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GONDWANAN PERSPECTIVES

A NEW LATE CRETACEOUS ABELISAURID SPECIES FROM LA RIOJA PROVINCE, NORTHWESTERN ARGENTINA

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Abstract. Abelisauridae is a group of ceratosaurian theropods that thrived mainly in Gondwana during the Cretaceous. Their fossil record is currently represented by more than 25 species, and their most complete and abundant records are from the Argentinean Patagonia. Outside Patagonia, the record of named Argentinean ceratosaurians has been limited to the Cretaceous of the Salta Province, with the noasaurid *Noasaurus*–represented by a fragmentary skeleton–and the brachyrostran abelisaurid *Guemesia*–represented by a nearly complete braincase and partial skull roof–. Here, we report a new abelisaurid theropod specimen (CRILAR-Pv 506) from the Late Cretaceous of La Rioja Province, northwestern Argentina. It was found at the Tama locality, in outcrops of the Campanian Los Llanos Formation, and associated with titanosaurian sauropod remains. The new abelisaurid specimen is represented by a first dorsal centrum, a second dorsal vertebra, a partial sacrum, left ilium, pubis and ischium, and other indeterminate elements. A unique combination of character states led us to propose the new genus and species *Vitosaura colozacani*. Phylogenetic analyses found *Vitosaura* either as a non-brachyrostran abelisaurid, closely related to Indo-Malagasy species in some trees, or a non-carnotaurinin furileusaurian. However, the interrelationships among abelisaurids are poorly supported. Our comparisons confirm the presence of abelisaurids in the Los Llanos Formation and this is the first named theropod taxon in the Cretaceous of La Rioja Province.

Key words. Theropoda. Ceratosauria. Abelisauridae. Upper Cretaceous. Los Llanos Formation.

Resumen. UNA NUEVA ESPECIE DE ABELISÁURIDO DEL CRETÁCICO TARDÍO DE LA PROVINCIA DE LA RIOJA, NOROESTE DE ARGENTINA. Abelisauridae es un grupo de terópodos ceratosaurios que prosperaron principalmente en Gondwana durante el Cretácico. Su registro fósil está representado actualmente por más de 25 especies, y sus registros más completos y abundantes provienen de la Patagonia argentina. Fuera de la Patagonia, el registro de ceratosaurios argentinos nombrados se ha limitado al Cretácico de la provincia de Salta, con el noasáurido *Noasaurus*, representado por un esqueleto fragmentario, y el abelisáurido braquirostro *Guemesia*, representado por una caja craneana casi completa y un techo craneano parcial. Aquí, informamos sobre un nuevo espécimen de terópodo abelisáurido (CRILAR-Pv 506) del Cretácico Superior de la Provincia de La Rioja, noroeste de Argentina. Fue hallado en la localidad de Tama, en afloramientos campanianos de la Formación Los Llanos, y asociado a restos de saurópodos titanosaurios. El nuevo ejemplar de abelisáurido está representado por el primer centro vertebral dorsal, la segunda vértebra dorsal, un sacro parcial, íleon, pubis e isquion izquierdos, y otros elementos indeterminados. Una combinación única de estados de carácter permitió proponer el nuevo género y especie *Vitosaura colozacani*. Los análisis filogenéticos encontraron a *Vitosaura* como un abelisáurido no braquirostro, cercanamente emparentado con especies indo-malgaches en algunos árboles, o como un furileusaurio no carnotaurinino. Sin embargo, las interrelaciones entre los abelisáuridos están pobremente soportadas. Nuestras comparaciones confirman la presencia de abelisáuridos en la Formación Los Llanos y este es el primer taxón de terópodo nombrado para el Cretácico de la Provincia de La Rioja.

Palabras clave. Theropoda. Ceratosauria. Abelisauridae. Cretácico Superior. Formación Los Llanos.

ABELISAURIDAE IS A CLADE of ceratosaurian theropods erected by Bonaparte and Novas (1985) and characterized by the presence of a robust, short, and tall skull, well-ornamented maxillae and frontals, a highly pneumatized axial skeleton, and reduced forelimbs (Bonaparte *et al.*, 1990; Ruiz *et al.*, 2011; Pol & Rauhut, 2012). The discovery of multiple abelisaurid species over the last few decades, mainly in Gondwanan landmasses, has significantly enhanced our understanding of this group of theropods (Krause *et al.*, 2007; Novas *et al.*, 2013). Abelisauridae was the dominant clade of theropod dinosaurs during the Cretaceous in Gondwana, with numerous records in northern Africa and

Indo-Madagascar, and they also reached Laurasia in what is current-day central Europe (*e.g.*, Wilson *et al.*, 2003; Sereno *et al.*, 2004; Krause *et al.*, 2007; Novas *et al.*, 2010; Tortosa *et al.*, 2014; Longrich *et al.*, 2017; Salem *et al.*, 2022; Buffetaut, 2024). Beyond these records, the group was astonishingly successful in South America, with a very abundant fossil record (Canale *et al.*, 2009; Ezcurra & Novas, 2016; Filippi *et al.*, 2016; Aranciaga-Rolando *et al.*, 2021; Iori *et al.*, 2021; Gianechini *et al.*, 2021; Agnolín *et al.*, 2022; Pol *et al.*, 2024). Late Cretaceous South American abelisaurids are represented by several nominal species in Argentina—17 valid species—and Brazil—4 valid species—(see Supplementary Online Information 1), in addition to indeterminate records from northern Chile (Amudeo-Plaza *et al.*, 2023) and Colombia (Ezcurra, 2009). The Argentinean abelisaurid record is the richest worldwide (Aranciaga-Rolando *et al.*, 2021; Agnolín *et al.*, 2022), with iconic abelisaurid species, such as *Abelisaurus*, *Carnotaurus*, and *Aucasaurus* (Bonaparte, 1985; Bonaparte & Novas, 1985; Coria *et al.*, 2002), and several other new species discovered in recent years, mostly from Patagonia (*e.g.*, *Skorpiovenator*, *Viavenator*, *Llukalkan*, *Niebla*, *Elemgasem*, *Koleken*) (see Supplementary Online Information 1). These new specimens have considerably expanded our anatomical knowledge of the group, their interrelationships, and evolution during the Late Cretaceous (Canale *et al.*, 2009; Filippi *et al.*, 2016; Aranciaga-Rolando *et al.*, 2021; Gianechini *et al.*, 2021; Baiano *et al.*, 2022; Pol *et al.*, 2024; Seculi-Pereyra *et al.*, 2025).

Outside Patagonia, the Argentinean record of abelisaurids is considerably more limited. The brachyrostran *Guemesia* is represented by an isolated braincase from the Upper Cretaceous Los Blanquitos Formation (Campanian) of the Salta Province (Agnolín *et al.*, 2022). Several isolated teeth of abelisaurids have been reported from the Upper Cretaceous Ciénaga del Río Huaco Formation, Quebrada Santo Domingo locality, western La Rioja Province (Juarez *et al.*, 2023). Finally, the Upper Cretaceous Los Llanos Formation of southeastern La Rioja Province yields a vertebrate faunal assemblage that includes two preliminarily reported abelisaurid specimens (Fiorelli *et al.*, 2016; Jiménez-Velandía *et al.*, 2023). Here, we describe one of these abelisaurid specimens in detail (CRILAR-Pv 506), and based on it, we name the first definitive abelisaurid theropod taxon from La Rioja Province (Fig. 1). This specimen was found at the type locality of the Los Llanos Formation, near the town of Tama, in association with several titanosaur remains (Hechenleitner *et al.*, 2018). This first Riojan abelisaurid taxon sheds light on the group, the tetrapod assemblage of the Los Llanos Formation, and possible paleobiogeographic relationship with other Campanian-Maastrichtian units of South America.

Geological settings. The remains of the new abelisaurid were discovered in exposures of the type locality of the Los Llanos Formation and come from the main dinosaur quarry of the Colozacán valley, a few kilometers south of the Tama village (Gral. Ángel V. Peñaloza Department), western slope of the Sierra de Los Llanos mountain range in the southeastern region of La Rioja Province (Fig. 1). The Los Llanos Formation has several outcrops in the eastern region of La Rioja and it is often associated with the Sierras Pampeanas system (Fig. 2.2) (Fiorelli *et al.*, 2016). The unit is widely exposed in the Sierra Brava region and on the eastern and western plains of the Sierra de Los Llanos (Fiorelli *et al.*, 2016), with some isolated but paleontologically relevant outcrops associated to the Sierra de Velasco (Fig. 2.3) (*i.e.*, Sanagasta valley; Grellet-Tinner & Fiorelli, 2010; Fiorelli *et al.*, 2012). The Los Llanos Formation is predominantly a sandstone succession represented by paleosol profiles (Fig. 2.1) (*i.e.*, in the type locality of Tama; Basilici *et al.*, 2017), but there are great sedimentological variations in other localities, with fluvial or even paleohydrothermal deposits, such as in the Sanagasta GeoPark (Fiorelli *et al.*, 2012).

The geology of the Los Llanos Formation, in particular at the Tama locality, has been recently addressed in detail (see Fiorelli *et al.*, 2012, 2016; Hechenleitner *et al.*, 2016, 2018; Basilici *et al.*, 2017). As a summary, in the type locality of Tama, the theropod fossil remains occur in association with titanosaur bones widely distributed in a sedimentary succession comprising sandstones and sandy conglomerates 28 meters above the contact with the underlying Permian Patquía Formation (Hechenleitner *et al.*, 2016; Basilici *et al.*, 2017). The Los Llanos Formation is approximately 150 meters in thickness, dips 3° WNW in this area, and shows upwards a manifested angular unconformity with a younger 5 meters thick undefined unit (Tertiary?) characterized by sandy conglomerates with planar cross stratifications (Basilici *et al.*, 2017). The whole succession of the Los Llanos Formation is composed of cumulative paleosol profiles (Basilici *et al.*, 2017). Although beds with high calcium carbonate content are present throughout the succession, they are particularly abundant in the lower section and characterize the Colozacán pedotype, a well-developed aridisol formed in semiarid and drained paleoenvironmental conditions (Fiorelli *et al.*, 2016; Basilici *et al.*, 2017). How-

