supraoccipital. The dorsal surface of the supraoccipital is smooth immediately ventral to the notch. The caudal margin of the bone forms part of the dorsal margin of the foramen magnum, which is wider than deep (Fig. 11A). In addition, the caudal margin of the supraoccipital bears a medial notch, resulting in a concave outline (Fig. 11B).

Prootic

Both elements are preserved in the specimen, but the right one is badly fractured. The left is well preserved but covered by other bones, preventing a detailed observation (Fig. 13). The cranial half of the dorsal margin receives the laterosphenoid, whereas the caudal half contacts the parietal and the supraoccipital. Caudally, the bone articulates against the opisthotic. The ventral margin of the prootic rests on the dorsal surface of the parabasisphenoid. A caudoventrally oriented notch that corresponds to the opening for cranial nerve V (trigeminal) excavates the rostral margin of

the bone, dividing it into two regions. The dorsal one is dorsoventrally larger and tapers to a point rostrally, whereas the ventral is mostly covered by the laterosphenoid. There is a wide depression on the dorsal portion of the lateral surface, which is usually related to the tympanic recess (Fig. 13). The rostral portion of the bone, ventral to the notch for cranial nerve V, corresponds to the clinoid process. It bears an oblique crest extending at the lateral surface. The caudolateral portion of the prootic extends almost as caudally as the caudal margin of the quadrate.

Exoccipital–opisthotic

Usually, both elements are co-ossified in dinosaurs, forming the otoccipital (Sampson & Witmer, 2007), but this does not seem to be the case in the specimen described here, because a putative exocciptalopisthotic suture is visible on the left side of the braincase (Fig. 14A). It starts dorsally on the lateral corner of the foramen magnum and extends ventrally. The opisthotic articulates laterally against the caudoventral margin of the supraoccipital and forms the ventral half of the lateral margin of the foramen magnum. Part of the rostral surface of the bone contacts the prootic and may also contact the caudal surface of the parietal. More dorsally, the bone receives both the squamosal and the quadrate.

The paraoccipital process is caudolaterally directed (Fig. 11B), and its caudal surface bears a transverse rugose ridge, which extends from the medial portion of the bone and merges on its lateral half. The surface ventral to the medial portion of that ridge is gently concave and possibly related to the insertion of

m. iliocostalis capitis (Snively & Russell, 2007). A perforating foramen is present dorsal to the ridge, close to the dorsal margin of the bone. The ventral and dorsal margins of the paroccipital process are parallel along their length, so that the process does not expand distally (Fig. 11A). The distal tip of the process is rounded, with a rough texture, which resembles the area related to the insertion of m. longissimus capitis superficialis in some theropods (Snively & Russell, 2007). In caudal view, the ventral ramus of the opisthotic extends further laterally than the lateralmost edge of the exoccipital. On its dorsocaudal surface, the opisthotic bears a pair of depressions for the articulation of the proatlas.

The rostralmost of the two exits for the hypoglossal nerve (XII) is rostroventrally positioned relative to the caudal exit (Fig. 14A). The fenestra ovalis is separated from the more caudally located metotic foramen by the descending process of the opisthotic. However, a subvertical and crest-like strut separates the exits for cranial nerve XII from the metotic foramen, which is rostrally located relative to the exits. The exoccipitals do not articulate against one another on the floor of the endocranial cavity. Ventrally, the exoccipital rests on the dorsal surface of the basioccipital, forming the lateral and part of the ventral margins of the foramen magnum. In addition, the exoccipital condyle (Fig. 11B).

Basioccipital

The basioccipital is entirely preserved, measuring 14 mm in width. Its dorsal surface forms the floor of the endocranial cavity (Fig. 11B), and the caudal portion



Figure 13. Left temporal region of the skull of CAPPA/UFSM 0035 in dorsolateral view. Abbreviations: dtr, dorsal tympanic recess; ec, ectopterygoid; ls, laterosphenoid; p, parietal; po, postorbital; popr, paraoccipital process; pro, prootic; q, quadrate; qj, quadratojugal; so, supraoccipital; sq, squamosal.



Figure 14. Caudal region of the skull of CAPPA/UFSM 0035. A, left lateroventral view. B, ventral view. Abbreviations: atr, anterior tympanic recess; bo, basioccipital; bpp, basipterygoid process; bpr, basisphenoid recess; bt, basal tubera; cpr, cultriform process; dpo, descending process of the opisthotic; hy, hyoid; mf, metodic foramen; oc, occipital condyle; pi, pit; popr, paraoccipital process; pt, pterygoid; q, quadrate; ssr, subsellar recess; XII, foramen for hypoglossal nerve.

contributes to the ventral margin of the foramen magnum. Together with the exoccipitals, the basioccipital forms the occipital condyle, which is heart shaped in occipital view (Fig. 11A). The occipital condyle is transversely narrower (7.5 mm) than the foramen magnum (9.5 mm). Ventrally, a subcondylar recess extends from the proximal margin of the occipital condyle to the basioccipital component of the basal tubera (Fig. 14). As in some other sauropodomorphs (Bronzati & Rauhut, 2017), the basioccipital component of the basal tubera corresponds to multiple protuberances on the ventrolateral surface of the bone, caudal to its rostromedial projection. A pair of protuberances occurs on each side of the basioccipital, medially separated by a U-shaped gap in occipital view. The lateralmost protuberances are located immediately dorsolateral to the medial ones and are smaller. The rostromedial projection of the basioccipital extends between those two caudolateral projections of the parabasisphenoid, carrying the basisphenoidal component of the tubera. This gives a U/Vshaped aspect to the contact between these two bones in ventral view. Within the rostromedial projection, a circular blind pit excavates the medial portion of the ventral surface of the basioccipital (Fig. 12). Inside the cranial cavity, a medial ridge occurs on the rostral portion of the dorsal surface of the basioccipital.

Parabasisphenoid

This 43-mm-long bone is almost entirely preserved (Fig. 12). It articulates rostrally with the pterygoid

and caudally with the basioccipital. Its contact with the prootic is covered by matrix. Both the parasphenoid and the basisphenoid are co-ossified, as in other dinosaurs (Sampson & Witmer, 2007). A portion of the ventral surface of the bone, corresponding to the cultriform process of the basisphenoid, is visible in palatal view, within the interpterygoid vacuity. It is ~26 mm long and bears a ventral longitudinal groove, bounded by laminae on each side. The ventral surface of the process is set below the ventral surface of the occipital condyle.

On the caudal portion of the parabasisphenoid, two caudolateral projections, separated by the rostromedial process of the basicccipital, support the basisphenoidal component of the basal tubera. More rostrally, the basipterygoid processes project ventrolaterally. Together, these four projections give an X shape to the main body of the parabasisphenoid in ventral view (Fig. 14B). Central to these, a shallow depression corresponds to the basisphenoid recess (Witmer, 1997), which is not as developed as in neotheropods (Rauhut, 2004). The lateral surface of the braincase bears another 6-mm-long recess, which corresponds to the anterior tympanic recess. A well-developed (~6-mm-broad) crest extends transversely between the proximal portions of the basipterygoid processes, forming the separation between the basisphenoid recess caudally and the subsellar recess rostrally. The crest expands caudoventrally, forming a convex caudal surface. A circular foramen is present within the subsellar

recess. The basipterygoid processes are rounded and robust, and their caudal surface bears a rugose ridge. A faint, transversely oriented ridge divides their ventral surface.

Laterosphenoid

The specimen preserves both laterosphenoids. The bone is 10 mm long, corresponding to approximately one-third of the length of the supratemporal fenestra. Indeed, the laterosphenoid contributes to the medial half of the rostral margin of that fenestra, also forming almost its entire medial margin (Fig. 13). The lateral surface of the bone is concave in dorsal view, except for a gently convex mid-length projection. The tip of the rostrolateral process contacts the postorbital (Fig. 9A). At this point, the laterosphenoid is dorsoventrally narrower (~1.5 mm deep) than in its caudal part (9 mm deep at the maximal dorsoventral extension). The parietal fits on the straight dorsal surface of the bone. The prootic articulates against its caudoventral margin, where a notch is present, corresponding to the laterosphenoid portion of the trigeminal nerve (V) foramen (Fig. 7B). Rostrally, a groove extends from the notch.

Dentary

Both elements are well preserved, except for their caudalmost ends. They are not fused together in the symphysis, which occupies only their rostral margin. Indeed, the elements are preserved with the rostral portions separated from one another. The preserved portion of the right dentary is 65 mm long (Fig. 15A), whereas the left one is 61 mm long. At the level of the sixth tooth, the bone is ~6 mm in height. As such, the long and slender dentary comprises most of the lower jaw, and contact with other bones is restricted to the medial surface, where it meets the splenial more rostrally, the surangular on the caudodorsal portion, and the angular in the caudoventral portion. The tip of the dentary is rounded and lacks a ventral projection, but has a ventrally bent dorsal surface (Fig. 15A). This surface accommodates the first two teeth and, ventrally along its lateral surface, two large foramina are present. In addition, a set of neurovascular foramina pierces the lateral surface of the dentary along its length. These are located inside a groove that extends parallel to the long axis of the bone at its rostral part, being dorsally directed in the caudal portion.

Except for the longitudinal groove, the lateral surface of the dentary is convex dorsoventrally, lacking any other prominent feature. The bone lacks a dorsally expanded coronoid process at its caudal portion, where both ventral and dorsal margins extend parallel to one another. Also in its caudal half, the dentary gradually becomes transversely narrower, so it is quite thin and fragile in the caudal third. As a result, both caudal processes are fractured and incomplete. Nonetheless, a slot in the lateral surface of the angular suggests that the ventral process was ~ 8 mm long, with the caudal extremity exceeding the midlength of the mandibular fenestra. The splenial mostly covers the medial surface of the dentary, but the rostral part of the Meckelian groove is still exposed (Fig. 15B), extending along the ventral edge of that surface.

Surangular

The rostral portion of the right surangular is covered by matrix (Fig. 15C), whereas the left element lacks part of its caudal portion (Fig. 15D). This bone forms the dorsal portion of the caudal part of the lower jaw. At 52 mm in length, it measures less than half of the total length of the jaw (111.5 mm). The rostral process contacts the dentary laterally. It is ~17 mm long and becomes dorsoventrally narrow from the caudal to the rostral portion. The lateroventral part of the bone bears a slot that receives the angular. On its medial surface, the surangular articulates with the prearticular. In addition, the articular rests on the dorsal surface of the caudal end of the bone. As the surangular contributes to the jaw articulation, it also articulates to both the guadratojugal and the guadrate. The bone also contributes to the dorsal and caudal margins of the external mandibular fenestra. In lateral/medial view, the dorsal surface of the surangular, usually recognized as the insertion area for m. adductor mandibulae externus superficialis (e.g. Dilkes et al., 2012; Button et al., 2016), is flat to gently convex. Close to the dorsal edge, the lateral surface bears a rostrocaudally oriented ridge, which extends from the caudal portion of the rostral process and does not reach the retroarticular process. There is a small surangular foramen between the ridge and the glenoid. The surangular portion of the retroarticular process is elongated and tapers caudally.

Angular

Both elements are preserved but fractured. The right angular is 45 mm long, and the entire length of the bone is preserved (Fig. 15C), whereas the left one lacks its caudal part (Fig. 15D). The angular forms most of the ventral part of the caudal portion of the lower jaw. Its rostral portion articulates with the dentary laterally, where a slot excavates the bone. On the opposite side, the angular also bears a slot to receive the splenial. The contact with the surangular occurs dorsomedially in the caudal half of the angular, whereas the prearticular articulates along the caudal half of its medial surface, ventral to the contact with the surangular. The dorsal margin of the rostral half of the angular forms the ventral margin of the external mandibular fenestra, and its ventrolateral surface could be related to the insertion of m. pterygoideus ventralis (Button et al., 2016).



Figure 15. Lower jaws of CAPPA/UFSM 0035. A, details of the right dentary in lateral view. B, right dentary and splenial in medial view. C, caudal portion of the right lower jaw in lateral view. D, caudal portion of the left lower jaw in lateral view. Abbreviations: a, angular; ar, articular; d, dentary; emf, external mandibular fenestra; f, foramen; gl, glenoid; gr, groove; ic, intercoronoid; mg, Meckelian groove; myf, mylohyoid foramen; pra, prearticular; qj, quadratojugal; rgd, ridge; rpsa, rostral process of the surangular; sa, surangular; sp, splenial.

