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DESCRIPTION OF A NEW SPECIES OF FOSSIL *CERATOPHRYS* (ANURA: CERATOPHRYSIDAE) FROM VERSALLES CAVE, SÃO PAULO, BRAZIL

LUCAS A. BARCELOS, ^{*1,2} DIEGO ALMEIDA-SILVA, ¹ CHARLES M. D. SANTOS, ¹ and VANESSA K. VERDADE ¹

¹Centro de Ciências Naturais e Humanas, Universidade Federal do ABC, Av. dos Estados, 5001–Bangú (09210-580), Santo André, São Paulo, Brazil;

²Laboratório de Paleontologia, Departamento de Biologia, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, Av. Bandeirantes, 3900–Vila Monte Alegre (14040-901), Ribeirão Preto, São Paulo, Brazil, lucasabarcelos@gmail.com

ABSTRACT—We describe a new fossil species of *Ceratophrys* from cave sediments in Brazil tentatively assessed as late Pleistocene–early Holocene in age. The specimen consists of a nearly complete skull that is missing only the right premaxilla and the right columella. A detailed description and comparative analysis, which considers both living and fossil species, supports the conclusion that the specimen represents a previously unknown, extinct species of *Ceratophrys*. Poorly represented and assessed characters, paleodistribution of Ceratophryidae, and the taxonomic rectification of the *Ceratophrys* fossil specimens described by Günther (1859) are also discussed.

<http://zoobank.org/urn:lsid:zoobank.org:pub:17DCC830-93AB-4FB6-9377-0467E8F3BDF9>

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

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INTRODUCTION

Anurans of the Neotropical clade Ceratophryidae are characterized by having a robust, medium-sized to large body (snout–vent length [SVL]: 40–50 mm) (Fabrezi, 2006; Evans et al., 2008), short limbs, broad skull, mandibular adductor muscles inserting in a broad coronoid process of angulosplenial, disproportionately large jaws in relation to SVL, and non-pedicellated and fang-like teeth in the maxilla and the premaxilla (Fabrezi, 2006). The skeleton is hyperossified (Wild, 1997a), possibly resulting from peramorphic heterochrony (Reilly et al., 1997; Fabrezi, 2006).

Ceratophryidae is a well-supported clade recovered in most recent phylogenetic analyses (e.g., Frost et al., 2006; Pyron and Wiens, 2011; Faivovich et al., 2014; Jetz and Pyron, 2018; Sabbag et al., 2018; Streicher et al., 2018). Living species of Ceratophryidae (sensu Faivovich et al., 2014; Frost, 2019) are placed in three genera: *Ceratophrys* (8 spp.), *Chacophrys* (1 sp.), and *Lepidobatrachus* (3 spp.). *Ceratophrys* is the most speciose of these and contains two species groups: the *C. aurita* group, including *C. aurita*, *C. cranwelli*, *C. joazeirensis*, and *C. ornata*; and the *C. cornuta* group, including *C. calcarata*, *C. cornuta*, *C. stolzmanni*, and *C. testudo* (Lynch, 1982; Faivovich et al., 2014).

The species in the *C. aurita* group occur in the Caatinga, Atlantic Forest, and Pampas biomes, in northeastern, eastern, and southern South America, respectively (Faivovich et al., 2014). The species in the *C. cornuta* group occur in the Amazon rainforest in northwestern South America (Faivovich et al., 2014). The species in *Lepidobatrachus* and *Chacophrys* occur in the Chaco, in southwestern South America (Faivovich, 1994; Faivovich et al., 2014).

The taxonomy and the systematics of Ceratophryidae were addressed by different authors based on adult osteology

(Lynch, 1982; Perí, 1994; Wild, 1997b), larval phenotypic characters (Wild, 1997b), immunological data (Maxson and Ruibal, 1988), and molecular markers (Faivovich et al., 2014). Yet, most of these works consider only living species, and the relationships of some extant species remain unstable.