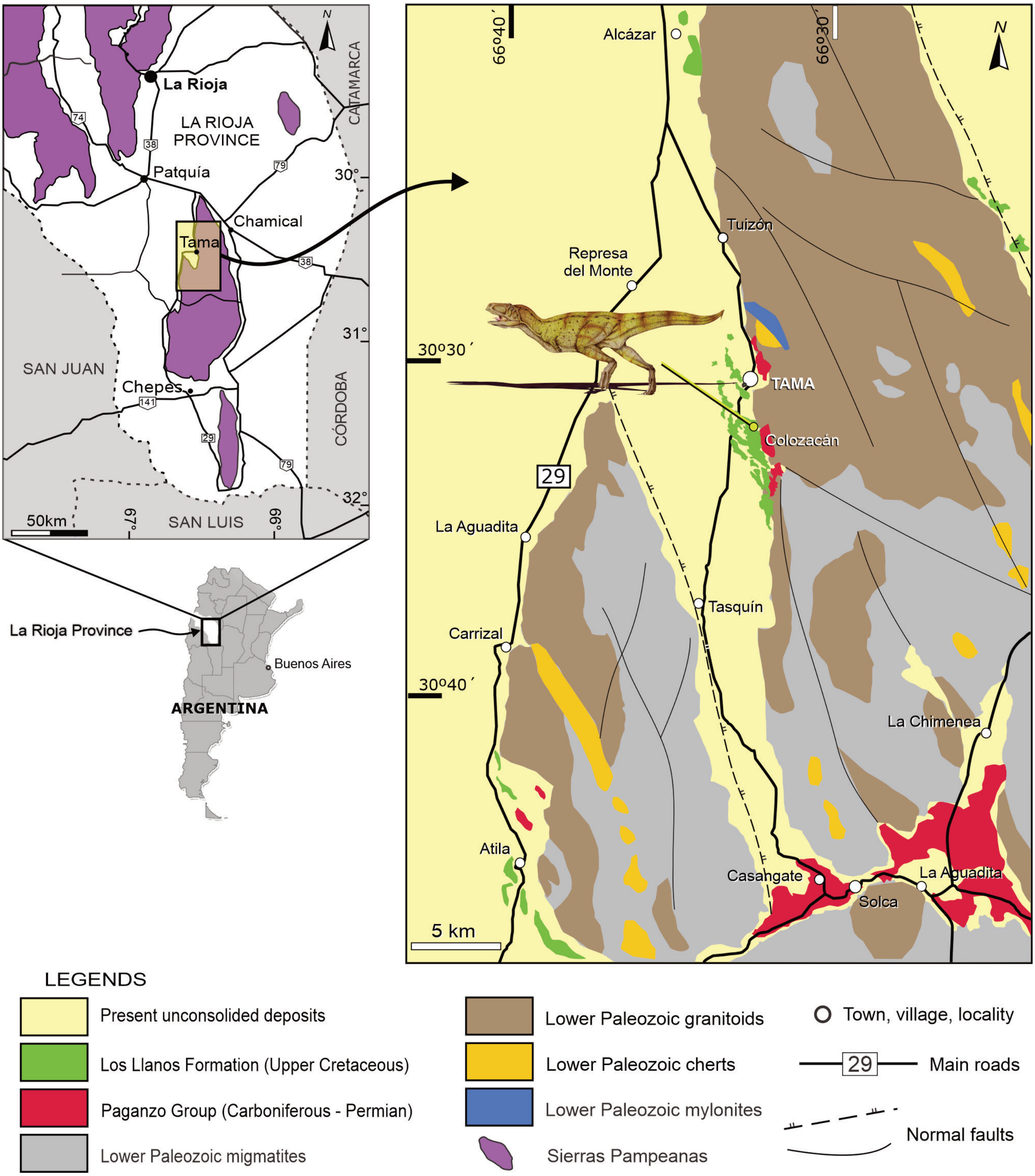

Figure 1. Regional and local geological map showing the location of ***Vitosaura colozacani*** gen. et sp. nov. (**CRILAR-Pv 506**) in the Los Llanos Formation, La Rioja Province, Argentina.

ever, the cumulative paleosol section is mostly dominated by a poorly developed inceptisol formed in semiarid and drained paleoenvironmental conditions corresponding to the Tama pedotype, which shows evidence of weak pedogenic maturity (Basilici *et al.*, 2017). The fossil-bearing level is located in the first meters of this pedotype succession in a fine Bk horizon, but between two predominant and well-developed Bw horizons with diffuse boundaries. The level comprises poorly to moderately sorted, fine to medium-grained sandstones with calcium carbonate micritic cement. Nodules of microcrystalline calcite and rhizoliths constituted of chalcedony root casts and calcareous rhizotubules are

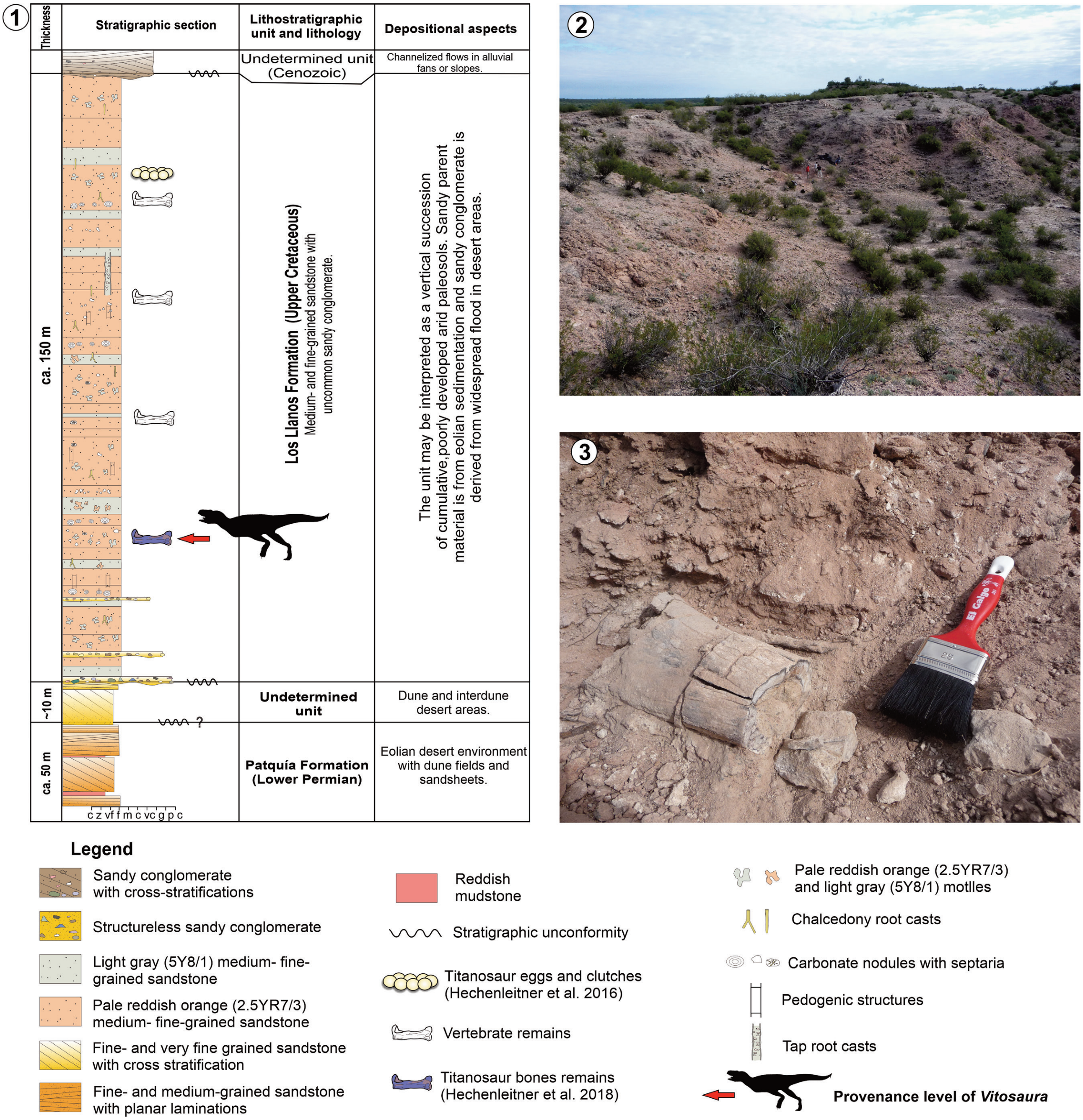

Figure 2. Stratigraphic context of ***Vitosaura colozacani*** gen. et sp. nov. (**CRILAR-Pv 506**). **1,** Regional stratigraphic column of the Tama pedotype (the black silhouette of a theropod shows the stratigraphic position of the bones of **CRILAR-Pv 506**); **2,** Panoramic photograph of the type locality of the Los Llanos Formation, located three kilometers south of the town of Tama, in the southeast of La Rioja Province; **3,** Photograph showing sauropod fossil remains in situ, in the outcrops of the Los Llanos Formation. Modified from Hechenleitner *et al.* (2016).

conspicuous. The unit has several typical crystalline calcitic and chalcedony pedofeatures (see Basilici *et al.*, 2017).

In addition to the first abelisaurid theropod remains described here, the fossil vertebrate assemblage of the Los Llanos Formation in the Tama pedotype is also composed of the sphagesaurian notosuchian *Llanosuchus tamaensis*, unnamed titanosaur bone remains and egg-clutches, other theropod remains, and turtle bones (Grellet-Tinner & Fiorelli, 2010; Fiorelli *et al.*, 2016; Hechenleitner *et al.*, 2016, 2018). The age of the Llanos Formation was first interpreted as Cretaceous (Bodenbender, 1911), but subsequently several authors erroneously considered it as Neogene (Dávila & Lithgow-Bertelloni, 2013; but see Hechenleitner *et al.*, 2014). However, the age of the unit was re-interpreted as Late Cretaceous based on the discovery in several localities of reptile fossil remains typical of other Cretaceous Gondwanan associations (Grellet-Tinner & Fiorelli, 2010; Fiorelli *et al.*, 2016; Hechenleitner *et al.*, 2016, 2018). More precisely, an association of microfossils in palustrine muddy facies of the Tama pedotype, including charophytes and freshwater ostracodes (Carignano *et al.*, 2013; De Sosa Tomas *et al.*, 2017), indicates a Campanian age for the Llanos Formation.

Institutional abbreviations. CRILAR-Pv, Centro Regional de Investigaciones Científicas y Transferencia Tecnológica de La Rioja, Paleontología de Vertebrados, Anillaco, Argentina; **DGM,** Departamento Nacional da Produção Mineral, Museu de Ciências da Terra, Rio de Janeiro, Brazil; **MACN-Pv,** Colección Nacional de Paleovertebrados, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Ciudad Autónoma de Buenos Aires, Argentina; **MAU-Pv,** Museo Municipal "Argentino Urquiza", Rincón de los Sauces, Argentina; **MCF-PVPH,** Museo Carmen Funes, Vertebrate Paleontology, Plaza Huincul, Argentina; **MMCh-PV,** Museo Municipal "Ernesto Bachmann", Villa El Chocón, Argentina; **MPCN-PV,** Museo Patagónico de Ciencias Naturales, General Roca, Argentina; **MUVP,** Mansoura University Vertebrate Paleontology Center, Mansoura, Egypt.

MATERIAL AND METHODS

Specimen

The specimen described here (CRILAR-Pv 506) was excavated during field trips in 2009 and 2010, using traditional paleontological methods, from the Los Llanos Formation at the Tama locality. The theropod remains were associated with several titanosaur postcranial remains in a quarry opened at the Colozacán Valley (see Hechenleitner *et al.*, 2018). The fossil specimens were mechanically prepared with pneumatic tools at the Paleontological Lab of the CRILAR (Anillaco, La Rioja, Argentina) and deposited in its Vertebrate Paleontology Repository.

Paleohistological sections

The thin section of the middle shaft of the left pubis was made at the Petrology Laboratory at CRILAR (La Rioja, Argentina), using the following protocol for petrographic sectioning: the specimen was washed in distilled water and cut with PetroThin and dried at 40°C in an oven for 24 hours. The section was glued with compound glue (Araldit CY 248 and hardening HY 956) on a glass slide of 28 × 48 × 1.8 mm and then ground smooth using progressively finer abrasive grit until the sample was only 30 μm thick. Observations were made using a Leica DM2500P petrographic microscope, and images were captured with a digital Leica camera attached to the microscope and connected to a computer for processing and editing. The Leica Application Suite was used to integrate the microscope and digital camera.