Splenial

Both elements are preserved in CAPPA/UFSM 0035. The splenial is elongated (55.5 mm) and transversely flat. Medially, it articulates with the dentary, covering the caudal part of the Meckelian groove (Fig. 15B). The dorsolateral surface receives the intercoronoid. The caudal part of the splenial articulates laterally with both the angular and the prearticular. There is no internal mandibular fenestra between the splenial and prearticular. The rostral portion of the bone is divided into two processes, with the ventral process extending more rostrally than the dorsal. A mylohyoid foramen is present on the rostral third of the splenial, located on its dorsoventral midpoint. Caudally, the splenial becomes dorsoventrally narrow, tapering to a point.

Coronoid

Only the dorsal portion of the left coronoid is exposed (Fig. 10), which is 13 mm long and 2 mm dorsoventrally deep. The bone rests against the dorsal margin of the prearticular. There is a gap between the rostral tip of the coronoid and the splenial. Its caudoventral process is overlapped by the prearticular. Rock matrix covers other bone contacts.

Intercoronoid

Only the right element is visible (Fig. 15B). The bone lies between the dorsomedial margin of the dentary and the dorsolateral margin of the splenial. The rostral tip extends until the rostral end of the rostroventral process of the right splenial. The caudal extension of the bone and its sutures are covered by the matrix.

The visible portion is rod like, slender, and $\leq 1 \text{ mm}$ in height. The lateral border of the bone contributes to the boundary of the alveolar margin of the dentary.

Prearticular

Both elements are preserved in CAPPA/UFSM 0035. The bone forms part of the medial portion of the caudal half of the lower jaw. Its total length is ~55 mm. The rostral portion of the prearticular is transversely narrow (Fig. 16A) and articulates with the coronoid dorsally and the splenial ventrally. This portion is connected to the caudal part of the bone by an elongated shaft that extends along the ventral portion of the lower jaw. The ventrolateral surface of the shaft bears a longitudinal ridge that bounds the slot for the articulation with the angular. A medial lip occurs on the dorsal margin of the caudal third of the bone (Fig. 16B), which probably received the insertion of m. pterygoideus dorsalis on its ventral surface (Button et al., 2016). In contrast, the dorsal surface of the lip contributes to the articular surface for the medial condule of the quadrate (Fig. 15A). In addition, the caudal third of the bone articulates with the surangular laterally and with the articular dorsally, forming the retroarticular process.

Articular

Only the right articular is preserved in CAPPA/UFSM 0035, but its caudomedial portion is missing (Fig. 11).

The bone forms the dorsal surface of the caudalmost portion of lower jaw and most of the jaw joint, receiving the quadrate condyles in two corresponding condylar surfaces, the medialmost of which is bounded by a caudal depression. In addition, the dorsal surface of the articular part of the retroarticular process receives the m. depressor mandibulae, contributing to the jaw abduction (Dilkes *et al.*, 2012). The surangular covers the lateral surface of the articular, whereas the prearticular fits in the ventral surface of the bone. The retroarticular process has a mostly caudal orientation, but its caudal tip is upturned (Fig. 15C). A large, 1.5-mm-long foramen, bounded ventrally by a medial ridge, is present on the medial surface of the articular (Fig. 16A).

Dentition

Two premaxillary teeth are preserved in the caudal half of the left premaxilla (Fig. 17A), corresponding to the two caudalmost of the four premaxillary teeth present in the holotype of *B. schultzi*. The apicobasal length of their crowns is \sim 3.5 mm, and the crown lacks a basal constriction. These dental elements are cylindrical along their length, but taper to a point at the tip. The main axes of the teeth are perpendicular to the premaxillary alveolar margin and oblique in relationship to that of the maxilla. Serrations are lacking in their mesial margins, whereas the distal margin of the



Figure 16. Caudal region of the lower jaw of CAPPA/UFSM 0035. A, medial view. B, ventral view. Abbreviations: a, angular; cppra, caudal portion of the prearticular; d, dentary; f, foramen; gl, glenoid; mlpra, medial lip of the prearticular; q, quadrate; rppra, rostral portion of the prearticular; sa, surangular; sp, splenial.



Figure 17. Teeth of CAPPA/UFSM 0035. A, last two premaxillary teeth in labial view. B, detail of the first preserved premaxillary tooth in labial view. C, maxillary teeth in labial view. D, labial view of a caudal maxillary tooth. E, labial view of a rostral maxillary tooth.

rostralmost tooth bears ~11 serrations per millimetre (Fig. 17B). These very small serrations bear convex tips and form right angles with the tooth margin.

The right maxilla bears ~24 tooth positions (Fig. 17C). They become gradually smaller caudally. For instance, the apicobasal lengths of the second and third preserved tooth crowns of the left maxilla are 4.5 and 5.0 mm, respectively, whereas the last two preserved teeth are slightly shorter than 2 mm. The maxillary tooth crowns are blade like, strongly caudally curved and labiolingually compressed. The mesial carina is convex, whereas the distal is concave to straight (Fig. 17D, E). Both mesial and distal margins bear fine serrations (approximately eight per millimetre) that form right angles to the tooth margin.

The number of dentary teeth cannot be estimated. The first three teeth lie on the dorsal, ventrally bent surface of the dentary, with the first tooth located slightly caudal to the rostral tip of the bone (Fig. 17C). Either matrix or other teeth generally cover the mesial margin of all crowns, so that the presence of serrations on this margin is uncertain. However, all teeth bear serrations on their distal margins. Teeth from the middle portion of the dentary are typically ziphodont, resembling the general morphology of the maxillary teeth (Fig. 7B).

Palatal dentition

There is a row of small teeth on the palatal process of the pterygoid (Fig. 18). The left process, better

preserved, bears at least 11 teeth aligned parasagittally, but the overlapped hyoid precludes a more precise quantification. The cross-sectional diameter and the apicobasal length of these teeth do not exceed 1 mm. The basal portion of the crowns is cylindrical, and their preserved portions lack serrations.

Hyoids

The hyoid apparatus comprises a pair of elongated bones preserved ventral to the palate, between the hemimandibles (Fig. 12). Both are broken, with their caudal portions missing. The preserved portion of the right element is 24 mm long, whereas the left one is 34 mm long. The hyoid shaft is rod like (2 mm broad), whereas the rostral portion is expanded (3 mm broad), forming a convex rostral margin. As preserved, their shafts are laterally bowed, although when completely preserved, the hyoid elements are generally sigmoid in other dinosaurs.

AXIAL SKELETON

Preserved axial elements include the cervical and trunk series, both complete and articulated, with sacral vertebrae and some ribs (Fig. 19). The tail was lost, possibly owing to erosion of the bearing rock. Nine cervical, 16 trunk and two primordial sacral vertebrae are preserved in the specimen.

Proatlas

Both proatlantal elements are preserved and articulate to one another rostrally (Fig. 20A). They are plate like (dorsoventrally compressed), and their total length is ~10 mm (Fig. 20B). Each element is bow like in dorsal view, with the concave margin facing medially. The cranial tip articulates against the occiput, covering part of the foramen magnum. The tips are medially directed, with each touching its opposite at a rostrocaudally straight margin. Each entire element forms a 2 mm dorsolateral wall over the foramen magnum. The midpoint of their lateral surfaces bears a ventrally facing protuberance (Fig. 20B). The caudal tip rests on the dorsal surface of the atlantal prezygapophysis, forming the roof of the neural canal. It tapers to a point and does not invade a large area between the dorsal margins of the atlantal neural arches.

Atlas

The atlas complex comprises the odontoid process (atlantal centrum), the intercentrum and paired neural arches (Fig. 20A, B). The odontoid process is coossified with the axis (Fig. 21A-E). Its dorsal surface is transversely concave, forming the floor of the neural canal. The cranial surface is smooth, 5 mm wide, and convex in dorsal/ventral views, articulating against the caudal surface of the occipital condyle. In addition, it is more cranially placed than the cranial margin of the axial intercentrum. On the lateral surface, an oblique sulcus is present, which starts cranially from the ventral margin of the odontoid process and reaches the caudodorsal border of that element (Fig. 21A). As a result, the ventral margin of the cranial portion of the odontoid process is transversely narrower than the dorsal margin. The caudal part of the process expands transversely towards the ventral portion, reaching 9.5 mm in width at the base.

The antlantal intercentrum is a small structure, 4.5 mm in length and 8 mm in width. It is subrectangular in dorsal/ventral views (Fig. 20C), U shaped in cranial/caudal views (Fig. 20D) and subtriangular in lateral view (Fig. 20B). The dorsal surface lacks a transverse ridge between its cranial and caudal portions, which are cranially and caudodorsally oriented, respectively. The cranial surface is larger and articulates with the ventral surface of



Figure 18. Palatal teeth of CAPPA/UFSM 0035. A, ventral view. B, ventrolateral view. Abbreviations: cpr, cultriform process; hy, hyoid; pt, pterygoid; t, tooth.



Figure 19. Axial skeleton of CAPPA/UFSM 0035. Abbreviations: ax, axis; c, cervical vertebra; cr, cervical rib; il, ilium; s, sacral vertebra; t, trunk vertebra; tr, trunk rib.

the occipital condyle. The caudal surface meets the sulcus on the cranioventral surface of the odontoid process. In addition, each dorsolateral margin bears an ovoid depression for the pedicle of the atlantal neural arch. The cranioventral surface of the bone is bumpy, contrasting with the opposite (caudoventral) surface, which is smooth, except for a U-shaped sulcus that receives the cranial projection of the ventral margin of the axial intercentrum. This sulcus divides the caudal surface into two regions; a dorsoventrally deeper and convex dorsal portion and a flat ventral portion (Fig. 20D).



Figure 20. Proatlas and atlas of CAPPA/UFSM 0035. A, dorsal view. B, lateral view. C, dorsal view of the atlantal intercentrum. D, caudal view of the atlantal intercentrum. Abbreviations: ai, atlantal intercentrum; ana, atlantal neural arch; poz, postzygapophysis; pro, proatlas; prz, prezygapophysis; s, sulcus.



Figure 21. Axis of CAPPA/UFSM 0035. A, photograph and interpretative drawing in left lateral view. B, photograph and interpretative drawing in right lateral view. C, photograph and interpretative drawing in dorsal view. D, photograph and interpretative drawing in cranial view. F, photograph and interpretative drawing in cranial view. Abbreviations: epi, epipophysis; hy, hyposphene; ic, axial intercentrum; nc, neural canal; ncs, neurocentral suture; ns, neural spine; odp, odontoid process; pa, parapophysis; poz, postzygapophysis; prz, prezygapophysis; slc, sulcus; vk, ventral keel.

Both atlantal neural arches are almost entirely preserved, except for the caudal part of the postzygapophyses (Fig. 20A). They form the roof and the lateral walls of the neural canal. Each prezygapophysis is short and receives the caudal tip of the proatlas. The cranial margin between the prezygapophyses is concave. More caudally, the medial margin of the atlantal neural arch, which has a flattened dorsal portion, contacts its counterpart. Although the caudal portions of the postzygapophyses are lacking, it is possible to recognize a lateral keel on the dorsal surface of this dorsoventrally compressed structure. In addition, the dorsal and the ventral surfaces of the postzygapophyses bear a longitudinal groove. The cranioventrally oriented pedicles (Fig. 20B) of the neural arch contact the intercentrum ventrally and the occipital condyle cranially. The lateral surface of the pedicle extends further ventrally than the medial, producing an oblique ventral surface in cranial or caudal views. In lateral view, its ventral margin is rounded.

Axis

The axis is composed of the intercentrum, centrum and neural arch and is fused to the atlantal centrum (Fig. 21). The intercentrum is fused to the centrum and, together, they form an 18-mm-long element. The intercentrum (Fig. 21A) is slightly shorter craniocaudally than the atlantal intercentrum, but transversely broader (9 mm in width). Its cranial surface bears two craniolaterally oriented articular facets that receive the atlantal intercentrum. The ventromedial margin of its cranial surface is cranially projected, and the caudolateral margin reaches the parapophysis of the axial centrum. The entire lateral surface of the intercentrum is rough.

The axial centrum is long, but shorter than the interzygapophyseal distance. Its cranial and caudal ends are subequal in height. The oval-shaped parapophysis is located on a rugose and raised subtriangular surface on the cranioventral portion of its lateral surface (Fig. 21A). There is no evident sign of a diapophysis above the parapophysis. At the dorsoventral level of the parapophysis, on the lateral surface, a series of small foramina pierce the centrum. Its ventral surface bears a 1-mm-thick (lateromedially) ventral keel. It is deeper than the concave ventral keel of the postaxial cervical vertebrae; in the axis, the keel is ventrally straight in lateral view.