Baurubatrachus pricei, *Beelzebufo ampinga* (both from the upper Cretaceous), and *Wawelia gerholdi* (lower Miocene) were previously considered the oldest ceratophryids, but the phylogenetic hypothesis proposing it was heavily scrutinized (e.g., Agnolin, 2012; Faivovich et al., 2014; Nicoli et al., 2016). The holotypes of these taxa were reassessed and their skeletal anatomy reinterpreted (Nicoli et al., 2016; Báez and Gómez, 2018). A late Miocene origin of Ceratophryidae was proposed to the exclusion of *Be. ampinga*, *Ba. pricei*, and *W. gerholdi* (Feng et al., 2017; Hutter et al., 2017). The phylogeny of Báez and Gómez (2018), which included fossils, recovered none of these taxa within Ceratophryidae, in congruence with a younger origin of Ceratophryidae. Under this hypothesis, the oldest, currently accepted species of Ceratophryidae is *Ceratophrys* sp. MD-CH-06-165 from the Arroyo Chasicó Formation, Buenos Aires Province, Argentina, which dates back to the late Miocene (Nicoli et al., 2017).

Ceratophryids are relatively common in the anuran fossil record, compared with other Neotropical clades. There are five recognized extinct species (*C. prisca* species inquirenda Ameghino, 1899, *C. ensenadensis* Rusconi, 1932, *C. ameghinorum* Fernicola, 2001, *C. rusconi* Agnolin, 2005, and *Lepidobatrachus australis* Nicoli, 2015) and many specimens are identified only to genus (see Günther, 1859; Vergnaud-Grazzini, 1968; Marshall and Patterson, 1981; Perí, 1993; Rinderknecht, 1998; Fernicola, 2001; Pardiñas, 2001; Mercadal de Barrio and Barrio, 2002; Stoessel et al., 2008; Turazzini, 2015; Nicoli, 2014, 2016, 2017; Nicoli et al., 2017; Table 1). Although the aforementioned phylogenies included fossils, none of them had a broad scope of ceratophryid fossil species. The differentiation between crown and stem groups of

*Corresponding author.

TABLE 1. Fossil specimens of Ceratophryidae. **Abbreviations:** BA, Buenos Aires; MH, Monte Hermoso; US, unnumbered specimen.