Phylogenetic analyses

The phylogenetic relationships of CRILAR-Pv 506 were tested using a modified version of the data matrix published by Pol *et al.* (2024), which is focused on ceratosaurian relationships (Supplementary Online Information 2). We added the new species *Vitosaura colozacani* and a new character (246) describing the occurrence of a transverse groove on the distal surface of the anterior dorsal neural spines. We deactivated MPCN-PV 69 and *Thanos* before the tree searches because of the low number of characters scored for them. The modified version of the data matrix is composed of 246 characters and 46 active terminals (Supplementary Online Information). The following 14 characters were considered as ordered following Pol *et al.* (2024): 29, 30, 34, 116, 118, 141, 159, 170, 174, 185, 191, 204, 207, and 222. The data set was analyzed under equal and implied weighting maximum parsimony in the program TNT version 1.6 (Goloboff & Morales, 2023). This decision of weighting against homoplasy follows the results of the analyses of Goloboff *et al.* (2018) (based on simulations) and Ezcurra (2024) (based on empirical data), in which implied weighting outperformed equal weighting in topological accuracy and stability, respectively. The data set was analyzed using a range of concavity constant values (k) between 3 and 8, following the suggestion of Ezcurra (2024) for a matrix of approximately 50 terminals.

The tree searches involved 1,000 replications of Wagner trees (with random addition sequence) followed by TBR (tree bisection reconnection) branch swapping (holding 10 trees per replicate). The shortest trees obtained were then subjected to a final round of TBR. Zero-length branches were collapsed in the recovered most parsimonious trees (MPTs). All the trees were rooted with *Herrerasaurus*. Homoplasy indices were calculated with the 'STATSb.run' script (Spiekman *et al.*, 2021). Group supports were quantified using Bremer decay indices and no-zero weight symmetric resampling with a probability of 25%. The resampling was conducted using 10,000 pseudo-replications, and both absolute and GC (group present/contradicted) frequencies were reported on the branches of a reduced strict consensus tree. Finally, a global strict consensus tree (GSCT) was generated from all the MPTs found in all the analyses under implied weighting using the different k-values. Similarly, absolute and GC resampling frequencies were calculated from all the resampling trees recovered using the different k-values and plotted on the branches of the GSCT. The analyses were implemented in one custom script written for TNT and named 'phylo_analyses_IW_and_eqW_1.1.run' (see the README file that accompanies this script for an explanation of how the script works; Supplementary Online Information).

Nomenclatural acts

This published work and its nomenclatural acts have been registered in ZooBank, the online registration system for the International Code of Zoological Nomenclature. The ZooBank Life Science Identifiers (LSIDs) and the associated information can be viewed through any standard web browser by appending the LSID to the prefix 'http://zoobank.org/'. The LSID for this publication is: urn:lsid:zoobank.org:pub:5F65F268-EF7E-4B94-8C38-2EC878E4F133

SYSTEMATIC PALEONTOLOGY

Dinosauria Owen, 1842
Theropoda Marsh, 1881
Ceratosauria Marsh, 1884
Abelisauroidea Bonaparte, 1991
Abelisauridae Bonaparte & Novas, 1985

Vitosaura gen. nov.

LSID urn:lsid:zoobank.org:act:349E766B-1517-4E15-BE8C-9D9392460BE7

Type and only known species. *Vitosaura colozacani* sp. nov.
Etymology. '*Vito*' in honor of Victoria "Doña Vito" Romero, a legendary woman and federal soldier from the mid-19th century. She was the partner of Ángel 'El Chacho' Peñaloza and fought against the unitary oligarchy. Victoria was born in 1804 in the Los Llanos region, eastern plains of La Rioja, near where the holotype was found. '*Saura*' (Greek), feminine for lizard.
Diagnosis. As for the type and only known species.

Vitosaura colozacani sp. nov.

Figures 3–6, Tables 1, 2

LSID urn:lsid:zoobank.org:act:97DB3D77-317F-494B-A0D2-6BF4C22F7A1B

Holotype. CRILAR-Pv 506, a partial postcranium including a first dorsal centrum, a nearly complete second dorsal vertebra, a partial sacrum, left ilium, pubis and ischium, and other indeterminate bony elements.
Stratigraphic and geographic occurrence. CRILAR-Pv 506 comes from the main dinosaur quarry of the Colozacán Valley in the vicinity of Tunacata and Guasamayo, 3 km south of Tama village (General Ángel V. Peñaloza Department), western slope of Sierra de Los Llanos Mountain range in the southeastern region of La Rioja Province, Argentina (Fig. 1). The holotype was found in a paleosol level of the Tama pedotype of the Los Llanos Formation, approximately 28 meters above the contact with the underlying late Paleozoic Patquía Formation (Fig. 2.1). A Late Cretaceous age (possibly Campanian) has been suggested for the Los Llanos Formation based on an association of microfossils, represented by charophytes, freshwater ostracods (Carignano *et al.*, 2013; Hechenleitner *et al.*, 2014), and vertebrates (Fiorelli *et al.*, 2016; Hechenleitner *et al.*, 2016, 2018).

Etymology. The specific epithet '*colozacani*' alludes to the Colozacán Valley, the type locality of the Los Llanos Formation and the site where the holotype was found.

Diagnosis. *Vitosaura colozacani* is a medium-sized abelisaurid theropod that differs from other ceratosaurs in the presence of the following unique combination of character states: anterior dorsal vertebrae without posterior pleurocoels in the centrum (posterior pleurocoels present in some ceratosaurs, *e.g.*, *Canotaurus*, *Koleken*), anterior dorsal vertebrae with a transverse groove on the distal

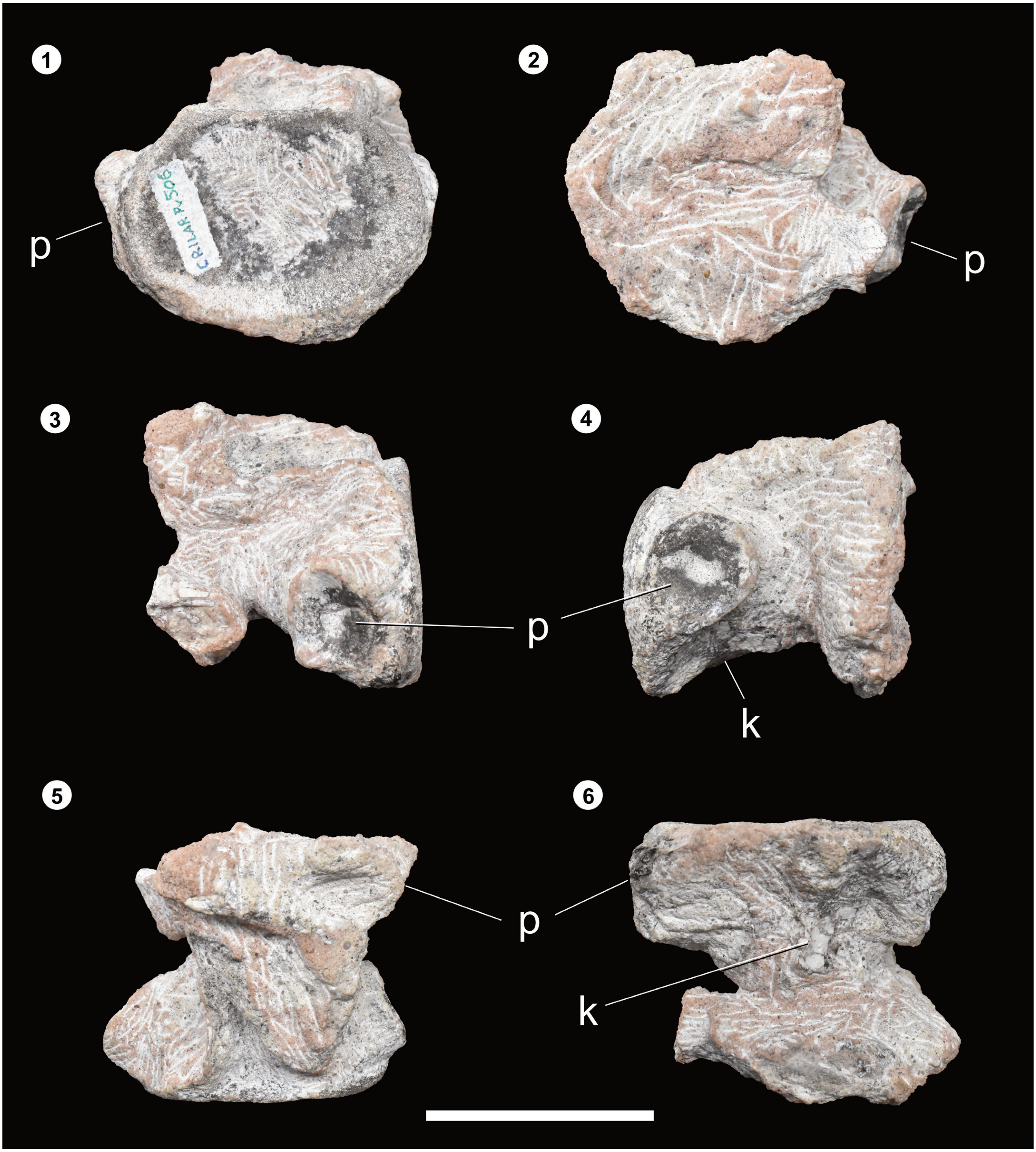

Figure 3. First dorsal vertebral centrum of ***Vitosaura colozacani*** gen. et sp. nov. (**CRILAR-Pv 506**) in **1,** anterior; **2,** posterior; **3,** right lateral; **4,** left lateral; **5,** dorsal; and **6,** ventral views. Abbreviations: **k,** keel; **p,** parapophysis. Scale bar equals 5 cm.