The axial neural arch is almost entirely preserved. It rests on the centrum, with a clear suture between both structures. The cranial opening of the neural canal is subtriangular (Fig. 21E), whereas the caudal is squared (Fig. 21F). The prezygapophysis is located in the cranial portion of the neural arch, below the level of the postzygapophysis. Indeed, the ventral margin of the prezygapophysis almost reaches the level of the ventral border of the neural canal. The prezygapophysis faces laterodorsally and is reduced in comparison with those of the postaxial cervical vertebrae. Its cranial margin is rounded in lateral view and slightly exceeds the cranial margin of the neural canal. The postzygapophysis is located higher in the neural arch than the prezygapophysis and reaches as caudally as the caudal margin of the centrum. The medial margin of the postzygapophysis projects ventrally, contacting its opposite. This arrangement forms a vertically oriented hyposphene, which has a flat ventral surface (Fig. 21F). The epipophysis rises from the caudodorsal margin of the postzygapophysis (Fig. 21C). It tapers caudally to a point, resulting in a triangular shape in dorsal or ventral views. The caudal tip of the epipophysis projects more caudally than the caudal margin of the centrum. The epipophysis has the cranial part of its dorsal surface crossed by a ridge that extends from the caudal bifurcation of the neural spine, which forms a Y-shaped structure in dorsal view. Except in this caudal portion, the neural spine is transversely compressed. Its cranial margin forms a pointed cranial projection, which extends cranially beyond the prezygapophyses (Fig. 21B). The dorsal margin of the neural spine is similar in height along the entire length, but the cranialmost margin is downturned, resulting in a rounded lateral view.

Postaxial cervical vertebrae

Although the complete series is preserved (Fig. 22), some vertebrae are incomplete. Their length generally decreases from the first to the last element, both for the length of the centrum and for the interzygapophyseal space. Yet, some adjacent elements are equivalent in size. The centrum of the third cervical vertebra (first postaxial element) is 23 mm in length, whereas the ninth cervical centrum is 15 mm long. Except for the caudalmost cervical vertebra, which has a centrum of similar length to that of the axis, all the others possess a more elongated centrum. The height of the centra is almost constant along the series. Other anatomical aspects of cervical centra include their transverse compression and the presence of a midline ventral keel, which is, however, reduced in the middle cervical vertebrae (fifth and sixth). Yet, the centrum of these two elements presents a longitudinal accessory lamina on each lateroventral surface (Fig. 22A). Both articular facets of the cervical centra are concave. The cranial articulation of the third to seventh elements is elevated in comparison with those of the

eighth and ninth cervical vertebrae. This arrangement gives a parallelogram shape to those vertebrae. In contrast, the caudal cervical centra (eighth and ninth) are subrectangular. The lateral surface of all cervical centra is concave, lacking pleurocoels. However, there are piercing foramina on the lateral surface of some centra (e.g. six, eight and nine). The parapophysis is located on the cranial border of the lateral surface of the centrum in the entire cervical series. In the third, fourth and fifth vertebrae, the parapohypsis is triangular, whereas from the sixth to the ninth vertebrae it varies from circular to ovoid in shape. Indeed, there is a longitudinal ridge rising from the caudal edge of the parapophysis, which extends caudally and merges smoothly into the centrum in the cervical vertebrae with a triangular parapophysis. CAPPA/UFSM 0035 lacks the oval scars on the lateral surface of the caudal border of the cervical centra present in the holotype of P. protos (PVSJ 874; Martinez & Alcober, 2009), but there are several craniocaudally oriented striations on their entire lateral surface.

The cervical neural arches are longer than their respective centra, because the zygapophysis projects beyond the cranial and caudal margins of the latter elements. The neurocentral suture is present in only some of them (i.e. fourth, seventh, eighth and ninth). In dorsal view, the divergence of the pre- and postzygapophyses gives to the neural arch an X shape. In cranial view, the neural canal of the postaxial cervical vertebrae is subcircular. The cranial part of the neural canal of the third cervical vertebra is 4 mm in height and 4.5 mm in width. Below the prezygapophysis, the cranial face of the neural canal is laterally concave, lacking any recess on this region. The prezygapophyses are significantly more cranially expanded than that of the axis, but they decrease in size from the sixth to ninth cervical elements. The cranial tip of the prezygapophysis of the third cervical vertebra is 4.5 mm more cranially projected than the cranial margin of its respective centrum. In contrast, in the ninth cervical vertebra, that projection is only 1 mm. The articular facet of the prezygapophysis is smooth and oblique, facing dorsomedially. In contrast, the ventromedial surface of the cranialmost portion of the prezygapophysis is marked by a rough texture. At the dorsolateral surface of the prezygapophysis, a ridge extends from the cranial tip of that structure to merge on the surface lateral to the middle of the neural spine, producing a triangular cross-section to the base of the prezygapophysis. Unlike E. lunensis (Sereno et al., 2013), the specimen lacks an accessory prezygapophyeal process on the middle surface of the prezygapophysis.

The diapophysis of the cranial (third and fourth) cervical vertebrae does not project much laterally and is located near the parapophysis. However, it gradually increases in size and moves upwards from the more



Figure 22. Postaxial cervical vertebrae and ribs of CAPPA/UFSM 0035. A, right lateral view. B, left lateral view. C, dorsal view. D, ventral view. Abbreviations: al, accessory lamina; c, cervical vertebra; ccdl, caudal centrodiapophyseal lamina; cr, cervical rib; dp, diapophysis; e, eminence; epi, epipophysis; f, foramen; ncs, neurocentral suture; ns, neural spine; pa, parapophysis; podl, postzygodiapophyseal lamina; poz, postzygapophysis; prdl, postzygodiapophyseal lamina; rdg, ridge; vk, ventral keel.

cranial to the more caudal cervical vertebrae, remaining close to the parapophysis until the middle caudal (fifth to seventh) cervical elements. In contrast, in the eighth and ninth vertebrae, both articular facets are well separated. The diapophysis is triangular in dorsal view and has articular facets that face lateroventrally (Fig. 22C). It bears an unusual protuberance that first appears on the sixth vertebra as a gentle eminence on the lateral surface of the neural arch and gradually increases in size in more caudal elements. In the sixth vertebra, the eminence is caudal to the diapophysis, but in the seventh and subsequent vertebrae, it merges into that element (Fig. 22B). Martinez & Alcober (2009) reported a similar feature in *P. protos*. Dorsal to the articular facet of the diapophysis in the middle to caudal (sixth to ninth) vertebrae, there is a rough surface that might relate to the m. longissimus capitis superficialis. A rudimentary prezygodiapophyseal lamina is present in the seventh cervical vertebra, which is well developed in the eighth element. Both eighth and ninth vertebrae present centrodiapophyseal and postzygodiapophyseal laminae.

The postzygapophysis of the cervical vertebrae forms a ventrolaterally directed oval facet. Cranioventral to each postzygapophysis, a C-shaped sulcus excavates the caudal margin of the pedicle and receives the tip of the prezygapophysis of the following vertebra. The tip of the postzygapophysis is as caudally projected as the caudal margin of the centrum. However, the epipophysis exceeds that margin in the cranial (fourth) and middle (fifth to sixth) cervical vertebrae. In the fourth cervical vertebra, the epipohypsis is well developed caudally. Its caudal tip tapers to a point, so that the structure is triangular in dorsal view. In contrast, in the last three cervical elements, the epipophysis reduces significantly. Indeed, there is only a faint eminence over the postzygapophysis of the ninth cervical vertebra.

The neural spines of the third, fourth and fifth cervical vertebrae are not completely preserved. The remaining cervical neural spines are transversely compressed and longer than tall. The dorsal margin of the neural spine of the sixth, seventh and eighth cervical vertebrae is straight (Fig. 22A, B). In the ninth element, the cranial half of the neural spine is slightly directed dorsally. The dorsal portion of the spines is longer than the ventral, as its cranial margin projects more cranially than the base. In contrast, the caudal portion merges smoothly into the neural arch. The spines become craniocaudally shorter from the sixth (12 mm in length) to the ninth (8 mm in length) elements.

Trunk vertebrae

As with the cervical series, the trunk vertebrae are also articulated along the entire series, which contains

16 vertebrae. In order to protect the integrity of the first nine elements, their left side was kept imbedded in the matrix (Fig. 23). Almost all vertebrae are well preserved, except from the 11nth to the 15nth element, which have damaged neural arches (Fig. 24). The general morphology of the centra approaches that from other early dinosaurs, because they are spool shaped and amphicoelous. The neurocentral suture is visible along all trunk elements. The first one is 15 mm long and 9.5 mm high (measured at the cranial articular facet), whereas the last is approximately 18 mm long and 13 mm high. The length of the seventh element is subequal to that of the last one, and so are the remaining between them, whereas the more cranial centra are craniocaudally shorter (e.g. fifth = 17 mm; sixth = 17.5 mm). All cranial trunk centra (first to fifth elements) are longer than deep, with cranial or caudal articular facets that are circular and similar in height. Conversely, the more caudal elements become significantly wider. In general, trunk centra lack pneumatic openings, but there is a shallow depression on each lateral surface. In contrast, in cross-section the centra are extremely hollowed internally. Only the first trunk centrum has a longitudinal ventral keel, whereas the others have a smooth ventral surface that is concave in lateral view. The contact of the ventral margin of the cranial articular facet of the first trunk centrum with its ventral keel does not form a hypapophysis.

The parapophysis is located at least partly in the centrum in the first three trunk vertebrae (Fig. 23A). In the first element, the parapophysis is ovoid and restricted to the centrum. In the second, the neurocentral suture traverses the middle of the parapophysis, resulting in an hourglass-shaped articulation. Only the ventral part of the parapophysis contacts the centrum of the third trunk vertebra. In the fourth, the parapophysis is completely restricted to the neural arch and subcircular in shape. In the subsequent elements, the parapophysis gradually moves upwards, reaching the transverse process and contacting the diapophysis in the caudalmost (fourteenth to fifteenth) elements.

The neural arch is not as dorsoventrally deep (disregarding the neural spine) as the respective centrum, but longer instead (considering the pre- to postzygapophyseal distance). In the first three trunk elements, the subretangular transverse process is horizontal and laterally directed, whereas from the fourth to the eighth elements it is slightly dorsocaudally directed. The transverse process of the last trunk vertebra is, however, craniolaterally oriented. The articular facet of the diapophysis is concave and located in the tip of the transverse process of all vertebrae in which the structure is preserved. In contrast to the same articular facet of the cervical vertebrae, those from the trunk are drastically larger and do not face ventrally. The prezygapophysis in the first three elements is more



Figure 23. First nine trunk vertebrae of CAPPA/UFSM 0035. A, right lateral view. B, vertebrae six and seven in right lateral view. C, vertebrae two and three in right lateral view. Abbreviations: ccdl, centrodiapophyseal lamina; dp, diapophysis; ncs, neurocentral suture; ns, neural spine; pa, parapophysis; padl, parapodiapohyseal lamina; podl, postzygodiapophyseal; poz, postzygapophysis; prdl, prezygodiapophyseal lamina; prz, prezygapophysis; przpl, prezygoparapophyseal lamina; t, trunk vertebra; tr, trunk rib; vk, ventral keel.

dorsally directed than in the subsequent ones (i.e. from fourth to 16th). Hence, the prezygapophysis projects slightly cranial to the cranial margin of the respective centrum, whereas that limit is further surpassed from the third to tenth elements. The articular facet of the prezygapophysis is oblique (forming a 45° angle) to the neural spine in cranial view. On the medial surface of the prezygapophysis, a ventrally oriented facet is observed, forming an accessory joint, which corresponds to the hypantrum. Correspondingly, the hyposphene originates from a small ventral projection of the medial portion of the postzygapophysis. The tips of the preserved postzygapophyses reach the caudal margin of the respective centrum.