N	Collection ID	Taxonomy	Geographical Provenance	Age	References
1	MMH 84.1.15	<i>Ceratophrys ameghinorum</i>	Farola de MH, BA, Argentina	Pliocene	Fernicola, 2001
2	MMP 664.S	<i>Ceratophrys ameghinorum</i>	Barranca de los Lobos, BA, Argentina	Pliocene	Fernicola, 2001
3	MMP 892.M	<i>Ceratophrys ameghinorum</i>	MH, BA, Argentina	late Miocene–early Pliocene	Fernicola, 2001
4	MMP 664.M	<i>Ceratophrys ameghinorum</i>	Playa de Los Lobos, Chapadmalal, Argentina	Pliocene	Fernicola, 2001
5	MMP 1063.M	<i>Ceratophrys ameghinorum</i>	Playa de Los Lobos, Chapadmalal, Argentina	Pliocene	Fernicola, 2001
6	MLP 88.VII.20.1/2	<i>Ceratophrys ameghinorum</i>	Miramar, Barranca Parodi, BA, Argentina	Pliocene	Fernicola, 2001
7	MACN 19731	<i>Ceratophrys ameghinorum</i>	Farola MH, BA, Argentina	Pliocene	Fernicola, 2001
8	MACN 14317-9	<i>Ceratophrys ameghinorum</i>	MH, BA, Argentina	late Miocene–early Pliocene	Rovereto, 1914; Fernicola, 2001
9	MACN 14323-6	<i>Ceratophrys ameghinorum</i>	MH, BA, Argentina	late Miocene–early Pliocene	Rovereto, 1914; Fernicola, 2001
10	NHMUK 18895/6	<i>Ceratophrys aurita</i>	Lagoa Santa, Minas Gerais, Brazil	Pleistocene	Günther, 1859; this paper
11	ZUFABC 038	<i>Ceratophrys aurita</i>	Versalles cave, São Paulo, Brazil	late Pleistocene–early Holocene	Barcelos and Verdade, 2019
12	PVL 699 (FHC 480), PVL 767 (FHC 481), 1 US in FHC (lost) and 1 US in MLP (lost)	<i>Ceratophrys ensenadensis</i>	Olivos, BA, Argentina	Pleistocene	Rusconi, 1932
13	US (MNHN)	<i>Ceratophrys ornata</i>	Chuquisaca, Bolivia	Pleistocene	Vergnaud-Grazzini, 1968
14	MMH 85.3.8	<i>Ceratophrys ornata</i>	MH, BA, Argentina	Holocene	Pardiñas, 2001
15	MMH 85.2.11	<i>Ceratophrys ornata</i>	Farola de MH, BA, Argentina	Holocene	Fernicola, 2001; Pardiñas, 2001
16	MMH 88.2.5	<i>Ceratophrys ornata</i>	MH, BA, Argentina	Holocene	Pardiñas, 2001
17	MMH 90.2.1	<i>Ceratophrys ornata</i>	MH, BA, Argentina	Holocene	Pardiñas, 2001
18	MLP 86.VIII.1.4	<i>Ceratophrys ornata</i>	G. Chávez, Los Tres Reyes, Argentina	late Pleistocene–early Holocene	Perí, 1993
19	MMP 692-S	<i>Ceratophrys ornata</i>	Chapadmalal, BA, Argentina	Pliocene	Reig, 1958
20	MMP 4846	<i>Ceratophrys ornata</i>	Daireaux District, BA, Argentina	late Pleistocene	Perez-Ben et al., 2019
21	US (lost)	<i>Ceratophrys prisca</i>	MH, BA, Argentina	Miocene	Ameghino, 1899
22	MACN 19744	<i>Ceratophrys rusconii</i>	Mar Chiquita, Playa Dorada, BA, Argentina	Pleistocene	Agnolin, 2005
23	ZUFABC037	<i>Ceratophrys sagani</i>	Versalles cave, São Paulo, Brazil	late Pleistocene–early Holocene	Barcelos et al., 2018
24	MLP 86.VIII.1.5/6	<i>Ceratophrys</i> sp.	G. Chávez Laguna Los Tres Reyes, Argentina	late Pleistocene–early Holocene	Perí, 1993
25	PVSJ 284	<i>Ceratophrys</i> sp.	Ullum Valley, San Juan, Argentina	late Miocene	Contreras and Acosta, 1998; Nicoli, 2016
26	FCS.SA1.M3.590.1 FCS.SA1.M3.590.2 FCS.SA1.S1.486.1 FCS.SA1.S1.506.1 FCS.SA1.S1.525.1 FCS.SA1.S1.534.1	<i>Ceratophrys</i> sp.	San Antonio (Río Colorado), BA, Argentina	late Holocene	Stoessel et al., 2008
27	MLP 52.IX.27.11	<i>Ceratophrys</i> sp.	Miramar, Mar del Sur, BA, Argentina	late Holocene	Frenguelli, 1921; Fernicola, 2001; Mercadal de Barrio and Barrio, 2002
28	MD-CH-06-165	<i>Ceratophrys</i> sp.	Arroyo Chasicó, BA, Argentina	late Miocene	Urrutia and Rosset, 2006; Nicoli et al., 2017
29	MLP 86.III.25.150/1	<i>Ceratophrys</i> sp.	Olavarría, Arroyo Tapalqué, Argentina	Holocene	Mercadal de Barrio and Barrio, 2002
30	MLP 96.V.18.12	<i>Ceratophrys</i> sp.	Gral. La Madrid, Fortín Necochea, Argentina	Holocene	Mercadal de Barrio and Barrio, 2002
31	MLP 88.V.20.1	<i>Ceratophrys</i> sp.	Gral. Pueyrredón, Mar del Plata, Argentina	Pleistocene	Mercadal de Barrio and Barrio, 2002
32	MACN 18074	<i>Ceratophrys</i> sp.	Chapadmalal, BA, Argentina	Pliocene	Mercadal de Barrio and Barrio, 2002
33	MACN 17585	<i>Ceratophrys</i> sp.	Arroyo Lobería, BA, Argentina	Pliocene	Mercadal de Barrio and Barrio, 2002