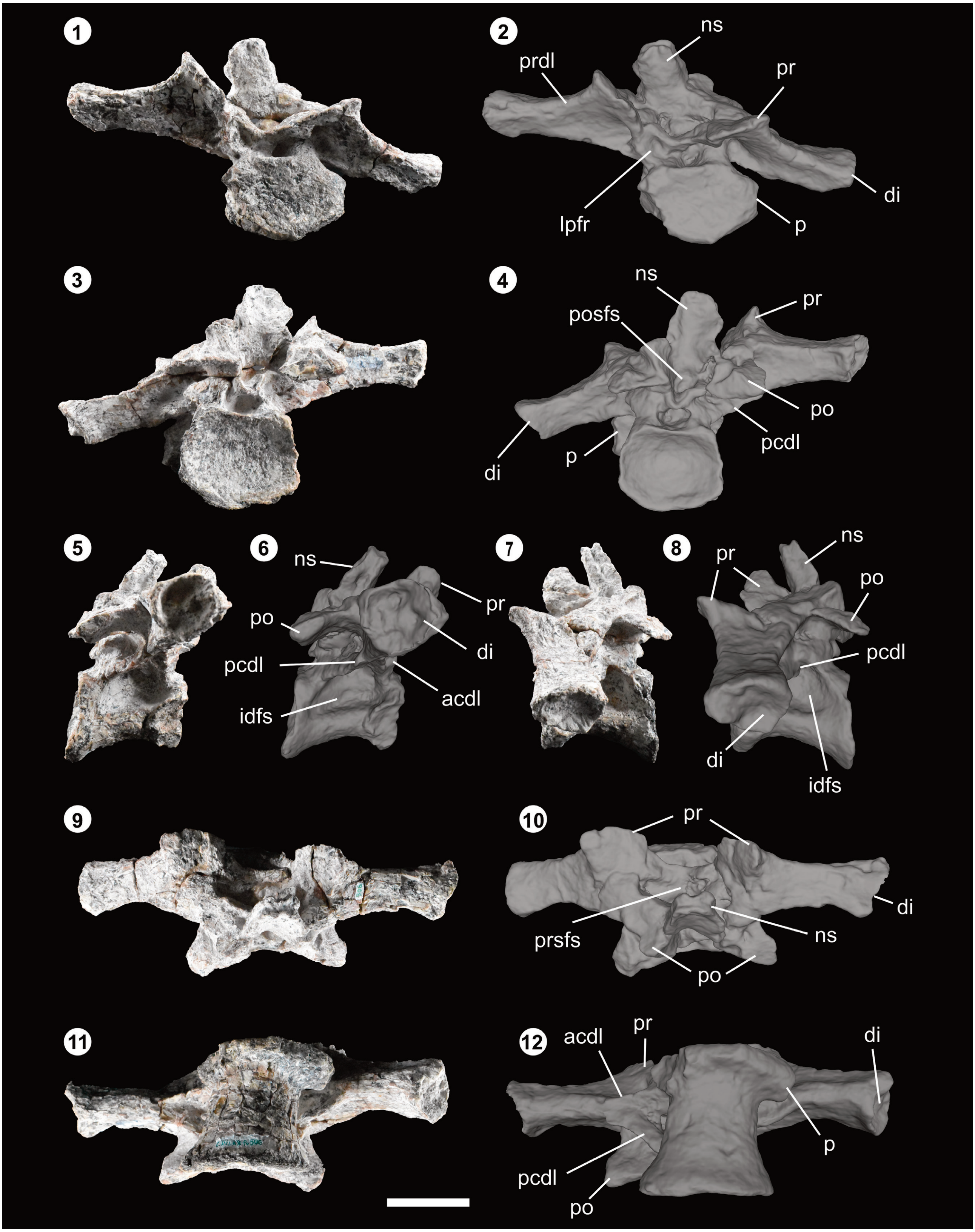

Figure 4. Second dorsal vertebra of ***Vitosaura colozacani*** gen. et sp. nov. (**CRILAR-Pv 506**) in **1, 2,** anterior; **3, 4,** posterior; **5, 6,** right lateral; **7, 8,** left lateral; **9, 10,** dorsal; and **11, 12,** ventral views. Abbreviations: **acdl,** anterior centrodiapophyseal lamina; **di,** diapophysis; **idfs,** infradiapophyseal fossa; **lpfr,** laminopeduncular foramen; **ns,** neural spine; **p,** parapophysis; **pcdl,** posterior centrodiapophyseal lamina; **po,** postzygapophysis; **posfs,** postspinal fossa; **pr,** prezygapophysis; **prdl,** prezygodiapophyseal lamina; **prsfs,** prespinal fossa. Scale bar equals 5 cm.

TABLE 1. Measurements in millimeters of the dorsal and sacral vertebrae.

	D1	D2	S2	S3	S4
Length of centrum	63.18	69.86	49.78*	77.76	78.58
Anterior height of centrum	51.63	52.16	68.20*	44.64	40.86
Anterior width of centrum	69.81	65.34	40.99	41.57*	30.02
Posterior height of centrum	69.66*	53.03	61.48	45.9	51.32
Posterior width of centrum	57.19*	66.93		24.58	
Length across zygapophyses		83.22/91.23			
Height neural spine		44.89			
Length neural spine at base		20.65			
Maximum height		141.57			

Values with an asterisk indicate incomplete measurements (owing to post-mortem damage) and the value given is the maximum measurable. Values with a slash indicate a double measurement due to deformation and the value given is the maximum measurable.

TABLE 2. Measurements in millimeters of the pelvic girdle.

	Acetabulum	Pubis	Ischium	Pubic peduncle	Ischial peduncle
Maximum height	149.15	4060.0*	35.21*	85.9	210.78
Maximum length	117.33	67.29	101.63	69.37	72.48

Values with an asterisk indicate incomplete measurements (owing to post-mortem damage) and the value given is the maximum measurable.

surface of the neural spine (shared with *Majungasaurus* and *Viavenator*, but absent in other taxa), ilium with subequal size of pubic and ischial articulation surfaces (only shared with *Rahiolisaurus* among abelisaurid taxa), and vertical ischial peduncle (shared with *Genusaurus*), and pubic shaft decreasing its anteroposterior depth distally (autapomorphy).

Ontogenetic assessment. The histological section of the pubis presents an external fundamental system in its outermost cortex, which indicates that somatic maturation was attained by the individual at the moment of death. In addition, features that include the full co-ossification between sacral centra and the bones of each hemipelvis indicate that CRILAR-Pv 506 was, at least, approaching skeletal maturity. The count of lines of arrested growth allows estimating a minimum age of 17 years for the specimen, assuming one period of slower growth per year.

RESULTS

Description and comparisons

Dorsal vertebrae. A vertebral centrum and a nearly complete vertebra, found in association, are interpreted here as the first and second dorsal vertebrae (D1 and D2) of *Vitosaura,* respectively. The centrum (Fig. 3.1–3.6, Table 1) is interpreted as a D1 due to the combination of a spool-shaped centrum, wider than it is long, and a parapophysis located at mid-height (Fig. 3.6). The D2 (Fig. 4.1–4.12, Table 1) lacks only the right parapophysis, but presents a marked deformation, very accentuated in the neural arch and mild to moderate in the centrum. This element is identified as a D2 due to the position of the parapophysis, the orientation of the transverse apophysis, the shape of the diapophyses, and the presence of laminopeduncular foramina. The centrum and neural arch are fused in D2, and no suture is observed (Fig. 4.1–4.8).

The centra of both anterior dorsal vertebrae are slightly transversely wider than dorsoventrally tall and anteroposteriorly long, as in the D1 of *Dahalokely* and the Abelisauridae indet. MAU-Pv-LI-665 (Méndez *et al*., 2022). By contrast, they differ from the longer-than-tall centra of *Carnotaurus* and *Majungasaurus* (MACN-Pv CH894; O'Connor, 2007). The centra are transversely compressed around mid-length in ventral view (Figs. 3.5, 3.6, 4.11, 4.12). The ventral surface is broad and slightly convex; D1 presents an incipient longitudinal keel (Fig. 3.4, 3.6), as in *Majungasaurus* and the Abelisauridae indet. MPM-99 (Martínez *et al*., 2004; O'Connor, 2007), whereas *Carnotaurus* has two longitudinal keels restricted to the anterior half of the centrum (MACN-Pv CH894). *Dahalokely* and *Skorpiovenator* lack a ventral keel (Farke & Sertich, 2013; Baiano, 2021). The centrum of the D2 of *Vitosaura* lacks ventral grooves or keels (Fig. 4.11, 4.12), as in the anterior dorsal centrum of *Aucasaurus*, *Dahalokely*, and *Skorpiovenator* (O'Connor, 2007; Méndez *et al*., 2022; Baiano *et al*., 2023), but keels are present in the D2 of *Carnotaurus* and *Majungasaurus* (MACN-Pv CH894; O'Connor, 2007). The anterior articular facet of D1 is well preserved (Fig. 3.1), being slightly concave, as in *Majungasaurus* and the Abelisauridae indet. MAU-Pv-Li-665 (Méndez *et al*., 2022). In D2, the articular facet is flat, as in the D2 of *Carnotaurus* and *Majungasaurus* (Bonaparte *et al*., 1990; O'Connor, 2007; Filippi *et al*., 2018), but contrasting with the concave surface of the D2 of *Aucasaurus*, *Majungasaurus*, and *Viavenator* (Sereno & Brusatte, 2008; O'Connor, 2007; Filippi *et al*., 2018; Baiano *et al*., 2023). The anterior articular surface of the D1 and D2 of *Vitosaura* has an oval contour (Figs. 3.1, 4.1, 4.2), with a transverse main axis, similar to that of MAU-Pv-LI-665, MPM-99, *Dahalokely,* and *Viavenator* (Martínez *et al*., 2004; Farke & Sertich, 2013; Filippi *et al*., 2016; Méndez *et al*., 2022). In particular, the dorsal margin of the anterior articular facet of the D2 is straight, as in MAU-Pv-LI-665, MPM-99, *Dahalokely*, and *Viavenator* (Martínez *et al*., 2004; Farke & Sertich, 2013; Filippi *et al*., 2016; Méndez *et al*., 2022). By contrast, the anterior articular facet of the D1 and D2 of *Carnotaurus* and *Majungasaurus* are subcircular (Bonaparte *et al*., 1990; O'Connor, 2007). The posterior articular surface of D1 is too poorly preserved (Fig. 3.2), but a subcircular outline can be inferred, as occurs in D2 (Fig. 4.3, 4.4). In the latter vertebra, the posterior facet is larger than the anterior one, as in most Abelisauridae (*e.g.*, Abelisauridae indet. MUVP 477, *Carnotaurus*, *Majungasaurus*; O'Connor, 2007). The posterior articular surface of D2 is strongly concave (Fig. 4.3, 4.4), as in most abelisaurids, but this facet is slightly concave in *Majungasaurus* and MAU-Pv-LI-665 (Méndez *et al*., 2022). The dorsal margin of this facet is also straight, similar to that of MAU-Pv-LI-665 (Méndez *et al*., 2022) and different from that of *Majungasaurus*, which has a dorsoventrally elongated oval outline (O'Connor, 2007).

The parapophyseal facet of D1 and D2 is concave, with a semicircular outline in D1 (Fig. 3.3, 3.4) and an oval profile in D2, with a dorsoventral main axis, as in *Aucasaurus*, *Carnotaurus*, *Dahalokely*, *Skorpiovenator*, and *Xenotarsosaurus* (Baiano *et al*., 2023). The parapophysis projects laterally and immediately posterior to the edge of the anterior articular facet, halfway along the dorsoventral height of the centrum, as in *Carnotaurus*, *Dahalokely*, and *Majungasaurus* (Bonaparte *et al*., 1990; O'Connor, 2007; Farke & Sertich, 2013). The lateral surface of the centra have a large elliptical fossa on its dorsal half, being better preserved in D2; this fossa is continued dorsally onto the centrodiapophyseal fossa of the neural arch. This fossa lodges a circular pneumatic foramen that is placed immediately posterodorsal to the base of the parapophysis and because of its position is interpreted as homologous to the anterior pleurocoel present in most other abelisauroids. There is no pneumatic foramen on the posterior half of the centrum, as in the anterior dorsal centrum of several other abelisaurids (*e.g.*, *Aucasaurus*, *Carnotaurus*, *Dahalokely*, *Eoabelisaurus*, *Xenotarsosaurus*; Martínez *et al*., 1986; Pol & Rauhut, 2012; Farke & Sertich, 2013; Baiano, 2021), but contrasting with its absence in *Carnotaurus* (MACN-Pv CH894). In dorsal view, the D1 possesses two parallel, longitudinal ridges that run along the centra and probably represent the base of the neural arch.