Several laminae are present on the lateral surface of the trunk vertebrae (Fig. 23B, C), and their arrangement changes along this series. A prezygodiapophyseal lamina is present from the first to the fifth element. In the sixth, this lamina connects the prezygapophysis with the parapophysis, forming a prezygoparapophyseal lamina. From the seventh vertebra onwards, this lamina is absent owing to the high placement of



Figure 24. Trunk vertebrae ten to 15 of CAPPA/UFSM 0035. A, right lateral view. B, left lateral view. C, ventral view. Abbreviations: f, foramen; hy, hyposphene; ncs, neurocentral suture; ns, neural spine; poz, postzygapophysis; prz, prezygapohypsis; t, trunk vertebra; tr, trunk rib.

the parapophysis. The paradiapophyseal lamina is restricted to the cranial (second and third) trunk vertebrae. All well-preserved vertebrae bear the caudal centrodiapophyseal lamina, in addition to the postzygodiapophyseal and spinopostzygapophyseal laminae. The cranial (from first to fifth) elements have three (cranial, middle and caudal) infradiapophyseal fossae bounded by the laminae. However, after the rearrangement of the parapophysis, the subsequent vertebrae lack the cranial infradiapophyseal fossa.

In the second trunk element, the neural spine is taller than long (Fig. 23C), whereas from middle to caudal (sixth to 16nth trunk vertebrae), the neural spine is subequal in those dimensions. For instance, the dorsal margin of the neural spine of the second trunk vertebra is 5 mm long and 6.5 mm high, whereas in the seventh it is respectively ~12 and 11 mm. The spines of the entire trunk series are transversely compressed (~0.5 mm broad in the tenth element) and subrectangular in lateral view. They lack any lateromedial expansion (spine tables) on their dorsal margins. The caudodorsal portion of the neural spine of the sixth element projects in a slightly caudal direction. The lateral surface close to the dorsal margin is rugose in the better-preserved neural spines.

Sacral vertebrae and ribs

There are two preserved vertebrae attached to the ilia, corresponding to the primordial sacral vertebrae (Fig. 25). The 16nth trunk vertebra rests between

the preacetabular iliac alae, but (although the tip is fractured) its transverse processes do not contact the ilium. Indeed, there is no sign of any contact area in the ilium. It resembles the condition of the putative first sacral vertebra of *E. lunensis* (PVSJ 512; Sereno *et al.*, 2013), which also does not contact the ilium.

The centra of the sacral vertebrae are not co-ossified and are subequal in length, at 18.5 mm (Fig. 25B). They are longer than tall, as the cranial height of the first element is 12 mm and the caudal height of the second element is 12.5 mm. The cranial articular facet of the first sacral centrum and the caudal articular facet of the second are concave. Their ventral surfaces are smooth, lacking keels or grooves. The transverse processes and ribs are partly hidden by both matrix and ilia, but it is possible to observe that the transverse processes are craniocaudally expanded. The height of the transverse process/rib of the first primordial sacral vertebra is inaccessible, but it forms, ventrally, an inclined platform. The transverse process/rib of the second element is 20.5 mm in height. In addition, the ventral margin of the structure reaches the



Figure 25. Sacrum of CAPPA/UFSM 0035. A, photograph and interpretative drawing in dorsal view. B, photograph and interpretative drawing in ventral view. Abbreviations: bf, brevis fossa; bs, brevis shelf; ib, iliac blade; ip, ichiadic peduncle; mb, medial blade; paa, postacetabular ala; pp, pubic peduncle; praa, preacetabular ala; ptb, protuberance; s, sacral vertebra; sac, supra-acetabular crest; t, trunk vertebra.

level of the ventral margin of its respective centrum, whereas in the first sacral vertebra the ventral margin of the transverse process/rib is slightly dorsal to the ventral margin of its centrum. The transverse process/ rib of the first sacral vertebra does not contact the cranial portion of the transverse process/rib of the second element dorsally (Fig. 25A). The dorsal portion of the transverse process/rib of the second sacral vertebra is caudolaterally directed and rests on the dorsal surface of the medially deflected ventral margin of the postacetabular ala of the ilium. However, the transverse process/rib does not reach the caudal end of that structure. That area probably hosts the contact of the additional caudosacral vertebra. From that point, the transverse process/rib extends cranioventrally and continues cranially as a ventral horizontal shelf, which contacts the ventral portion of the transverse process/rib of the previous vertebra. The neural spine of the first primordial sacral vertebra is almost entirely preserved. It is transversely compressed, following the shape of the trunk series spines. In addition, spine tables are absent on the dorsal end of the neural spines. Only the basal portion of the spine of the second element is preserved.

Cervical ribs

Only the left side has preserved elements, probably owing to taphonomic processes. Except for the rib of the ninth cervical vertebra, all other preserved elements are articulated with their respective vertebrae. In addition, there is no evidence of fusion between them. The ribs are generally tetraradiate, because they are formed by three processes (capitulum, tuberculum and spinous) and by a slender shaft. The capitulum is medially oriented and articulates to the parapophysis. The tuberculum rests on the diapophysis, whereas the shaft of the previous rib lies close to the medial surface of the spinous process. Both the tuberculum and the capitulum of the rib of the third cervical vertebra are short, and the spinous process is also poorly developed (Fig. 26A). The shaft is broken, but part of it reaches the middle of the centrum of the fourth cervical vertebra. Therefore, the shaft is ≥ 30 mm in length.

The rib of fourth cervical vertebra bears more developed processes than the previous one (Fig. 26A). The total length of the preserved portion is 27.5 mm. The spinous process is long (4.5 mm in length), with its pointed tip exceeding cranially the caudal margin of the third cervical centrum. The slender, rod-like shaft follows the craniocaudal orientation of the previous rib, but is partly broken, so that its total length cannot be confirmed. The fifth cervical vertebra does not have its associated rib preserved. The rib of the sixth cervical element is more robust than that of the third one, but their tuberculi are similar in size (Fig. 26B). The preserved portion is 35.5 mm long. The spinous process is longer (5.5 mm) than the previous one and slightly curved dorsally. The preserved portion of the shaft extends along the ventral surface of the rib associated with the seventh cervical element and reaches its midlength (Fig. 26C). The subsequent cervical rib lacks, almost entirely, its shaft. Its morphology resembles that of the previous elements, but the spinous process is 8 mm in length.

The rib of the ninth cervical vertebra is almost completely preserved (Fig. 26D). It is 51 mm long, with the tuberculum more developed than those from the remaining cervical ribs, but smaller than the capitulum. The medial surface between both articulations is concave, and a spinous process is absent, with no indication that this could have been broken. The shaft is about three times longer than its respective centrum. In contrast to the slender and straight shaft of the previous ribs, this is more robust and curved ventrally along its length. In its medial surface, a shallow sulcus extends along the entire length of the shaft.

Trunk ribs

Trunk ribs are preserved on both sides. The left ribs are articulated with their respective vertebrae, whereas those from the right side are disarticulated. No trunk rib is entirely preserved, so their total length is unknown. The first trunk rib (Fig. 27) is longer and more robust than the last cervical one, and its capitulum is longer (8 mm) than the tuberculum (3.5 mm). There is a gap separating both processes in the cranial (visible in the first two trunk ribs) elements, but it reduces in size along with the upward displacement of the parapophysis throughout the trunk series. Unlike the cervical ribs, the elements from the trunk series completely lack a spinous process. Also, whereas the shafts of the cervical ribs are almost entirely directed caudally, they are more ventrally directed in the trunk series. In addition, the cranial surface of the trunk ribs is transversely convex, whereas a longitudinal groove extending from the region between the tuberculum and capitulum excavates their caudal surface.

PECTORAL GIRDLE AND FORELIMB

The pectoral girdle and forelimb elements were found disarticulated in the field, but closely associated with the specimen. Only the left side has preserved elements, including a partial scapula, coracoid and humerus (Fig. 28). The scapula lacks the cranial part of its basal portion, including the acromion and the distal end of the blade. Only the caudal half of the coracoid is preserved. The lateral half of the proximal portion of the humerus is preserved. Despite their incompleteness, these bones have well-preserved surfaces.

Scapula

The scapula is lateromedially flattened and laterally arched in cranial/caudal views (Fig. 28C, D). As



Figure 26. Cervical ribs of CAPPA/UFSM 0035. A, ribs associated with the cervical vertebrae three and four in left lateral view. B, ribs associated with the cervical vertebrae six and seven in left lateral view. C, ribs associated with the cervical vertebrae six and seven in ventral view. D, rib associated with ninth cervical vertebra in medial view. Abbreviations: c, cervical vertebra; ca, capitulum; cr, cervical rib; sh, shaft; slc, sulcus; sp, spinous process; tu, tuberculum.



Figure 27. First trunk rib of CAPPA/UFSM 0035 in lateral view. Abbreviations: ca, capitulum; sh, shaft; tu, tuberculum.

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Figure 28. Left pectoral girdle and forelimb of CAPPA/UFSM 0035. A, photograph and interpretative drawing in lateral view. B, photograph and interpretative drawing in medial view. C, photograph and interpretative drawing in caudal view. Abbreviations: c, coracoid; cf, coracoid foramen; gl, glenoid; gr, groove; h, humerus; lf, lateral fossa; li, lip; ra, rugose area; rdg, ridge; scp, scapula; sgb, subglenoid buttress; str, striations.

indicated by the preserved portion of its cranial margin, the blade expands gradually from the neck. The thinnest part is 10 mm in craniocaudal breadth, reaching 12 mm more distally. The lateral surface of the scapular blade is mainly smooth (Fig. 28A), but there are some longitudinal scars generally associated with the m. deltoideus scapularis (e.g. Langer, França & Gabriel, 2007; Remes, 2008). In contrast to the lateral surface, the medial surface bears a long longitudinal ridge located in the caudal half of the craniocaudal breadth (Fig. 28B). Caudal to the ridge, there is a parallel longitudinal groove for either m. serratus superficialis or m. scapulohumeralis posterior (Remes, 2008; Burch, 2014). Cranial to the ridge, a gentle depression is occupied by longitudinal muscle scars from the m. scapularis. Towards the scapular body, the cranial margin of the scapular blade starts to expand more distally than the caudal, but the cranial expansion is more gradual. This cranial expansion culminates in the acromion, not preserved in the specimen.

The body of the scapula rests on the dorsal surface of the coracoid, and the bones are clearly unfused. The preserved portion of the coracoid articulation forms a straight ventral margin. The lateral and medial surfaces near the coracoid articulation are densely marked with dorsoventrally oriented striations, a pattern also present in the adjacent portion of the coracoid. The cranial half of the scapular body is craniomedially compressed and bears a wide fossa on its lateral surface for the m. supracoracoideus (Fig. 28A). In contrast, the caudal half is transversely broad, forming the scapular part of the glenoid. The scapular body is laterally depressed immediately cranial to the ventral margin of the glenoid; therefore, the dorsal part of the scapular glenoid expands more laterally than the ventral, forming a lip (Fig. 26D). Together with its coracoid portion, this forms a C-shaped glenoid, with the convexity facing slightly lateral. The scapular part of the glenoid is flat, except for a shallow groove that extends from the dorsal to the lateroventral margin. A rugose area (6 mm in length) for the attachment of the m. triceps brachii scapularis is present on the lateral surface of the scapular body neighbouring the glenoid (Fig. 28D), where a pit is present in Saturnalia tupiniquim (Langer et al., 2007).

Coracoid

The dorsal half of the preserved portion of the coracoid is dorsoventrally oriented and thicker than the ventral half (Fig. 28C). The maximal transverse breadth (7 mm) occurs at the articulation with the scapula. The caudal tip of the coracoid is more caudally placed than the maximal caudal extension of the scapula, but they have similar participation in the glenoid (Fig. 28B). The caudal border of the glenoid forms a gently subglenoid buttress, ventral to which there is a lateromedially oriented groove that does not reach the medial margin of the coracoid; hence, no marked notch ventral to the glenoid is observed in medial view. The caudal half of the coracoid foramen is preserved and visible in lateral view, close to the dorsal margin of the coracoid (Fig. 28A). The contact of the dorsal portion of the coracoid with its plate-like (2-mm-thick) ventral portion is marked by a wide fossa in medial view, because the ventral part is medially inflected. This fossa is probably related to the m. subcoracoideus (Remes, 2008). This arrangement makes the medial surface of the coracoid markedly concave, with the opposite configuration occurring on the lateral surface.

Humerus

The recovered part of the humerus is 32 mm long (Fig. 29). The proximal end expands craniocaudally when compared with the preserved part of the shaft. Its caudal margin expands caudally and forms a convex edge in proximal view (Fig. 29D), which is more evident in its central part, where the projection forms a lip. On the caudal surface of the humerus, this lip probably separated the proximal portions of the insertions of m. scapulohumeralis cranialis and m. scapulohumeralis caudalis (Remes, 2008). In addition, the proximal portion of the lateral surface



Figure 29. Left humerus of CAPPA/UFSM 0035. A, cranial view. B, caudal view. C, lateral view. D, dorsal view. Abbreviations: dpc, deltopectoral crest; li, lip.

of the humerus is rugose, which could be associated with m. scapulohumeralis cranialis and m. deltoideus scapularis.