(Continued)

TABLE 1. Continued.

N	Collection ID	Taxonomy	Geographical Provenance	Age	References
34	MACN 17936	<i>Ceratophrys</i> sp.	Pta. Lobería, BA, Argentina	Pliocene	Mercadal de Barrio and Barrio, 2002
35	MLP 34.V.10.8	<i>Ceratophrys</i> sp.	Punta Varohué, BA, Argentina	Pliocene	Mercadal de Barrio and Barrio, 2002
36	MLP 94.II.1.171	<i>Ceratophrys</i> sp.	Quequén Salado, BA, Argentina	Pliocene	Mercadal de Barrio and Barrio, 2002
37	MLP 48.XII.16.195	<i>Ceratophrys</i> sp.	MH, BA, Argentina	late Miocene–early Pliocene	Fernicola, 2001; Mercadal de Barrio and Barrio, 2002
38	MACN 14322	<i>Ceratophrys</i> sp.	MH, BA, Argentina	late Miocene–early Pliocene	Fernicola, 2001
39	MLP 136	<i>Ceratophrys</i> sp.	MH, BA, Argentina	late Miocene–early Pliocene	Fernicola, 2001
40	FMNH-P 14402	<i>Ceratophrys</i> sp.	Corral Quemado, Catamarca, Argentina	late Miocene–early Pliocene	Marshall and Patterson, 1981
41	MHNM 1560	<i>Ceratophrys</i> sp.	Colonia, Uruguay	late Pleistocene	Rinderknecht, 1998
42	US (MNH)	<i>Ceratophrys</i> sp.	Tarija, Bolivia	Pleistocene	Vergnaud-Grazzini, 1968
43	MMH FMH 85.12.2a	<i>Lepidobatrachus australis</i>	Farola MH, BA, Argentina	Pliocene	Tomassini et al., 2011; Nicoli, 2015
44	GHUNL Pam 8633	<i>Lepidobatrachus</i> sp.	Quehué, La Pampa, Argentina	late Miocene	Scanferla and Agnolín, 2015, Nicoli, 2017
45	IANIGLA-PV 112	<i>Lepidobatrachus</i> sp.	Huayquerías, Mendoza, Argentina	late Miocene	Turazzini, 2015

ceratophryids cannot be determined with rigor and the necessary analyses of variation within *Ceratophrys* are beyond the scope of this study. Here we describe a new species of fossil *Ceratophrys* based on a nearly complete skull. We also provide much needed discussion concerning the anatomy and phylogenetic distribution of ceratophryid characters, the paleodistribution of the group, and the taxonomic status of *Ceratophrys* fossils described by Günther (1859).