The neural arch, only preserved in the D2 (Fig. 4.1–4.10), is low, with a maximum height reaching 1.5 times the height of the anterior articular facet of the centrum. The neural canal is cylindrical, with an elliptical outline in anterior view, and a subcircular outline in posterior view. The shape differences in the anterior and posterior openings are the result of deformation. The prezygapophyses project anterodorsally and beyond the level of the anterior margin of the centrum in lateral view (Fig. 4.7–4.10), as in *Majungasaurus* (O'Connor, 2007) and *Carnotaurus* (MACN-Pv CH894). By contrast, the prezygapophyses do not project beyond the anterior margin of the centrum in the D1 of MAU-Pv-LI-665 (Méndez *et al.*, 2022) and *Dahalokely* (Farke & Sertich, 2013). It is not possible to determine precisely the angle formed between the prezygapophyseal and postzygapophyseal articular facets and the sagittal plane, but it was likely approximately 45°, as in *Dahalokely* (Farke & Sertich, 2013). The margins of the prezygapophyses are positioned dorsal to the level of those of the postzygapophyses, a condition also observed in *Dahalokely* and MAU-Pv-LI-665 (Farke & Sertich, 2013; Méndez *et al.*, 2022). The infraprezygapophyseal fossa deepens medially and is delimited by the centroprezygapophyseal lamina, as in MAU-Pv-LI-665 and *Viavenator* (Filippi *et al.*, 2018; Méndez *et al.*, 2022). The centroprezygapophyseal lamina intersects the prezygapophysis near its anterior apex, as in *Dahalokely* and *Carnotaurus*, but the lamina contacts the prezygapophysis medially in *Majungasaurus* (Farke & Sertich, 2013). Laminopeduncular foramina are located on the anterior surface of the neural arch (Fig. 4.1, 4.2), dorsolateral to the neural canal, as in the D1/D2 of MAU-Pv-LI-665, *Carnotaurus*, *Dahalokely*, and *Majungasaurus* (Farke & Sertich, 2013). The transverse processes are subhorizontal and directed laterally, resembling MAU-Pv-LI-665 and the D2 of *Dahalokely*, *Majungasaurus*, and *Carnotaurus* (Méndez *et al.*, 2022). The diapophyseal facet is concave, with the anterior margin projecting more laterally than the posterior one, and faces slightly ventrally (Fig. 4.5–4.8). This facet has a circular contour, contrasting with the quadrangular diapophyseal facet of the D2 of *Majungasaurus* (O'Connor, 2007). The prezygodiapophyseal, anterior centrodiapophyseal, posterior centrodiapophyseal, and postzygodiapophyseal laminae are well-developed.

The postzygapophyses have a subtriangular articular facet, with a posterolateral apex, that faces mainly ventrally (Fig. 4.3, 4.4, 4.9, 4.10), as in *Majungasaurus, Carnotaurus,* and *Dahalokely* (Farke & Sertich, 2013), but not as in MAU-Pv-LI-665, in which the postzygapophyseal facet is subrectangular (Méndez *et al.*, 2022). The postzygapophyses form an angle of ca. 45° with the transverse processes in dorsal view (Fig. 4.9, 4.10), as in the D1 of *Dahalokely* (Farke & Sertich, 2013). Due to deformation, the left postzygapophysis exceeds the level of the posterior edge of the centrum, but it probably did not originally. The infrapotzygapophyseal fossa is large and deep, as in MAU-Pv-LI-665 (Méndez *et al.*, 2022). The hyposphene is V-shaped, with a ventral apex, and poorly posteriorly developed, as in the D2 of *Carnotaurus*, the D1 and D2 of *Majungasaurus*, and the D2 of *Dahalokely* (Bonaparte *et al.*, 1990; Farke & Sertich, 2013).

The neural spine is sub-rectangular in anterior view (Fig 4.1, 4.2), with rounded edges at the distal apex. The neural spine slants slightly anteriorly in lateral view, but we interpret that this is an artifact produced by deformation. On the anterior surface, a very large and deep prespinal fossa is located between the base of the neural spine and the prezygapophyses, being delimited posterolaterally by weak spinoprezygapophyseal laminae. The postspinal fossa is slightly smaller and shallower, extending onto the posterior surface of the neural spine up to its top. The neural spine is almost half the length of the centrum, as in *Dahalokely* (Farke & Sertich, 2013), the D2 of *Carnotaurus* (MACN-Pv CH894), and the D1 of *Majungasaurus* (O'Connor, 2007). The neural spine is more compressed anteroposteriorly than transversely. Between the spinopostzygapophyseal and spinoprezygapophyseal laminae, the prezygapophyseal-spinodiapophyseal fossa is shallow on the lateral surface of the neural spine. The dorsal surface of the neural spine possesses a deep transverse groove (Fig. 4.5-4.10), as in *Majungasaurus* and MAU-Pv-LI-665, but this feature is absent in other ceratosaurs (O'Connor, 2007; Méndez *et al.*, 2022).

Sacral vertebrae. Three sacral centra are preserved in three blocks, with irregular margins associated with fractures in a dorsoventral direction (Fig. 5). They are adhered to the anteromedial surface of the ilium and exposed on the right side. The three sacral centra are fused to each other, as occurs between the second and fifth sacral vertebrae of most Abelisauridae (*e.g.*, MMCh-PV 69, *Aucasaurus*, *Caletodraco*, *Carnotaurus*, *Eoabelisaurus*, *Koleken*, *Majungasaurus*, *Rahiolisaurus*, *Rajasaurus*; Bonaparte *et al.*, 1990; Wilson *et* *al*., 2003; Baiano, 2021; Baiano *et al*., 2023). The sacrum is transversely compressed, as in *Caletodraco*, *Carnotaurus*, and *Koleken* (Bonaparte *et al*., 1990; Baiano *et al*., 2023; Buffetaut *et al*., 2024; Pol *et al*., 2024). The sacral centra are apneumatic, as those of *Aucasaurus*, *Majungasaurus*, and other abelisaurids (O'Connor, 2007; Baiano *et al*., 2023). The lateral surface of the centra is almost flat to slightly concave, lacking fossae, as in MAU-Pv-LI 547, MMCh-PV 69, *Aucasaurus*, *Carnotaurus*, and *Majungasaurus* (Baiano *et al*., 2023). The centrum rims have an oval cross-section, with a dorsoventral main axis.

Pelvic girdle*.* Both hemipelves are partially preserved (Fig. 5.1–5.13, Table 2). The left one preserves the acetabular region of the ilium, the proximal end of the ischium, a small portion of the ischial peduncle of the pubis, and most of the pubic shaft (Fig. 5.2–5.7). The right hemipelvis preserves the pubic peduncle of the ilium, a small portion of the iliac blade, and the proximal end of the pubis (Fig. 5.8–5.13). The surface of the bones is deteriorated and, in some regions, preserved as small, overlapping, or isolated bone fragments that hamper the recognition of some structures and shapes.

The bones of the hemipelves are co-ossified with each other, but it is still possible to distinguish the boundaries

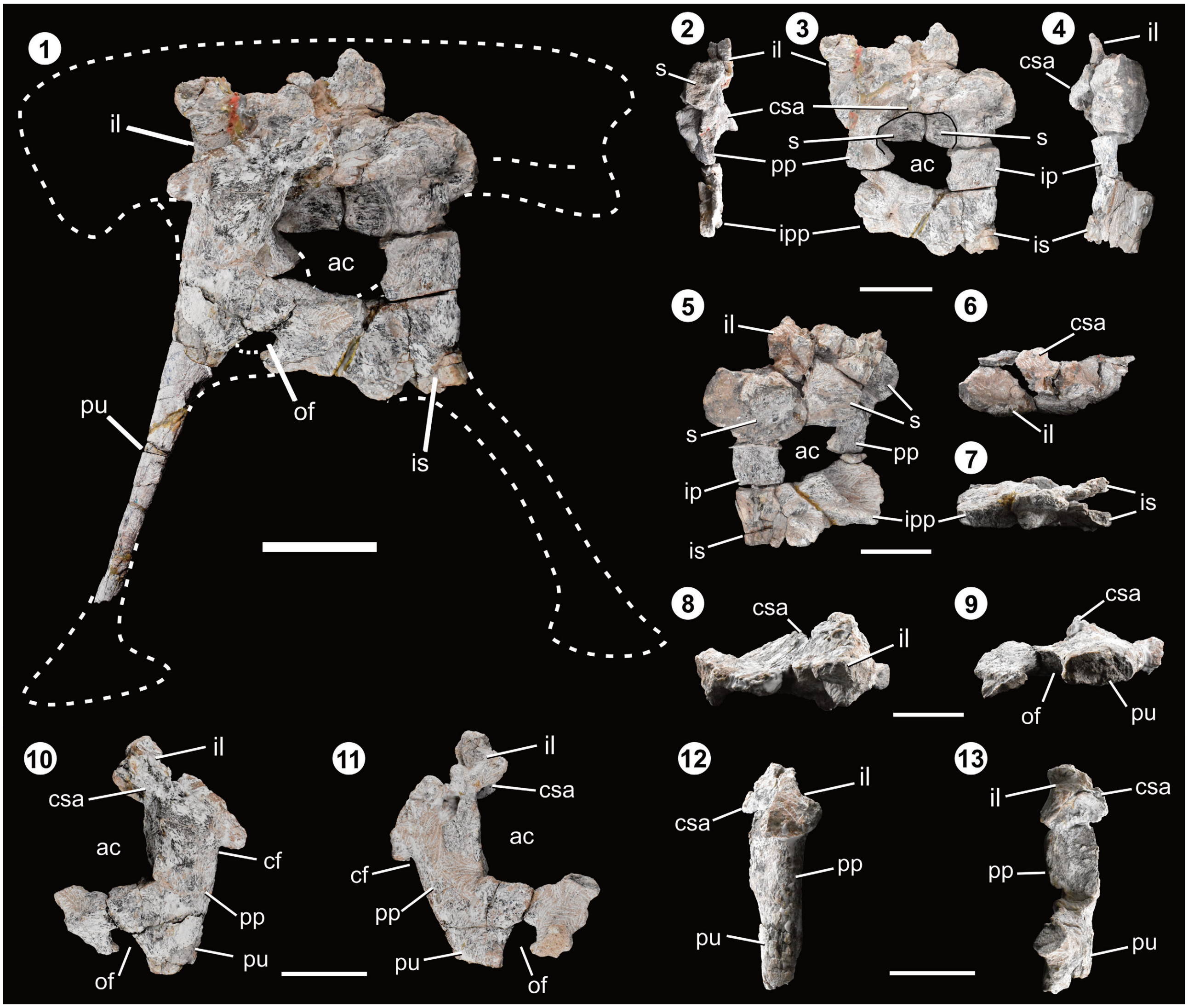

Figure 5. Partial pelvic girdle of ***Vitosaura colozacani*** gen. et sp. nov. (**CRILAR-Pv 506**). **1,** Reconstruction of left hemipelvis; **2–7,** left acetabular region; and **8–13,** right anterior acetabular region in **1, 3, 10,** lateral; **2, 12,** anterior; **4, 13,** posterior; **5, 11,** medial; **6, 8,** dorsal; and **7, 9,** ventral views. Abbreviations: **ac,** acetabulum; **cf,** cuppedicus fossa; **csa,** supraacetabular crest; **il,** ilium; **ip,** ischial peduncle; **ipp,** ischial pubic peduncle; **is,** ischium; **of,** obturator foramen; **pp,** pubic peduncle; **pu,** pubis; **s,** sacral vertebrae. Scale bars equal 10 cm.