The cranial surface of the proximal portion of the humerus is slightly concave and striated at the proximalmost region, which is generally associated with m. coracobranchialis (e.g. Langer et al., 2007; Remes, 2008; Burch, 2014). Only a proximal portion of the deltopectoral crest is preserved (Fig. 29A-C). The cranial folding of the proximal articular surface of the humerus forms the proximal portion of the crest, which expands craniolaterally and is lateromedially compressed. The transition from the humeral head to the crest is smooth (Fig. 29C). The proximal half of the humerus also expands medially, as observable on its concave medial margin. The medial portion that includes the internal tuberosity is not preserved in the specimen. The distalmost preserved portion probably corresponds to part of the attachment area of m. triceps brachii medialis.

PELVIC GIRDLE AND HINDLIMB

Both pelvic girdle and hindlimb elements were preserved in articulation on both sides, but the right elements are more complete. Both ilia are complete, but some portions are fractured and displaced. A portion of the iliac peduncle of the left pubis is preserved. The right element is better preserved, but also composed of the proximal part only. The ischia are represented by only one fragment corresponding to the iliac peduncle of the right element. The right femur is almost completely preserved, whereas the left is represented by only a fragment of the proximal portion and part of the shaft. The left tibia is unknown, but a partial right tibia was recovered, although poorly preserved and lacking its distal end. A partial right fibula is also preserved, the distal portion of which was lost. Right pedal digits III and IV are partly preserved. The ungual phalanx of digit III is incomplete. In contrast, digit IV preserves the ungual, but lacks phalanx 1 and part of phalanx 2.

Ilium

The ilium is 76 mm in total length (Figs 30, 31). The acetabulum is 16 mm deep and the upper iliac blade 30 mm deep. The entire dorsal margin of the blade is covered with muscle insertion striations (Fig. 30). The lateral surface of the cranial half of the blade is concave, probably corresponding to the attachment area of m. iliofemoralis. In lateral view, the dorsal margin of the iliac blade is nearly straight, but the cranial tip folds down, forming the rounded dorsocranial margin of the preacetabular ala. The cranioventral surface of the preacetabular ala is also rounded. The whole structure is short, because its cranial tip does not reach

the cranial margin of the pubic peduncle. The transition from the preacetabular ala to the pubic peduncle is concave in lateral view, although the medial surface is gently excavated for the attachment of the m. puboischiofemoralis 1.

The postacetabular ala is longer than the preacetabular and tapers caudally. On the lateral surface of its caudal end, a rugose protuberance (subtriangular and 12 mm long) is present in the left ilium (Fig. 30B). The homologous surface of the opposite bone is densely marked by muscle scars (Fig. 30A), but no similar protuberance is seen. This might be related to recent weathering, given that this portion was exposed in the outcrop when the specimen was discovered. In any case, this protuberance could be related to either m. flexor tibialis externus or m. iliofibularis. The brevis shelf expands lateroventrally and does not merge cranially with the supra-acetabular crest. Laterodorsally, the shelf set the limits of the brevis fossa, whereas its medial border is set by the medially deflected ventral margin of the postacetabular ala, forming the point of attachment to the m. caudofemoralis brevis. The medial blade is ~9 mm in width at its widest transverse point, whereas the brevis shelf is ~7.5 mm, resulting in an asymmetrical brevis fossa in caudal view. The arrangement of these two blades, associated with the dorsal iliac blade, forms an inverted Y in caudal view (Fig. 31B).

The supra-acetabular crest forms the roof of the acetabulum. It is lateroventrally oriented and reaches its maximal lateromedial extension above the centre of the acetabulum. The crest extends along the pubic peduncle, merging cranially with the iliac surface slightly before (4 mm) the distal margin of the peduncle. The lateral margin of the supra-acetabular crest is convex when observed in dorsal or ventral views. The acetabulum is craniocaudally longer (26 mm) than dorsoventrally deep (13 mm) and has a semilunate shape in ventral view (Fig. 25B). A transversely compressed bone extension that corresponds to the acetabular wall connects the iliac and pubic peduncles, closing the acetabulum medially. It extends caudally from the medial surface of the pubic peduncle and reaches the cranial margin of the ischiatic peduncle medially. The ventral margin of the wall is almost straight, although there is a gentle concavity near the cranial margin, close to the pubic peduncle.

The pubic peduncle is cranioventrally oriented and forms the cranialmost tip of the ilium. In cranial view (Fig. 31A), it is almost as high as broad. It bears two distinctly oriented surfaces for articulation with the pubis. One is cranially oriented and bears a central depression, whereas the other is ventrally oriented and C shaped in ventral view. Those surfaces are separated by a cranioventrally directed convex protuberance that rests in a



Figure 30. Sacrum of CAPPA/UFSM 0035. A, photograph and interpretative drawing in right lateral view. B, photograph and interpretative drawing in left lateral view. Abbreviations: at, antitrochanter; bs, brevis shelft; ib, iliac blade; ip, ischiatic peduncle; mw, medial wall; paa, postacetabular ala; pp, pubic peduncle; praa, preacetabular ala; ptb, protuberance; s, sacral vertebra; sac, supra-acetabular crest; t, trunk vertebra.

depression on the iliac articulation of the pubis. The dorsal surface of the pubic peduncle is lateromedially rounded and lacks crests or ridges. The lateral surface is also rounded, whereas the medial is flat. The ischiatic peduncle projects ventrocaudally. It is ovoid in crosssection, with a ventrocaudally convex articular surface. The cranioventral surface of the peduncle is convex, corresponding to the antitrochanter.

Pubis

The pubis (Fig. 32) is cranioventrally projected from the acetabulum. In proximal view, its iliac articulation is ovoid (Fig. 32D), with a 20 mm long axis and 9 mm transverse axis. It is formed by two main surfaces that form an angle of ~110° to one another. In addition, a bony wall bounds the medial margin of the articulation, resulting in a transversely concave articular surface. The preserved lateral surface of the pubis is covered by muscle scars and has a protuberance related to the m. ambiens (Fig. 32B). The obturator process expands from the medioventral surface of the pubis, in the dorsal portion of which a foramen pierces the bone (Fig. 32C). The pubic shaft is more craniocaudally flattened in its medial portion, where it forms the medial lamina. This starts proximally as a medioventrally expanding lamina and becomes limited to the medial surface along the preserved remnant of the bone, becoming progressively more expanded distally (Fig. 32A).

Ischium

The iliac peduncle is ovoid in proximal view (Fig. 33C), with the medial margin almost straight and the lateral margin convex. The preserved portion is ~20 mm in dorsoventral height and is 11 mm transversely. The proximal articulation is divided into dorsal and lateroventral surfaces. The former is concave, meets the ischial peduncle of the ilium, and is laterally bounded by a bump. Lateroventrally, the antitrochanteric surface is ventrally descending, with the medial margin more expanded than the lateral. Yet, its lateral margin also shows a slight expansion, forming the acetabular margin and resulting in a lateral ridge (Fig. 33A). A thin bone wall expands ventrally and forms the medioventral edge of the antitrochanter (Fig. 33B). This indicates the medial closure of the concavity between the iliac and pubic peduncles.



Figure 31. Sacrum of CAPPA/UFSM 0035. A, photograph and interpretative drawing in cranial view. B, photograph and interpretative drawing in caudal view. Abbreviations: bf, brevis fossa; bs, brevis shelf; ip, ischiatic peduncle; mb, medial blade; nc, neural canal; pp, pubic peduncle; praa, preacetabular ala; s, sacral vertebra; sac, supra-acetabular crest; t, trunk vertebra; tp, transverse process.

Femur

The left femur is 136 mm long (Fig. 34), with the long axes of the proximal and distal ends measuring, respectively, 24 and 22 mm. The femoral head is craniomedially directed in proximal view, and the shaft is sigmoid in cranial/caudal and lateral/medial views. A straight, shallow groove extends along the proximal surface (Fig. 35A), from the level of the caudomedial tuber to the craniolateral tuber. The proximal surface is gently convex in caudolateral/craniomedial views. The craniolateral tuber is poorly developed and distally connected to a descendant ridge (craniomedial crest of Bittencourt & Kellner, 2009) that reaches the proximal tip of the cranial trochanter. The craniomedial tuber is rounded and separated from the caudomedial tuber by the sulcus for the ligamentum capitis femoris. Although both tuberi are equivalent in size, the craniomedial is more expanded distally. Lateral to the caudomedial tuber, a distally descended surface corresponds to the facies articularis antitrochanterica.



Figure 32. Right publis of CAPPA/UFSM 0035. A, cranial view. B, lateral view. C, medial view. D, proximal view. Abbreviations: ap, ambiens process; bw, bone wall; f, foramen; ml, medial lamina; opb, obturator process.

The femoral head bears several muscle and soft tissue scars (Fig. 35C). Between the craniomedial crest and the dorsolateral trochanter, a rounded bone protuberance is present, which is possibly equivalent to a scar found in some individuals of Asilisaurus kongwe (NMT RB159, NMT RB216, NMT RB221; Griffin & Nesbitt, 2016) and Silesaurus opolensis (ZPAL AbIII/361/21, ZPAL AbIII/411/4R; Piechowski, Tałanda & Dzik, 2014). The cranially convex dorsolateral trochanter is protuberant, but merges smoothly to the femoral shaft proximally, completely disappearing at the ventral surface of the femoral head. Some dorsolateral trochanter scars reach the caudal portion of the bone, at the level of the trochanteric shelf (Fig. 35D). The cranial trochanter is knob like and bears an extremely striated surface (Fig. 35C). The proximal tip is distal to the tip of the dorsolateral trochanter and separated from the femoral shaft by a cleft. However, the cleft possibly resulted from taphonomic processes, which is suggested by the presence of a fracture between the dorsal tip of the trochanter and the femoral shaft. The distal portion of the cranial trochanter is associated with a well-developed trochanteric shelf, which is also marked by a striated surface and reaches the caudolateral margin of the femoral shaft. The caudolateral portion of the trochanteric shelf extends distally, reaching the level of the proximal tip of the fourth trochanter. At the same level of the trochanteric shelf, the medial surface of the femoral head bears striations that correspond to muscle insertions.

The fourth trochanter is located at the caudomedial surface of the proximal half of femoral shaft (Fig. 34C). It corresponds to a large (20 mm) proximodistally oriented crest, densely covered by muscle scars. The proximal portion of the trochanter merges with the shaft smoothly, whereas the distal forms a more acute angle, so that the structure has an asymmetrical shape. The lateral surface of the fourth trochanter possesses a longitudinal rugose margin probably related to the m. caudofemoralis brevis. In contrast, the medial surface bears a concavity with a rough surface (Fig. 34D), which extends onto the femoral shaft. A faint ridge bounds the distal margin of this concavity, and the entire region has been suggested as an insertion point for the m. caudofemoralis longus (Langer, 2003; Grillo & Azevedo, 2011; Müller et al., 2016). Distal to the fourth trochanter, the femoral shaft is ovoid in crosssection. In addition, two intermuscular lines extend longitudinally along the shaft. The cranial intermuscular line extends from the distal end of the cranial trochanter to the distal quarter of the bone (Fig. 34A). The proximal portion of the caudolateral intermuscular line rises approximately on the middle point of the shaft and extends distally until the distal quarter of the bone (Fig. 34C). The femoral shaft expands gradually from its middle point to the distal margin.

The cranial surface of the distal portion of the femur is strongly marked by longitudinal muscle scars, mostly grouped densely in the craniomedial margin (Fig. 34A). Muscle scars extend to the craniolateral surface, but no concavity or depression, as found in *Herrerasaurus ischigualastensis* (PVS J373; Novas, 1994), is present in that area. The distal surface of the femur bears three condyles (Fig. 35B). The medial one is subequal in size to the crista tibiofibularis, and both are caudally separated by a craniocaudally broad (6.5 mm), but proximodistally short (13 mm) popliteal fossa. The lateral condyle is ventrally larger than the crista tibiofibularis, and both are separated distally by a groove. The cranial edge of the distal femoral end is convex in distal view.

Tibia

The preserved length of the partial tibia (Fig. 36) is 109 mm. Its proximal end is craniocaudally expanded (~33 mm long) and subtriangular in proximal view (Fig. 36D), with a slightly convex proximal surface in lateral or medial view. On the cranial margin of the proximal end, there is a craniolaterally arched cnemial crest, which projects proximally relative to the caudal edge of the proximal end of the bone. Both cranial and lateral margins of the crest are rounded in proximal view. However, its caudomedial portion is separated from the main body of the tibia by a concavity, which forms a depression in proximal view. Also in that view, the caudal continuation of the medial margin is convex. The lateral margin bears the fibular (or lateral) condyle (Fig. 36A), which is located in the middle of its caudal half. The proximal part of this structure is missing, but it is possible to observe that it is as laterally expanded as the cnemial crest. The medial condyle is subequal in size relative to the lateral condyle, but it is more caudally located, forming the caudomedial edge of the proximal end of the tibia.

The transition from the proximal end to the tibial shaft is relatively smooth, with the caudal margin narrowing distally, slightly more abruptly (in lateral/ medial views) than the cranial. A craniocaudally oriented striated zone occurs on the medial surface of the proximal part of the tibia (Fig. 36B), probably related to m. gastrocnemius medialis. On the lateral surface of the proximal portion, rising from the distal edge of the fibular condyle, a proximodistally oriented and rugose fibular crest is present, which is sigmoid in lateral view and ~21 mm long. Probably, this crest received ligamentum tibiofibularis (Langer, 2003). The tibial shaft is almost equal in width (craniocaudal breadth of ~10 mm) along



Figure 33. Right ischium of CAPPA/UFSM 0035. A, lateral view. B, medial view. C, proxiaml view. Abbreviations: ats, ati-trochanteric surface; bmp, bump; bw, bone wall; lrdg, lateral ridge.





Figure 35. Right femur of CAPPA/UFSM 0035. A, proximal view. B, distal view. C, proximal portion in lateral view. D, proximal portion in medial view. Abbreviations: cmc, craniomedial crest; cmt, caudomedial tuber; crlt, craniolateral tuber; crmt, craniomedial tuber; ct, cranial trochanter; ctf, crista tibiofibularis; dg, distal groove; dlt, dorsolateral trochanter; faa, facies articularis antitrochanterica; lc, lateral condyle; mc, medial condyle; pg, proximal groove; ptrb, protuberance; slcf, sulcus for ligamentum capitis femoris; ts, trochanteric shelf.

its length. The preserved portion is proximodistally straight and subcircular in cross-section.

Fibula

The fibula (Fig. 37) is gracile and possesses a straight shaft. It is 121 mm long as preserved. The proximal portion is craniocaudally expanded (with a 21 mm long axis) and transversely narrow. The cranial margin of the proximal portion is more proximally expanded than the caudal. In contrast, the caudal margin is far more caudally projected from the shaft. Therefore, the caudal margin of the bone depicts a concave transition between the shaft and the proximal end, in lateral view. The lateral margin of the proximal end is convex in proximal view, whereas the medial is concave and articulates against the tibia. In lateral or medial view, there is a gentle concavity on the caudal half of the proximal end, whereas the cranial half is convex.

Figure 34. Right femur of CAPPA/UFSM 0035. A, photograph and interpretative drawing in cranial view. B, photograph and interpretative drawing in caudal view. C, photograph and interpretative drawing in lateral view. D, photograph and interpretative drawing in medial view. Abbreviations: 4t, fourth trochanter; cil, cranial intermuscular line; clil, caudolateral intermuscular line; cmc, craniomedial crest; cmt, caudomedial tuber; ct, cranial trochanter; ctf, crista tibiofibularis; dlt, dorsolateral trochanter; lc, lateral condyle; mc, medial condyle; ms, muscle scars; pf, popliteal fossa; prtb, protuberance; ts, trochanteric shelf.



Figure 36. Right tibia of CAPPA/UFSM 0035. A, photograph and interpretative drawing in lateral view. B, photograph in medial view. C, photograph and interpretative drawing in caudal view. D, photograph and interpretative drawing of tibia and fibula in proximal view. Abbreviations: cc, cnemial crest; dpr, depression; fb, fibula; fc, fibular condyle; fcr, fibular crest; mc, medial condyle.

On the medial surface of the proximal part of the fibula, a 20-mm-long rugose faint ridge is visible (Fig. 37C), rising from the caudal edge of the proximal end and extending craniodistally along the medial surface of the bone, reaching the cranial edge of the shaft. This structure is related to the fibular crest of the tibia, as it should also support the ligamentum tibiofibularis. The lateral surface of the fibular proximal portion is almost flat, but bears some faint scattered longitudinal scars. More distally, a proximodistally oriented ridge extends along the lateral surface of the shaft (Fig. 37A), probably corresponding to an attachment point of m. iliofibularis. This 18-mm-long ridge has its proximal tip rising from the cranial margin of the shaft, whereas its distal portion merges to the lateral surface of the shaft. It is, therefore, slightly oblique to the fibular shaft. The rough surface texture of this structure differs from that surrounding it, which is smooth. This distinct rough surface extends craniomedially from the ridge until a protruding tubercle on the craniomedial surface of the shaft (Fig. 37B, C).

The long and slender fibular shaft has a fairly constant diameter, 8 mm in craniocaudal width. The entire lateral surface is craniocaudally convex, whereas the medial surface is flat. This gives a semilunar shape to the shaft in cross-section. A foramen pierces the medial surface of the shaft slightly distal to the middle point of the preserved length of the bone (Fig. 37C). Close to the foramen, on the caudomedial margin of the shaft, a small bony salience is visible.

Pedal phalanges

Pedal digit III has four preserved phalanges (Fig. 38A, B), including a partial ungual. The phalanges are proportionally larger than those preserved for digit IV. Their sizes decrease from the proximal to the distal elements (not considering the incompletely preserved ungual). Phalanx 1 is 20 mm long, phalanx 2 is 16.5 mm, and phalanx 3 is 13 mm. All non-terminal phalanges of this digit are longer than lateromedially wide. Their midshaft is constricted, and both extremities are equally broad transversely. The dorsal margin of the proximal portion of phalanx 1 is poorly preserved where the other phalanges bear a dorsal intercondylar process. The dorsal surface of the distal portion of the non-terminal phalanges has a marked depression for the insertion of m. extensor digitorum brevis. In addition, the sides of both distal condyles bear deep collateral ligament pits. A flexor tubercle is absent or poorly developed on the ventral margin of the articular surface of the ungual phalanx of digit III. That phalanx is triangular in cross-section, with lateral and medial surfaces gently convex.

Following the phalangeal formula of several other early dinosaurs (Sereno *et al.*, 2013), we presume that digit IV of CAPPA/UFSM 0035 has phalanges 2–5

preserved, with phalanx 5 being the ungual (Fig. 38C, D). Phalanx 2 is heavily fractured. Phalanges 3 and 4 are subequal in length, ~8 mm. Together, they are only slightly longer than the ungual of that digit, which is 14 mm long. Only phalanx 4 has the dorsal intercondylar process preserved. All non-terminal phalanges bear a deep dorsal extensor depression and collateral ligament pits. The medial and lateral surfaces of the ventral margin of the proximal portion of phalanges 3 and 4 bear a rugose bump with irregular striations. The ungual phalanx is pointed at the distal extremity, but does not significantly curve ventrally, because the margin between its distal tip and the ventral surface of the proximal half is straight to slightly concave. The lateral and medial surfaces of the ungual bear a sharp ridge, which should have been covered by a keratinous sheath. Below those ridges, a longitudinal groove extends until the distal tip of the phalanx. The ventral surface is flat, except for the most proximal portion, which is convex in lateral view and densely striated, probably for m. flexor digitalis longus. The ungual is triangular in cross-section.

RESULTS

PHYLOGENETIC ANALYSIS

The first analysis recovered 54 MPTs of 853 steps each (consistency index [CI] = 0.345; retention index [RI] = 0.639). CAPPA/UFSM 0035 forms a clade with *B. schultzi*, with both forming the sister group to all other Sauropodomorpha in all MPTs (Fig. 39A). The CAPPA/UFSM 0035 plus *B. schultzi* clade is supported by the presence of a pedicel caudally projecting the forking part of the caudal process of the jugal. The rest of the strict consensus topology is the same as that recovered by Cabreira *et al.* (2016).

The second analysis also recovered 54 MPTs, but of 851 steps (CI = 0.347; RI = 0.637). The combined *B. schultzi* nests as the sister group of all other sauropodomorphs in all MPTs (Fig. 39B), similar to the results of Cabreira *et al.* (2016). In addition to the ten originally proposed character states, three additional conditions support the clade Sauropodomorpha, all of which are related to the cervical vertebrae: the absence of deep recesses on the cranial face of the neural arch, lateral to the neural canal [80(0)]; absence of pleurocoels in the cranial portion of the centra [86(0)]; and neural arches higher than caudal articular facets of the centra [87(0)]. The rest of the strict consensus tree is also the same as the former analysis.

The third analysis recovered 32 MPTs of 854 steps (CI = 0.349; RI = 0.636), with *B. schultzi* still as the sister taxon of all other sauropodomorphs in all the MPTs (Fig. 39C). Character states that support this position are the same as those found in the second analysis, except for an additional character related to the acute angle





Figure 38. Pedal digits of CAPPA/UFSM 0035. A, photograph and interpretative drawing of digit III in lateral view. B, photograph and interpretative drawing of digit III in dorsal view. C, photograph and interpretative drawing of digit IV in lateral view. D, photograph and interpretative drawing of digit IV in dorsal view. Abbreviations: bmp, bump; clp, collateral ligament pit; ded, dorsal extensor depression; dip, dorsal intercondylar process; ph, phalanx; rdg, ridge; un, ungual phalanx.

formed between the ascending and caudal processes of the jugal [259(1)]. Unlike the results of Cabreira *et al.* (2016), *Pampadromaeus barberenai* and *P. protos* are sister taxa, supported by the absence of a sheet of bone between the rostral and ventral processes of the prefrontal [258(1)]. This node is sister to a clade including Saturnaliinae (*S. tupiniquim* and *C. novasi*) and other sauropodormohps. There are no other differences relative to the strict consensus trees of the previous analyses.

In the analysis with implied weighting (k value = 3–4), B. schultzi still nests within Sauropodomorpha in all the three MPTs (Fig. 39D), but as the sister taxon of E. lunensis, both forming the sister group of the clade including P. barberenai and P. protos. Those four species form a clade in a sister-group relationship with a large clade that includes Saturnaliinae and other sauropodomorphs. The clade comprising B. schultzi, E. lunensis, P. barberenai and P. protos is supported by the following synapomorphies: presence of a caudomedial process in the premaxilla (character 8, state 1); presence

of a sharp longitudinal ridge on the ventral margin of the antorbital fossa of the maxilla [12(1)]; long axis of the jugal body nearly horizontal to the alveolar margin of the maxilla [26(0)]; presence of pterygoid teeth on palatal process [75(0)]; absence of a caudal groove on the astragalus [217(1)]; and the acute angle between the ascending and caudal processes of jugal [259(1)]. Another difference from the previous analyses performed here is the position of *T. hallae*, *Chindesaurus* briansmalli, E. murphi and Guaibasaurus candelariensis nested within Theropoda, because they were previously placed outside the clade formed by Theropoda plus Sauropodomorpha. The sister-group relationship between T. hallae and C. briansmalli remains supported in this analysis. Further increase of k recovers the same topology as the third analysis.

The fifth analysis recovered 40 320 MPTs of 1922 steps (CI = 0.274; RI = 0.621), seven steps shorter than the analysis by Langer *et al.* (2017). *Buriolestes schultzi* lies within Sauropodomorpha in all the MPTs

Figure 37. Right fibula of CAPPA/UFSM 0035. A, photograph and interpretative drawing in lateral view. B, photograph and interpretative drawing in medial view. D, magnification of the rectangle in C. Abbreviations: bs, bone salience; f, foramen; rdg, ridge; rs, rough surface; tb, tuberosity.



Figure 39. Results of the phylogenetic analyses (first to fourth). A, abbreviated strict consensus tree of the first analysis depicting the phylogenetic position of CAPPA/UFSM 0035. B, abbreviated strict consensus tree of the second analysis depicting the phylogenetic position of the combined *Buriolestes schultzi*. C, abbreviated strict consensus tree of the third analysis depicting the phylogenetic position of the combined *B. schultzi* using the modified data matrix. D, abbreviated strict consensus tree of the fourth analysis using implied character weighting with k = 3. Numbers below nodes represent Bremer support values (left) higher than one and Bootstrap values (right) higher than 50% (in A, B, C) and symmetric resampling values > 50% (in D).