between bones because of faint suture scars. Only small portions of the base of the preacetabular process are preserved in both ilia. The transition between the pubic peduncle and the preacetabular process is slightly transversely broader than the more dorsal extension of the iliac blade. The supraacetabular crest projects laterally and slightly ventrally, and bows ventrally to accompany the strongly anteroposteriorly concave dorsal contour of the acetabulum, as in *Aucasaurus*, *Eoabelisaurus*, *Skorpiovenator*, and *Kurupi* (Baiano, 2021; Cerroni *et al.*, 2022; Iori *et al.*, 2021; Pol *et al.*, 2024). By contrast, the dorsal margin of the acetabulum is flatter in MCF-PVPH-237, *Carnotaurus*, *Genusaurus*, *Majungasaurus*, and *Spectrovenator* (Carrano, 2007; Pol *et al.*, 2024). The supraacetabular crest extends posteriorly over the level of the ischiadic peduncle, and this indicates that it was continuous with the brevis shelf of the postacetabular process, as occurs in other ceratosaurs (Tykoski & Rowe, 2004). The pubic peduncle of the ilium has a sub-oval cross-section with an anteroposterior main axis and a flat medial surface. The cuppedicus fossa, if originally present, is not preserved. Posteriorly, the central region of the iliac blade is only represented by the first six to eight centimetres above the supraacetabular crest. The preserved lateral surface of the blade is slightly concave. The pubic peduncle is anteroventrally oriented, as in the Brazilian abelisaurid DGM 927-R, *Rahiolisaurus*, and *Majungasaurus* (Sampson *et al.*, 1998; Carrano, 2007; Novas *et al.*, 2010; Brum *et al.*, 2016). By contrast, the pubic peduncle of *Aucasaurus* has a more vertical orientation (Baiano, 2021). The ischial peduncle projects almost vertically, as in MMCh-PV 69 and *Genusaurus* (Canale *et al.*, 2016; Pol *et al.*, 2024), but it has a distinct posteroventral orientation in *Aucasaurus*, *Koleken*, *Majungasaurus*, *Kurupi*, and *Rahiolisaurus* (Carrano *et al.*, 2007; Novas *et al.*, 2010; Baiano, 2021; Iori *et al.*, 2021; Pol *et al.*, 2024). The articular facet of the ischial peduncle is anteroposteriorly as deep as that of the pubic peduncle. By contrast, in the vast majority of abelisaurids, to the exclusion of *Rahiolisaurus*, the pubic facet is deeper (Novas *et al.*, 2010). Similarly, the pubic and ischial peduncles have similar lengths, as in *Majungasaurus* (Carrano & Sampson, 2008; Pol *et al.*, 2024), whereas the pubic peduncle is longer in most other abelisaurids (Carrano & Sampson, 2008; Pol *et al.*, 2024). The lateral surface of the ischial peduncle has a distinct, comma-shaped antitrochanter, as in other ceratosaurs (*e.g.*, *Ceratosaurus*, *Eoabelisaurus*). The medial surface of the ilia is mostly obscured by matrix, mixed with bone fragments, and the sacral vertebrae.

Both pubes are partially preserved, lacking part of the pubic plate and the distal region of the bone (Fig. 5.1, 5.10–5.13). The proximal end of the pubis is fused to the ilium and the ischium. The fusion between the pubis and ilium occurs in skeletally mature specimens of other abelisaurids (*e.g.*, MCF-PVPH-820; MMCh PV 69; MCF-PVPH-237, *Carnotaurus*, *Eoabelisaurus*, *Koleken*, *Skorpiovenator*; Baiano, 2021; Pol *et al.*, 2024). In anterior view, the proximal end of the pubes converge medially, showing a slightly concave lateral border, as in MCF-PVPH-820, *Aucasaurus, Carnotaurus*, and *Pycnonemosaurus* (Coria *et al.*, 2006; Baiano, 2021; Delcourt, 2017). The iliac peduncle has a sub-oval cross-section, with an anteroposterior main axis, a slightly rounded lateral edge, and a flat medial edge. In lateral view, the iliac peduncle has a quadrangular outline, as in MCF-PVPH-820 and *Aucasaurus* (Baiano, 2021). The iliac and ischial peduncles are broadly separated from each other by a concave non-articular surface that forms the acetabular border, as occurs in other dinosaurs (Nesbitt, 2011). The pubis is transversely broader closer to the sutures with the ilium and ischium, and it is thinner where the peduncles converge. The pubic plate encloses the obturator foramen dorsally, anteriorly, and posteriorly, but it is likely that the foramen was also closed ventrally by the bony plate, as in MCF-PVPH-237, *Aucasaurus*, and *Carnotaurus* (Bonaparte *et al.*, 1990; Coria *et al.*, 2006; Sereno & Brusatte, 2008). The obturator foramen is oval in lateral view, with an anteroventral-to-posterodorsal main axis, different from the subhorizontal condition in *Koleken*, *Carnotaurus*, *Ceratosaurus*, *Eoabelisaurus*, and *Skorpiovenator* (Cerroni *et al.*, 2022; Pol *et al.*, 2024). A rough protuberance for anchoring of the *M. ambiens* occurs on the lateral to anterolateral surface of the proximal end of the pubis of MCF-PVPH-820, MMCh PV 69, *Aucasaurus, Carnotaurus, Ceratosaurus, Eoabelisaurus, Rajasaurus,* and *Skorpiovenator* (Wilson *et al.*, 2003; Baiano, 2021; Cerroni *et al.*, 2022), but its presence cannot be determined in *Vitosaura* due to poor surface preservation.

The preserved portion of the pubic shaft is straight and anteroventrally oriented in lateral view, as in MMCh PV 69, *Aucasaurus,* and *Carnotaurus* (Bonaparte *et al.*, 1990;

Canale *et al.*, 2016; Baiano, 2021), but unlike the anteriorly bowed shaft of MMCh-PV 69, MCF-PVPH-237, *Genusaurus*, *Eoabelisaurus*, and *Skorpiovenator* (Accarie *et al.*, 1995; Baiano, 2021). The pubic apron is poorly preserved as a thin longitudinal ridge. The shaft gradually decreases its anteroposterior depth distally, contrasting with the condition in other ceratosaurs, such as *Ceratosaurus* (Gilmore, 1920), *Masiakasaurus* (Carrano *et al.*, 2002), *Eobaelisaurus* (Pol & Rauhut, 2012), *Rahiolisaurus* (Novas *et al.*, 2010), and *Carnotaurus* (Bonaparte *et al.*, 1990). The pubic apron lacks the external surface of the bone, and it is difficult to determine its shape. The posterior surface of the shaft is moderately concave. The shaft has a triangular cross-section around mid-length.

The proximal end of the left ischium contributes, together with the ilium, to the well-developed antitrochanter that delimits posteriorly the acetabulum (Fig. 5.1–5.7). Although the ischium is co-ossified with the ilium and pubis, it can be determined that their contact lengths are subequal. The base of the ischial shaft is preserved and has a suboval cross-section with an anteroposterior main axis. Overall, the preserved morphology of the ischium of *Vitosaura* is congruent with that of other abelisaurids.

Histology

A thin transverse section of the left pubic mid-shaft was prepared for histological analysis (Fig. 6.1). It has distortions due to biogenetic processes. The cross-section of the bone is oval, with an anteroposterior main axis, and the medullary cavity is also oval, but with a near-transverse main axis (Fig. 6.2). In the cortex, the few fractures are radial and almost perpendicular to the lines of arrested growth (LAGs). Most of the medullary cavity is filled by a fine sedimentary matrix of chalcedonic quartz and calcite, with subangular, almost spherical, moderately sorted, matrix-supported clasts. It is mainly composed of quartz, plagioclase, and rock fragments (Fig. 6.4). At the posterolateral border, a portion of spongy tissue is preserved within the medullary cavity, represented by trabeculae that delimit the labyrinthine system and intertrabecular spaces, which are also filled by sediment. The thin internal circumferential layer is discontinuous, composed of lamellar tissue, and delimits the trabeculae and the secondary osteons of the medullary cavity (Fig. 6.5–6.6). Immediately outwards the posterior border of the medullary cavity, there is a small irregular strip that does not resemble any bone tissue and is interpreted as a diagenetic product from silica (Fig. 6.7). On the other hand, the cortex is mainly formed by a dense Haversian tissue that is a result of the resorption of the compact tissue (Fig. 6.8). The secondary osteons are abundant, located around the perimedullar region and extend over a large part of the anterior surface, medially reaching the subperiosteal cortex and laterally they are concentrated in the middle cortex. In this same region and with an abrupt transition, compact primary tissue is observed, characterized by low vascularity, with circumferential and oblique vascular channels. In the posterolateral region, radial channels predominate (Fig. 6.10). The primary bone, deposited in the subperiosteal cortex, is formed by a layer of avascular lamellar tissue and possesses LAGs. This region is interpreted as an external fundamental system (Chinsamy-Turan, 2005). Its preservation is limited only to the anterolateral-lateral border of the thin section, and the LAGs have moderate continuity along this region. At least 16 growth cycles (including single and double LAGs and rings) are observed (Fig. 6.9). In the anteromedial region, a fibrous tissue is distinguished, which is here interpreted as Sharpey's fibers (Fig. 6.11).

Phylogenetic relationships

The phylogenetic analysis under equal weights (EW) recovered >500,000 most parsimonious trees (MPTs) of 562 steps, with a consistency index of 0.46838 and a retention index of 0.70353. The optimal results were found 182 times of the 1,000 replicates. The strict consensus tree of these MPTs shows a massive polytomy composed of all the ceratosaur species, including *Vitosaura*, and only recovering Elaphrosaurinae as a lesser inclusive clade. The iterPCR protocol detected that the a posteriori pruning of *Quilmesaurus*, *Afromimus*, *Kryptops*, and *Huinculsaurus* resulted in the recovery of considerably more resolved interrelationships within Ceratosauria (Fig. 7). This reduced strict consensus tree recovers the traditional dichotomy between Noasauridae and Abelisauridae, in which *Vitosaura* is positioned within the latter clade. Brachyrostra is found within Abelisauridae and it is composed mainly of South American species, but also the European *Arcovenator* and *Genusaurus*. *Vitosaura* and the Indian *Rahiolisaurus* are