(Fig. 40). In contrast with the first three analyses, the taxon is not recovered as the sister to all other members of the group, but as a member of a clade composed exclusively by all coeval South American forms. This group is supported by 13 synapomorphies, but none is exclusively shared by their members among the OTUs of the analysis. This clade has a sister-group relationship to a clade formed by *Pantydraco caducus* and all other sauropodomorphs. The Carnian South American

clade has a pectinate structure, starting with *E. lunensis*, followed by *B. schultzi* and by *P. protos* as the sister group to a clade formed by *P. barberenai* and *S. tupiniquim*.

MORPHOLOGICAL DISPARITY ANALYSIS

As expected, the analysis using all characters recovered *B. schultzi* within the morphospace occupied by



Figure 40. Strict consensus tree of the fifth phylogenetic analysis depicting the phylogenetic position of *Buriolestes schultzi* (ULBRA-PVT280 plus CAPPA/UFSM 0035). Numbers represent Bremer support values higher than one.



Figure 41. Bivariate plots showing the results of the morphospace occupation analysis. A, using all the characters. B, using cranial characters. C, using non-dentary cranial characters. D, using postcranial characters. Green convex hull corresponds to morphospace of sauropodomorphs, blue convex hull corresponds to morphospace of ornithischians, and red convex hull corresponds to morphospace of theropods. Squares correspond to non-dinosaur archosaurs, triangles correspond to basal saurischians outside the theropod–sauropodomorph dichotomy, and the red dot corresponds to *Buriolestes schultzi*.

sauropodomorphs (Fig. 41A). Morphospaces of ornithischians, sauropodomorphs and theropods are well defined, without overlap among convex hulls. In the analysis using solely cranial characters (Fig. 41B), these three groups also do not overlap, but *B. schultzi* lies outside their respective morphospaces, instead occupying a region occupied by other faunivorous dinosauriforms, such as *H. ischigualastensis*, *T. hallae* and *Daemonosaurus chauliodus*. It is clear that dentition influences this result, because *B. schultzi* lies deeply in the morphospace of sauropodomorphs when the analysis is run only with non-dentary cranial characters (Fig. 41C). In this analysis, although there is some degree of overlap among the morphospaces of sauropodomorphs, theropods and ornithischians, the area occupied by *B. schultzi* is restricted to sauropodomorphs.

The PCoA of postcranial characters (Fig. 41D) shows overlap between the convex hulls of Sauropodomorpha and Ornithischia. *Buriolestes schultzi* lies slightly outside the morphospace of sauropodomorphs, but within the morphospace of ornithischians. On the contrary, the three main dinosaur groups are well separated in the analysis with characters from the axial skeleton alone (Fig. 42A), with *B. schultzi* found within the morphospace occupied by sauropodomorphs. In the analysis of the pectoral girdle and forelimb characters (Fig. 42B), a common area occupied by ornithischians



Figure 42. Bivariate plots showing the results of the morphospace occupation analysis. A, using axial characters. B, using pectoral and forelimb characters. C, using pelvic and hindlimb characters. Green convex hull corresponds to morphospace of sauropodomorphs, blue convex hull corresponds to morphospace of ornithischians, and red convex hull corresponds to morphospace of theropods. Squares correspond to non-dinosaur archosaurs, triangles correspond to basal saurischians outside the theropod–sauropodomorph dichotomy, and the red dot corresponds to *Buriolestes schultzi*.

and sauropodomorphs is found. However, *B. schultzi* lies outside any of the convex hulls of the three main groups. *Buriolestes schultzi* also lies outside the different morphospace areas of sauropodomorphs and ornithischians in the PCoA of pelvic girdle and hindlimb (Fig. 42C) but is close to both areas.

DISCUSSION

BURIOLESTES SCHULTZI INCLUSIVITY AND DISTINCTION FROM COEVAL SAUROPODOMORPHS

Sauropodomorphs are significantly less numerous in Carnian strata when compared with other vertebrates

(Martínez et al., 2011). The group was, however, apparently taxonomically diverse, with at least six coeval species in Argentina and Brazil (Sereno et al., 1993; Langer et al., 1999; Martínez & Alcober, 2009; Ezcurra, 2010; Cabreira et al., 2011, 2016). Therefore, the assignation of CAPPA/UFSM 0035 to *B. schultzi* should not rely solely upon topotypic principles. Indeed, even the sister-group relationship between the new specimen and the holotype of *B. schultzi* brings ambiguous evidence regarding its taxonomic affinity, because a close phylogenetic affinity does not necessarily indicate alpha taxonomy inferences. Cabreira et al. (2016) proposed that the caudal projection of the medial condyle of the tibia, medial to the intercondylar notch,



Figure 43. Specimens ascribed to Dinosauria from the Buriol outcrop.

is an autapomorphic trace of B. schultzi, but CAPPA/ UFSM 0035 unfortunately does not have that part of the tibia preserved. Nonetheless, several skeletal parts preserved in both ULBRA-PVT280 and CAPPA/ UFSM 0035 are similar and, together, they reveal a unique combination of features among coeval sauropodomorph taxa. These include the following: (1) a skull very slightly shorter than the femur; (2) short caudodorsal process of premaxilla; (3) lack of promaxillary fossa on the medial maxillary wall; (4) marked subnarial gap; (5) forking part of the caudal process of the jugal projected from a pedicel; (6) zyphodont dentition; (7) craniocaudally short, raised rugose process on the dorsocaudal margin of the iliac blade; (8) marked protuberance between the craniomedial crest and the dorsolateral trochanter of the femur; and (9) ovoid striated tuberosity on the craniomedial margin of the proximal third of the fibula.

In addition to CAPPA/UFSM 0035, there are at least three other dinosaur specimens (Fig. 43) excavated from the same layer/site that yielded the holotype of *B. schultzi*. ULBRA-PVT289 corresponds to an isolated right femur ~118 mm in length. Its morphology matches those of the femora of CAPPA/UFSM 0035 and ULBRA-PVT280, including the presence of a marked protuberance between the craniomedial crest and the dorsolateral trochanter of the femur. ULBRA-PVT056 includes two cervical vertebrae, ilium, proximal portion of the pubis, and femur from the right side, plus some phalanges. This individual is the smallest known dinosaur specimen from the site, with an 89-mm-long femur. Indeed, it lacks several muscle attachment structures that are present in the femora of both ULBRA-PVT280 and CAPPA/UFSM 0035, suggesting that it represents a less mature individual than the others. CAPPA/UFSM 0179 corresponds to an isolated axis (Müller et al., 2017). Its morphology resembles that of CAPPA/UFSM 0035, but it is 12% larger, corresponding to the largest dinosaur from the Buriol outcrop. The attribution of these three additional specimens to B. schultzi is uncertain, but plausible for topotypic reasons. In paleoecological terms, if all specimens correspond to *B. schultzi*, this taxon was relatively abundant in comparison to other taxa from the Buriol outcrop and surrounding localities, such as Polesinesuchus aurelioi and Prozostrodon brasiliensis, which are recorded in the area based on a single specimen each (Roberto-da-Silva et al., 2014; Pacheco et al., 2017). On the contrary, Hyperodapedon sp. is widely sampled.

Corroborating its affinity to *B. schultzi*, it is possible to differentiate CAPPA/UFSM 0035 from all the other coeval sauropodomorphs as discussed below. Compared with E. lunensis (Sereno et al., 1993; PVSJ 512, 559, 745, 852, 855, 860, 862, 876), the preorbital region of CAPPA/UFSM 0035 is longer than that of PVSJ 512. The rostral process of the maxilla of PVSJ 512 tapers rostrally to form a triangular portion, whereas the rostral margin of the maxilla of CAPPA/ UFSM 0035 is delimited by a concavity. CAPPA/UFSM 0035 possesses more maxillary teeth than PVSJ 512. The rostroventral process of the nasal overlaps the caudodorsal process of the premaxilla in CAPPA/ UFSM 0035, whereas the inverse condition occurs in PVSJ 512. Unlike that specimen, CAPPA/UFSM 0035 lacks a ventral notch on the caudalmost portion of the quadratojugal. CAPPA/UFSM 0035 bears a parasagittal tooth row on the pterygoid, but lacks the diagonal row seen in PVSJ 512 (Sereno *et al.*, 2013). A mylohyoid foramen is absent in the splenial of PVSJ 512 (Sereno *et al.*, 2013) but present in CAPPA/UFSM 0035. On the lateral surface of the surangular, CAPPA/UFSM 0035 has a longitudinal ridge that is absent in PVSJ 512. Unlike PVSJ 512, CAPPA/UFSM 0035 lacks an accessory articular process on the medial side of the base of the prezygapophysis of the fifth and sixth cervical vertebrae. The coracoid foramen is slightly more ventrally located in CAPPA/UFSM 0035 than in PVSJ 512. The articular surface of the pubic penducle of the ilium is triangular in PVSJ 512 (Sereno *et al.*, 2013) but subovoid in CAPPA/UFSM 0035.

CAPPA/UFSM 0035 also differs from S. tupiniquim (Langer et al., 1999; MCP 3844-PV, 3845-PV, 3846-PV). The ridge between the slot for the postorbital and the supratemporal fossa in the frontal of MCP 3845-PV is more slender than in CAPPA/UFSM 0035. The humerus of CAPPA/UFSM 0035 lacks the ligament ridge that is present on the caudolateral surface of the proximal portion of the humerus of MCP 3844-PV (Langer et al., 2007). The craniodorsal corner of the ischium of MCP 3844-PV is fairly expanded, embracing the caudal surface of the ischiatic peduncle of the ilium. In CAPPA/ UFSM 0035, this portion is less developed, so the contact occurs with only the ventral surface of the ischiatic peduncle. Another difference in the ischium is the lateral extension of the acetabular margin, which is more developed in MCP 3844-PV than in CAPPA/UFSM 0035. The scar on the craniolateral surface of the distal portion of the femur of MCP 3844-PV is circular, but forms an inverted U in CAPPA/UFSM 0035. Unlike CAPPA/UFSM 0035, MCP 3844-PV lacks a circular bone protuberance between the craniomedial crest and the dorsolateral trochanter. The dorsalmost extension of the tibia occurs in the centre of the proximal surface in MCP 3844-PV, whereas in CAPPA/UFSM 0035 this is located on the proximal portion of the cnemial crest.

As for P. protos (Martínez & Alcober, 2009; PVSJ 874), its prefrontal lacks a bony sheet between the rostral and ventral processes (Cabreira et al., 2011), seen in CAPPA/UFSM 0035. The slot for articulation with the postorbital of the frontal is straight in PVSJ 874 and sinuous in CAPPA/UFSM 0035. The longitudinal ridge on the dorsal surface of the parietal is more marked in PVSJ 874, whereas the nuchal crest of the occipital is broader in CAPPA/UFSM 0035. The articular region that receives the medial condyle of the quadrate projects more dorsally in PVSJ 874. Unlike PVSJ 874, CAPPA/UFSM 0035 lacks an oval scar on the lateral surface of the centra of the cervical vertebrae. The scapular blade of PVSJ 874 is craniocaudally broader than that of CAPPA/UFSM 0035. The iliac peduncle of the ischium is slightly wider in PVSJ 874.

Chromogisaurus novasi (Ezcurra, 2010; Martínez, Apaldetti & Abelin, 2013; PVSJ 845) has the glenoid lip of the scapula less laterally expanded than in CAPPA/UFSM 0035. In addition, the fossa on the caudal surface of the scapular blade of PVSJ 845 almost reaches the glenoid rim on the scapular body, whereas in CAPPA/UFSM 0035 an equivalent sulcus merges with the scapular blade and disappears distant from the dorsal margin of the glenoid rim. The dorsoventral height of the iliac acetabulum is proportionally larger in PVSJ 845 than in CAPPA/UFSM 0035, and the dorsocaudal margin of the iliac blade bears a raised rugose process along its entire length that expands caudally. In CAPPA/UFSM 0035, the homologous surface is marked by striations and bears a raised process only at the caudalmost portion of the postacetabular ala. The femora of PVSJ 845 possess a lateral fossa (Ezcurra, 2010) that is absent in CAPPA/UFSM 0035, but the PVSJ 845 condition might be related to preservational biases (Martínez et al., 2013). Likewise, the proximal articular surface of the tibia of PVSJ 845 has a deep concavity that, according to Martínez et al. (2013), has been exaggerated by sedimentary compression. On the contrary, the same surface of CAPPA/ UFSM 0035 is convex to smooth. Also, unlike CAPPA/ UFSM 0035, PVSJ 845 lacks the ovoid tuberosity on the craniomedial margin of the proximal third of the fibula.

CAPPA/UFSM 0035 also differs from P. barberenai (Cabreira et al., 2011; Müller et al., 2016; ULBRA-PVT016; CAPPA/UFSM 0027). The alveoli from the rostral portion of the maxilla are concave in lateral view in ULBRA-PVT016 but straight in CAPPA/ UFSM 0027. The medial wall of the antorbital fossa of the maxilla projects more caudally in CAPPA/UFSM 0035 than in ULBRA-PVT016. Unlike CAPPA/UFSM 0035, the dentary of ULBRA-PVT016 lacks a rostralmost edentulous surface. According to Cabreira et al. (2011), the prefrontal of ULBRA-PVT016 lacks a sheet of bone covering the lacrimal. This differs from the condition of CAPPA/UFSM 0035, in which the prefrontal covers part of the caudolateral surface of the lacrimal. The caudal process of the postorbital of CAPPA/UFSM 0035 is proportionally longer and slender. In CAPPA/UFSM 0035, the bifurcation of the caudal process of the jugal does not occur as rostrally as in ULBRA-PVT016. The scapular blade of ULBRA-PVT016 is slightly more caudally oriented in comparison to CAPPA/UFSM 0035. The sulcus for the ligamentum capitis femoris is narrower in ULBRA-PVT016. The crista tibiofibularis of the femur of CAPPA/UFSM 0035 is transversely wider than in ULBRA-PVT016 and CAPPA/UFSM 0027. Unlike CAPPA/UFSM 0027, the craniolateral surface of the distal portion of the femur of CAPPA/UFSM 0035 lacks an ovoid depression.



Figure 44. Reduced strict consensus tree of the third phylogenetic analysis within geographical distribution of the major groups. A, time-calibrated phylogeny. B, geographical distribution of theropods (red dot) and sauropodomorphs (green dot) of the analysis along the Carnian. C, geographical distribution of post-Carnian theropods (red dot) and sauropodomorphs (green dot) of the analysis.

THE FIRST STEPS FROM DISTINCT POINTS OF VIEW

than to provide additional arguments for one or other scheme.

The differences seen in the strict consensus topologies of the analyses indicate that the phylogeny of early dinosaurs can be affected by the choice of different weighting schemes and taxon samples. Discussions regarding the usefulness of implied weighting over unweighted analyses are still ongoing (Congreve & Lamsdel, 2016), and our discussion here attempts only to evaluate alternative evolutionary scenarios, rather

In the first scenario (i.e. based on the results from the third analysis), the Carnian sauropodomorphs are arranged in low-diversity groups along the stem leading to latter sauropodomorphs (Fig. 44). In this scheme, the anatomical features characterizing sauropodomorphs as a whole are not related to the dentition, suggesting that herbivorous feeding habits were not

the main drive in the origin of the group. In this scenario, the acquisition of a dental morphology related to herbivore/omnivore diets occurred in a second step, as seen in forms nested in the clade including *E. lunensis* and other sauropodomorphs, but not *B. schultzi*. These have maxillary and dentary tooth crowns that are labiolingually expanded in distal/medial view and have fewer denticles per millimetre, contrasting with the blade-like morphology present in faunivorous forms, such as *T. hallae*, *Coelophysis bauri* and *B. schultzi*. In the sister clade to *E. lunensis*, the distal margin of the maxillary/dentary tooth crowns is markedly expanded at the base, as in typically herbivorous forms, such as *P. mertii*, *S. opolensis* and *Unaysaurus tolentinoi*. Finally, the clade including *P. caducus*, *Efraasia minor* and *Plateosaurus engerlhardi* acquires maxillary/dentary teeth with large serrations forming oblique angles with the margin of the teeth. In sum, this first scenario





indicates that faunivory was the ancestral condition for Sauropodomorpha (Cabreira *et al.*, 2016) and that taxa such as *E. lunensis*, *Pampadromaeus barbarenai* and *S. tupiniquim* represent the first steps of a stepwise acquisition of traits related to a more herbivorous diet. As such, the high diversity of Carnian sauropodomorphs might be related to the adoption of slightly different feeding strategies (also true for the next scenario).

In the alternative scenario, based on the analysis with implied weighting, the sauropodomorphs B. schultzi, E. lunensis, P. barberenai and P. protos form a clade (Fig. 45). Indeed, early South American sauropodomorphs share a particular set of traits, so the recovery of a clade including some of these forms is not unexpected. Although weakly supported, this arrangement leads to distinct interpretations regarding character evolution. For instance, some features related to herbivorous/omnivorous feeding habits, such as the reduction in the number of serrations per millimetre in middle maxillay/dentary teeth, are reconstructed for the node including all sauropodomorphs, and reverted to the plesiomorphic condition in *B. schultzi*. Overall, in this scenario, dentition plays an important role in the initial evolution of the group. However, most character states that support the Carnian sauropodomorph clade are ambiguous, because their condition in S. tupiniquim and C. novasi is unknown. One exception is character 217, related to the apomorphic absence of a caudal groove on the astragalus of P. protos, E. lunensis and B. schultzi, which is present in S. tupiniquim and Plateosaurus engelhardti. Besides, although the set of character states that supports Sauropodomorpha is slightly distinct from that of the previous analysis, some features, such as the ventrally inclined dorsal surface of the rostral tip of the dentary, still characterize the group. Also synapomorphic for Sauropodomorpha, a low mandibular articulation occurs convergently in Ornithischians. Finally, another outcome of the implied weighting analysis is the reinterpretation of T. hallae, C. briansmalli, E. murphi and G. candelariensis as theropods.

The scenario derived from the analysis using the data matrix by Baron *et al.* (2017a) modified by Langer *et al.* (2017) differs from that based on the analysis with implied weighting because a more inclusive clade of sauropodomorphs from the Carnian of South America was recovered. Nevertheless, it supports the existence of this clade, in contrast with the first three analyses. In that hypothesis, *S. tupiniquim* is recovered within the group, as the sister taxon to *P. barberenai* (Fig. 40), based on the sharing of the first dentary tooth inserted in the extreme rostral end of the dentary [(0)149] and the slightly concave dorsal margin of the ilium in lateral view [(1)301]. The clade

composed by Carnian forms lacks synapomorphies related to a herbivorous diet, whereas the clade supporting *P. caducus* plus other sauropodomorphs is supported by several characters related to a herbivorous feeding behaviour: crown of the premaxillary teeth is at least moderately expanded above root [(1)152]; large and coarse denticles on maxillary and dentary teeth [(2)169]; majority of maxillary and dentary teeth weakly recurved [(1)174]; and caudal cutting edge of the caudal maxillary teeth convex [(1)175]. The placement of *E. murphi* as a saurischian basal to the Theropoda–Sauropodomorpha dichotomy implies, in the absence of theropods in the Carnian, agreement with the first scenario discussed here.

Regardless of the parameters applied in the phylogenetic analysis, B. schultzi is consistently nested within Sauropodomorpha, reinforcing the taxonomic assignation of Cabreira et al. (2016). Yet, and perhaps even more interesting, none of the disparity morphological analyses places B. schultzi in an area occupied by theropods, suggesting that its skeleton does not comprise a marked mosaic of theropod and sauropodomorph traits, but instead a combination of sauropodomorph and common saurischian traits. Our partitioned data matrix with characters from the axial skeleton also reveals well-delimited groups in the morphological disparity analysis. In contrast, other portions of the skeleton are generally less delimited, as indicated by the overlapped morphospace of the groups. These results suggest that axial traits played a relevant role in the evolution of the first dinosaurs. Indeed, sauropodomorphs are known for their peculiar axial skeleton, which in later members developed to conciliate feeding behaviours and their extremely large bodies (Wedel, 2003; Fronimos & Wilson, 2017; Ibiricu et al., 2017). The neural arches of the sauropodomorphs' neck vertebrae become tall, a feature already observed in the new specimen of B. schultzi. This condition, associated with the absence of pleurocoels, results in a unique morphology for the early members of the group, as already reported in the literature (e.g. Martínez, 2009; Apaldetti et al., 2011; Wang, You & Wang, 2017). The increase in neck length typical of later sauropodomorphs has, however, not yet taken place in B. schultzi and other Carnian members of the group (e.g. P. protos).

CONCLUSIONS

The anatomy of the new specimen described here is consistent with that of *B. schultzi*, sharing with its holotype a unique combination of traits among coeval taxa. In addition, there is no significant difference in the repeated elements of both specimens. Accordingly, we identify CAPPA/UFSM 0035 as a second individual of *B. schultzi*, substantially expanding our knowledge of the anatomy of this dinosaur. As such, *B. schultzi* is now as complete as the best-known early dinosaurs, such as *E. lunensis* and *H. ischigualastensis*.

The phylogenetic analyses performed fully support *B. schultzi* as a member of Sauropodomorpha, corroborating previous assignations. In fact, the morphological disparity analyses failed to find any indication of convergences with Theropoda in its skeletal parts. Indeed, such analyses demonstrate that the main dinosaur groups (Ornithischia, Sauropodomorpha, Theropoda) overlap in morphospace occupation for most skeletal parts, with a clear exception being the axial skeleton. We also propose an alternative evolutionary scenario for the first members of Sauropodomorpha, where some Carnian South American taxa are nested in a monophyletic group, rather than being arranged in low-diversity groups on the stem leading to later sauropodomorphs.

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APPENDIX

FULL CODING TO CAPPA/UFSM 0035 IN THE FIRST PHYLOGENETIC ANALYSIS

FULL CODING TO *BURIOLESTES SCHULTZI* (ULBRA-PVT280 PLUS CAPPA/UFSM 0035) IN THE SECOND PHYLOGENETIC ANALYSIS

01111111?00001102010010011?10???110????000100? ??00111111010001111100111

DATA MATRIX PROCESSED IN THE THIRD AND FOURTH PHYLOGENETIC ANALYSES

Euparkeria capensis

Lagerpeton chanarensis

Dromomeron gregorii

Dromomeron romeri

Ixalerpeton polesinensis

Marasuchus lilloensis

Saltopus elginenis

Lewisuchus admixtus

Pseudolagosuchus major

Asilisaurus kongwe

Diodorus scytobrachion

Eucoelophysis baldwini

Silesaurus opolensis

0?00000?0010000????101?110?010100110111000?0 1010?000001002001100111100[01]?10001001100010 10101010101011100100[01]1111000000000????????? ???????10002[01]01101011100101010111110110[12]111101210[01]0111001100100[12]11002000101011 0010?001100 010???1010010?100001021?1000110?0

Sacisaurus agudoensis

Pisanosaurus mertii

$Scutellos aurus \ lawleri$

Lesothosaurus diagnosticus

Eocursor parvus

Heterodontosaurus tucki

Herrerasaurus ischigualastensis

Staurikosaurus pricei

Sanjuansaurus gordilloi

Panphagia protos

Eoraptor lunensis

 $\begin{array}{l} 0110111?0011011110110111100011100100?????1000\\ 10001?000010?101[01]100000000000??1??001100000\\ 1111010100??1??0?00010121210110??100010111100\\ 002010100121011101?0110000111011[12]121???1??1\\ 011??1?1?111?00001102010010011010011111?002000\\ 01011101011111 01111111?????101 \end{array}$

Pampadromaeus barberenai

Buriolestes schultzi

Saturnalia tupiniquim

Chromogisaurus novasi

Pantydraco caducus

Efraasia minor

Plateosaurus engelhardti

Chindesaurus briansmalli

Guaibasaurus candelariensis

Tawa hallae

Eodromaeus murphi

Coelophysis bauri

Liliensternus liliensterni

Syntarsus rhodesiensis

01221211?011000110010?101?????10011111??00?1?? ?0000000?????112000000?010011???11112111101?10

$\begin{array}{l} 1?111111001010011111111210?11211111?1111101\\ 1121?1210122111101?1?100??1011111121211102211\\ [12]01[01]111100?00000112220020111010010111?00\\ 20111?1?010111101101011?0111?1101012??\\ \end{array}$

Syntarsus kayentakatae

Zupaysaurus rugeiri

Daemonosaurus chauliodus

Petrified forest theropod

Dilophosaurus wetherelli

FULL CODING TO *BURIOLESTES SCHULTZI* (ULBRA-PVT280 PLUS CAPPA/UFSM 0035) IN THE FIFTH PHYLOGENETIC ANALYSIS