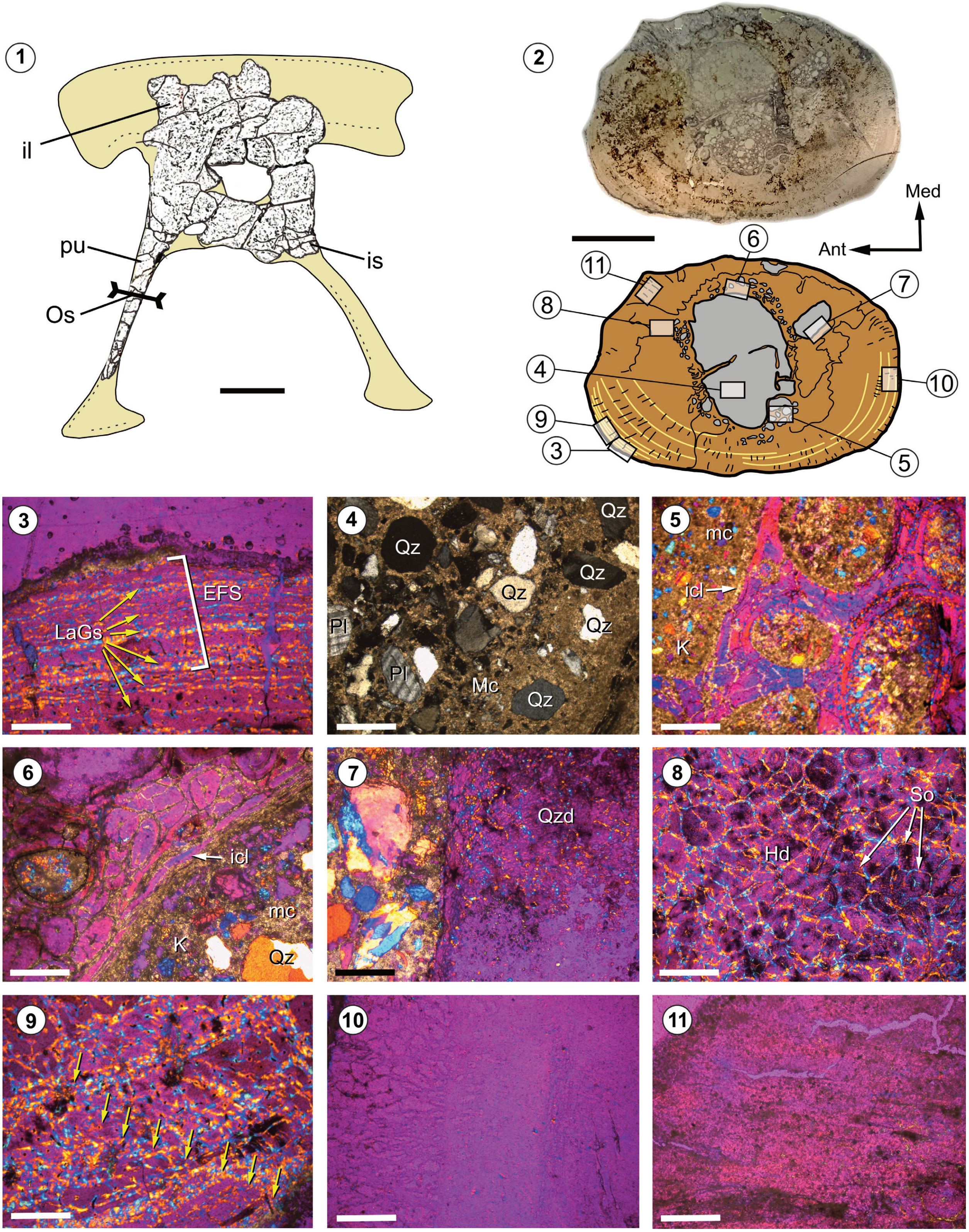

Figure 6. Osteohistology of ***Vitosaura colozacani*** gen. et sp. nov. **1,** Pelvic girdle of **CRILAR-Pv 506** indicating the osteohistological thin section made in the left pubis. **2,** Transverse thin section of pubis and drawing restoration based on the specimen. **3** to **11,** Petromicrographs of different microregions of the thin section of the pubis showing osteohistological features of **CRILAR-Pv 506** such as the medullary bone, lines of arrested growth (yellow arrows), secondary osteons and the infill sedimentary matrix. Abbreviations: **LaGs,** growth lines; **mc,** medullary cavity; **cl,** inner circumferential layer; **Hs,** Haversian system; **Mc,** matrix of chalcedonic quartz and calcite; **Os,** osteohistological section; **Pl,** plagioclase; **Qz,** quartz; **Qzd,** diagenetic product from silica; **So,** secondary osteons. Scale bars equal 10 cm in 6.1, 1 cm in 6.2, and 0.5 mm in 6.3–6.11.

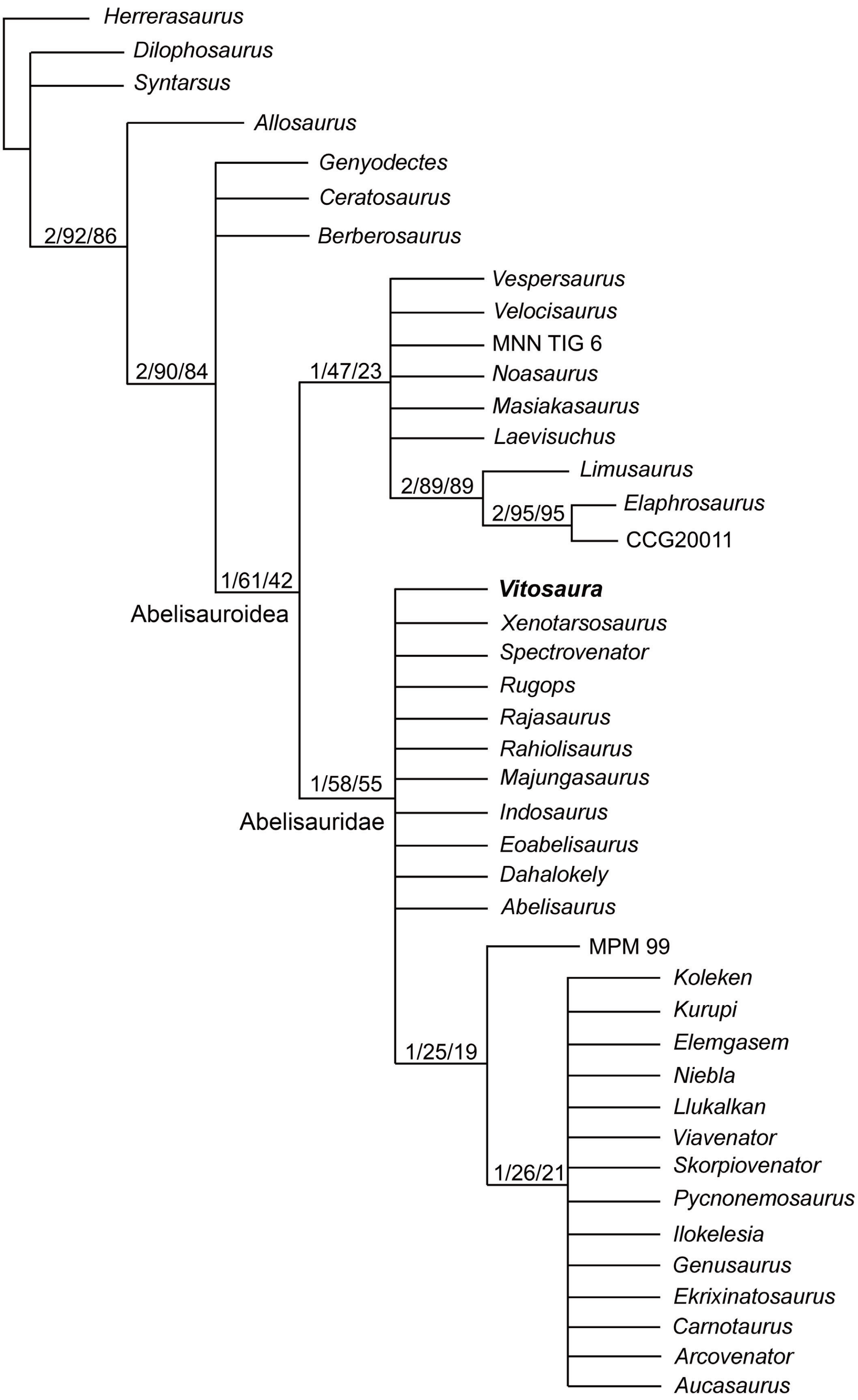

Figure 7. First reduced strict consensus tree showing the phylogenetic relationships of ***Vitosaura colozacani*** gen. et sp. nov. (**CRILAR-Pv 506**) among ceratosaurs found in the analysis under equal weights. Values above each branch are Bremer supports (left), and no-zero weight symmetric (probability = 25%) absolute (center) and GC (right) resampling frequencies.

recovered as sister taxa to each other in all the MPTs. The additional a posteriori pruning of *Vitosaura* and *Rahiolisaurus* resulted in an even more resolved second reduced consensus tree (Fig. 8), in which Majungasaurinae and Brachyrostra are recovered within Abelisauridae. The *Vitosaura* + *Rahiolisaurus* clade adopted multiple alternative positions among the non-brachyrostran abelisaurids in the MPTs. These reduced consensus trees are all consistent with those of other recent analyses of previous iterations of this data matrix (*e.g.*, Pol *et al.*, 2024; Seculi-Pereyra *et al.*, 2025).

The sister taxon relationship between *Vitosaura* and *Rahiolisaurus* is supported by the subequal relative sizes of the iliaco-pubic and iliaco-ischiatic joints (character 187: 0→1). When *Vitosaura* + *Rahiolisaurus* are recovered within Majungasaurinae, the Argentinean taxon is positioned in this clade because of the presence of a transverse groove on the apex of the neural spine (character 246: 1→0). *Vitosaura* does not preserve any of the synapomorphies of Abelisauridae optimized in our analysis. The branch supports for Abelisauridae are low, with minimal Bremer support and absolute and GC symmetric resampling frequencies below 60%. Similarly, the branch supports of the abelisaurid branches are also poorly supported. Only one additional step allows forcing the position of the *Vitosaura* + *Rahiolisaurus* clade within Carnotaurini, *i.e.*, deeply nested within Brachyrostra.

The global strict consensus tree (GSCT) recovered from all the MPTs found under implied weighting (IW) (see tree metrics in Table 3) and using the different concavity constant values (k = 3–8) shows completely unresolved relationships within Abelisauridae (Fig. 9), contrasting with the recognition of Brachyrostra in the analysis under EW. The a posteriori pruning of *Dahalokely*, *Kryptops*, *Rahiolisaurus*, *Elemgasem*, *Kurupi*, and *Vitosaura* resulted in a much more resolved reduced GSCT, with only a trichotomy within Majugasaurinae and a polytomy at the base of Furileusauria. *Vitosaura* is recovered in multiple positions within Abelisauridae among the MPTs, namely as a member of an early-diverging clade also composed of *Eoabelisaurus* and *Xenotarsosaurus* (k = 4, 5), as the sister taxon of the clade formed by *Rugops* and more deeply nested abelisaurids (k = 6–8), within Majungasaurinae (k = 3), or as a non-brachyrostran Furileusauria (k = 3). The position of *Vitosaura* as a majungasaurine is supported by the presence of the transverse groove on the top of the anterior dorsal neural spine (character 246: 1→0), as was the case under EW. In addition, *Vitosaura* is positioned as closely related to *Viavenator* within Furileusauria because it shares character state 246(0) with the latter genus. The placement of *Vitosaura* around the base of Abelisauridae is because it is recovered as sister taxon to *Rahiolisaurus,* and they share the absence of a posterior pleurocoel in postaxial presacral vertebrae (character 105: 2→0). In these analyses, *Rahiolisaurus* is excluded from the clade composed of *Rugops* and more deeply nested abelisaurids because it lacks cervical vertebrae with mediolaterally elongated zygapophyses, with the lateral half greatly expanded anteroposteriorly (character 107: 0→1).

TABLE 3. Number of most parsimonious trees (MPTs) found and homoplasy indices of the six analyses under implied weighting with the different concavity constant values.

Concavity constant value (k)	Number of MPTs	Consistency index	Retention index	Fit (adjusted homoplasy)
3	56,892	0.484956	0.722593	57.02143
4	12,612	0.48582	0.72355	47.34286
5	12,612	0.48582	0.72355	40.52976
6	>100,000	0.48754	0.72545	35.45411
7	>100,000	0.48754	0.72545	31.51515
8	>100,000	0.48754	0.72545	28.37203

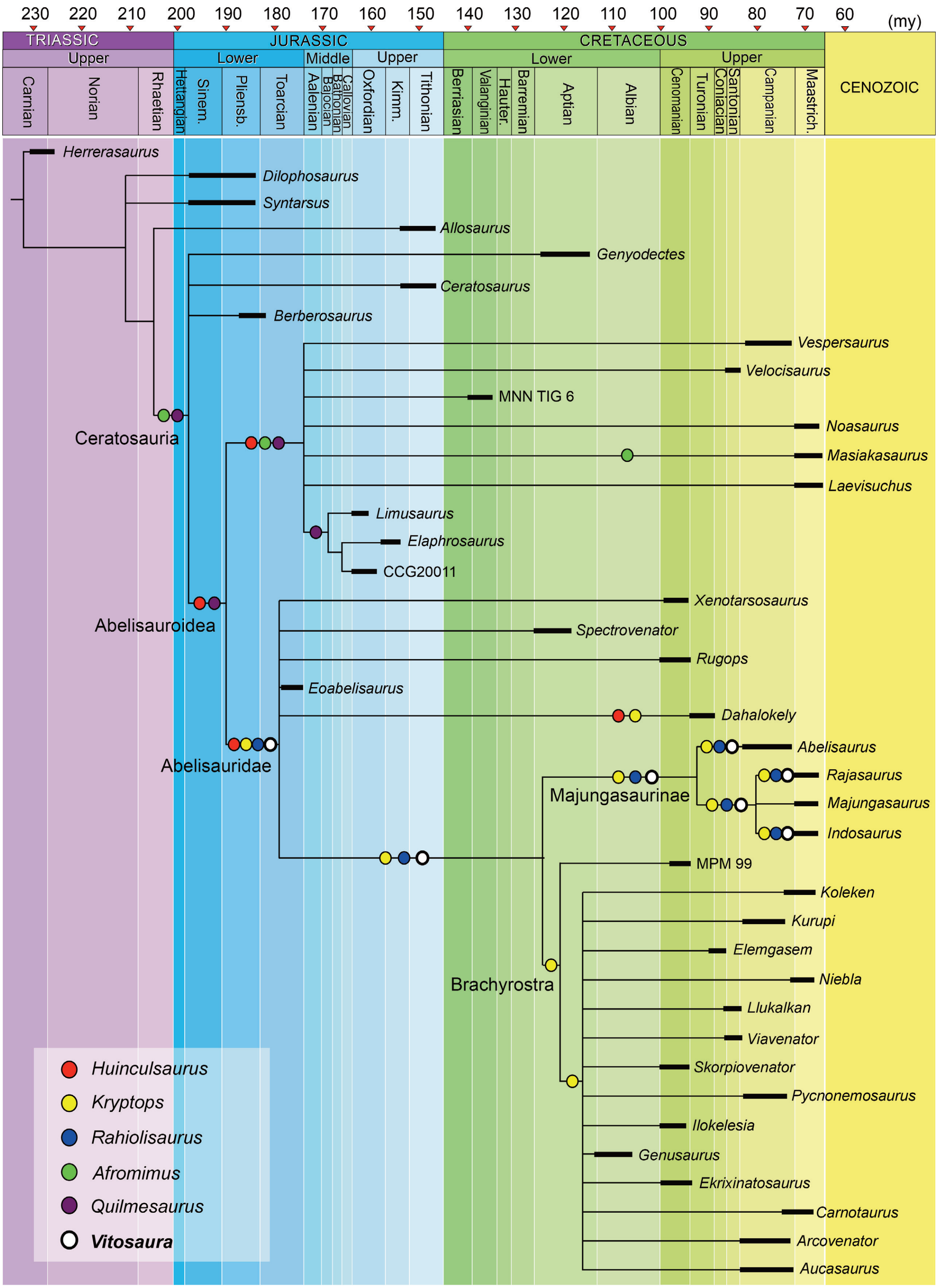

Figure 8. Time-calibrated second reduced strict consensus tree showing the alternative positions of topologically unstable terminals among the most parsimonious trees found in the analysis under equal weights.

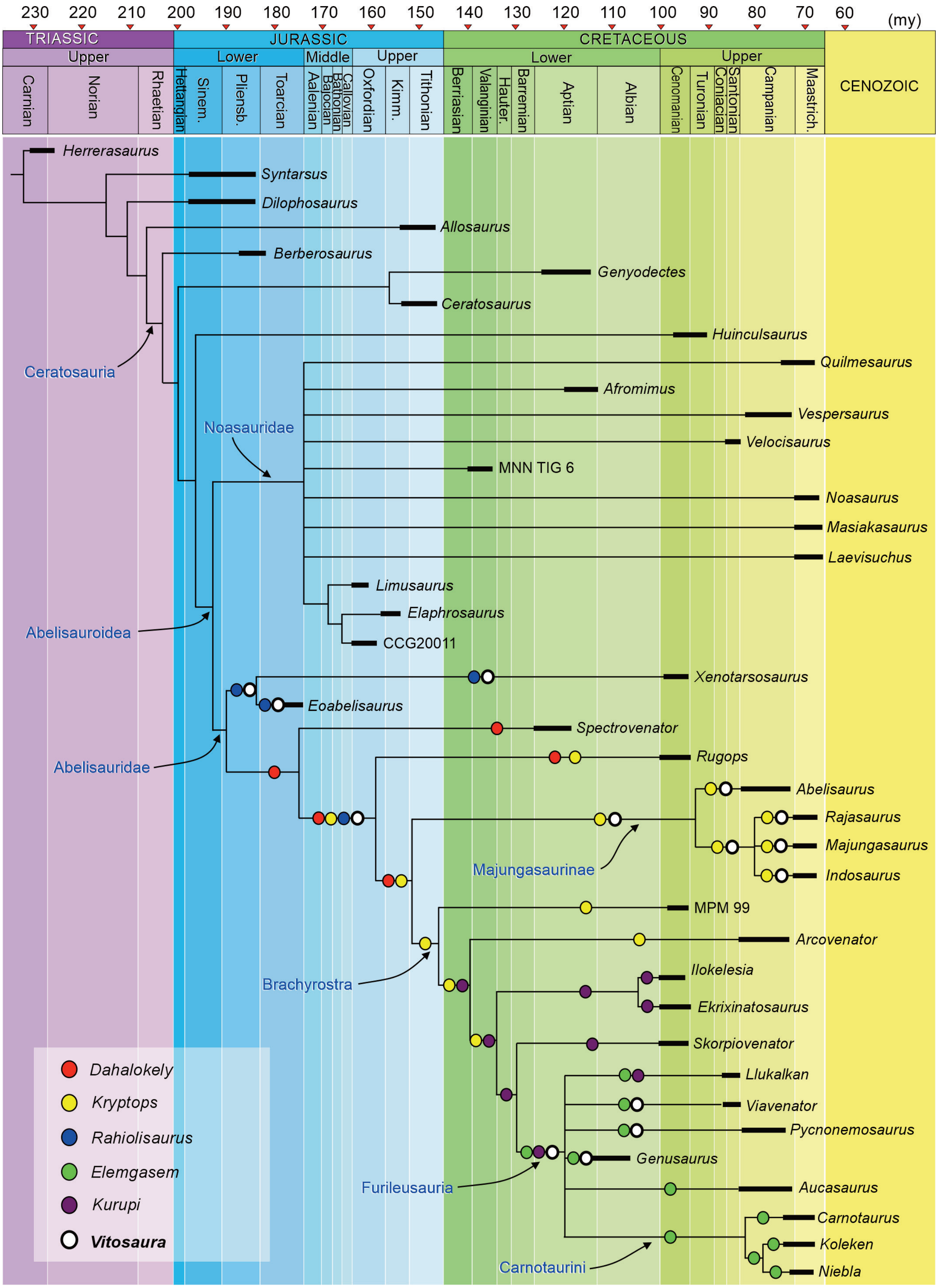

Figure 9. Time-calibrated reduced global strict consensus tree showing the alternative positions of topologically unstable terminals among the most parsimonious trees found in the analyses under implied weighting (k = 3–8).

DISCUSSION

Although fragmentary, the holotype of *Vitosaura colozacani* possesses a unique combination of character states that allow it to be distinguished from other nominal abelisaurid species. In particular, the pelvic girdle has an autapomorphic distally tapering pubic shaft that we have not observed in other ceratosaurs that we are aware of. Beyond the combination of character states listed in the diagnosis, *Vitosaura colozacani* also possesses a series of features with a striking distribution among abelisaurids. It shares with the Malagasy *Majungasaurus* and the Patagonian *Viavenator* and MAU-Pv-LI-665 the presence of a transverse groove on the top of the neural spine of the anterior dorsal vertebrae. Indeed, this latter groove was originally considered an autapomorphy of *Majungasaurus crenatissimus* (O'Connor, 2007). The preserved features in the holotype of *Vitosaura colozacani* indicate that the body plans of the Late Cretaceous abelisaurids were more diverse than thought.

Vitosaura is added as a new element of the vertebrate assemblage of the Los Llanos Formation, which is also composed of the sphagesaurian notosuchian *Llanosuchus tamaensis*, and other still unnamed or indeterminate theropods and titanosaurs (Fiorelli *et al.*, 2016; Hechenleitner *et al.*, 2016, 2018). *Vitosaura* roamed a seasonal, semi-arid, and drained environment (Fiorelli *et al.*, 2016; Basilici *et al.*, 2017), with average annual rainfall fluctuating between 230 mm/year and 450 mm/year in the Tama region (Basilici *et al.*, 2017). The holotype of *Vitosaura colozacani* represents a somatically mature individual because of the presence of an external fundamental system in the paleohistological thin section of the left pubis. This indicates that this individual was fully grown or very close to stopping the growth and allows it to be compared with the body size of other abelisaurids. The measurements of the preserved elements of *Vitosaura* indicate that it is a medium-sized abelisaurid with a total length between 4.5–5.5 m, similar in size to the holotypes of *Aucasaurus* and *Koleken*, but smaller than *Carnotaurus*, *Rajasaurus*, *Rahiolasaurus*, and *Majungasaurus*.

Vitosaura could be scored only for 5.6% of the characters of the phylogenetic data matrix, and hence, future discoveries could likely change the results recovered here and allow for a more precise placement for the taxon. Nonetheless, with the evidence at hand, we can discuss some implications based on the most parsimonious phylogenetic hypotheses recovered by our analyses. The position of *Vitosaura* as a non-brachyrostran abelisaurid recovered in the analysis under EW and some of the analyses under IW differs from the brachyrostran affinities found for the other Late Cretaceous abelisaurid species recorded in northwestern Argentina, *Guemesia ochoai*. This would suggest that the abelisaurid assemblage of northwestern Argentina was composed of both early-diverging abelisaurids (*i.e.*, non-brachyrostrans) and deeply nested abelisaurids (*i.e.*, brachyrostran), as recent phylogenetic analyses indicate for the abelisaurids of northern Patagonia (*e.g.*, Agnolín *et al.*, 2022; Pol *et al.*, 2024). Unfortunately, the hitherto known Late Cretaceous abelisaurids from Brazil (*e.g.*, Kellner & Campos, 2002; Delcourt, 2017; Delcourt & Iori, 2018; Iori *et al.*, 2021) are fairly incomplete and little osteological elements are comparable, hampering proper comparisons with *Vitosaura*. The sister taxon relationship between *Vitosaura* and the Indian *Rahiolasaurus* has potentially interesting biogeographic implications, indicating that the close affinities between South American and Indo-Malagasy species persisted until the latest Cretaceous. This biogeographic pattern is also suggested by some recent results that recovered the Patagonian *Abelisaurus* as a member of Majungasaurinae (Pol *et al.*, 2024). By contrast, the alternative position of *Vitosaura* as a furileusaurian brachyrostran, which is found in one of the analyses under IW, would indicate that the abelisaurid assemblage of northwestern Argentina was similar to that of central-northern Patagonia, in which brachyrostrans are the most diverse and abundant abelisaurid taxa (Pol *et al.*, 2024).

Finally, the discovery of *Vitosaura colozacani* in the Campanian beds of the Los Llanos Formation in La Rioja Province expands the geographic distribution of abelisaurids, but the implications of the new taxon are limited by its incompleteness and the state of flux that we note in multiple, recent phylogenetic analyses focused on the abelisaurid interrelationships. We consider that it is necessary to carry out new studies to improve the topological robustness of the phylogeny of Abelisauridae and discover new material assignable to *Vitosaura* to test more robustly the phylogenetic hypotheses discussed here.

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