Institutional Abbreviations—**cas:herp**, Department of Herpetology, California Academy of Sciences, U.S.A.; **CM-HERPS**, Carnegie Museum of Natural History, U.S.A.; **DNPM-MP**, Museu de Ciências da Terra, Departamento Nacional de Produção Mineral, Brazil; **FCS**, Facultad de Ciencias Sociales, Universidad Nacional del Centro de la Provincia de Buenos Aires, Argentina; **FHC**, Frederico Hennig Collection; **FMNH-P**, Field Museum of Natural History, Geology Department, Chicago, Illinois, U.S.A.; **GHUNL-Pam**, Facultad de Ciencias Exactas y Naturales, Universidad de La Pampa, Santa Rosa, La Pampa, Argentina; **IANIGLA-PV**, Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales-Paleovertebrados, Argentina; **KU**, University of Kansas Biodiversity Institute, U.S.A.; **MACN**, Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia,’ Buenos Aires, Argentina; **MCZ**, Museum of Comparative Zoology - Harvard University, U.S.A.; **MD-CH**, Museo Municipal de Ciencias Naturales ‘Carlos Darwin,’ Arroyo Chasicó collection, Punta Alta, Buenos Aires, Argentina; **MLP**, Museo de La Plata, La Plata, Argentina; **MMH**, Museo Municipal de Ciencias Naturales Vicente Di Martino, Monte Hermoso, Buenos Aires, Argentina; **MMP**, Colección de Paleontología de Vertebrados Museo Municipal de Ciencias Naturales de Mar del Plata ‘Lorenzo Scaglia,’ Mar del Plata, Buenos Aires, Argentina; **MHNM**, Museo de Historia Natural de Montevideo, Uruguay; **MNHN**, Muséum national d’Histoire naturelle, Paris, France; **MZUSP**, Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil; **NHMUK**, Natural History Museum, London, U.K.; **NRM**, Swedish Museum of Natural History, Sweden; **PVL**, Colección de Paleontología de Vertebrados del Instituto Miguel Lillo, San Miguel de Tucumán, Argentina; **PVSJ**, Museo de Ciencias Naturales, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de San Juan, Argentina; **UF-H**, Herpetology collection, University of Florida, Florida Museum of Natural History, U.S.A.; **uf:herp**, Herpetology

collection, University of Florida, Florida Museum of Natural History, U.S.A.; **ZUFABC**, Coleção Zoológica, Universidade Federal do ABC, São Bernardo do Campo, Brazil.

MATERIALS AND METHODS

Alessandro Marques de Oliveira and the Espeleo Grupo de Rio Claro (EGRIC) collected the holotype (ZUFABC 037), and only known specimen, in September 2014. It was found with megafauna fossils and other anuran remains, all disarticulated and fragmented (Oliveira, 2018). The skull was covered by mud and a carbonate crust that was removed mechanically. The geological age of the fossil horizon/layer is unknown, but remains of *Nothotherium maquinense* that were found in the same cave during the same paleontological expedition are dated to 13,037 and 12,790 BP (before present) (Oliveira, 2018). The holotype ZUFABC 037 is housed at the Coleção Zoológica of the Universidade Federal do ABC, São Bernardo do Campo–Brazil.

The extant and fossil specimens studied were measured directly with a Vernier caliper to the nearest 0.01 mm and through ImageJ Fiji software (Schindelin et al., 2012) on μ CT-scanned specimens. Morphometric measurements follow Reig and Cei (1963), with the addition of diameter of the supratemporal fenestra (Table S1). The osteological nomenclature follows Lynch (1971) and Wild (1997b).

The holotype (ZUFABC037) was compared with at least one specimen from each extant Ceratophryidae species, and to fossil specimens of Ceratophryidae (see Appendix) using a Zeiss Stemi V11 stereomicroscope; and μ CT-scanning images provided by the Laboratory of Computerized Tomography at Museu de Zoologia da USP (MZUSP). The μ CT-scan images were prepared in v tome \times m microfocus μ CT scanner Version 2.3.0.1032 (General Electric Company, Wunstorf, DE; Voltage = 85KV, Current = 170 μ A). The parameters of the μ CT-scan resulting images are: pixel size (0.2), voxel size (0.04521586), resolution (96 dpi), and number of images (2500). Specimens were scanned using a tungsten target, an air background medium, and no filter, and were rendered as 16-bit TIFF files. Scan data were analysed using 3DSlicer software, version 4.10.1 (Fedorov et al., 2012). Photos of the fossils were taken with a LGK10 cell phone 13 MP, f/2.2, AF (LTE model).

SYSTEMATIC PALEONTOLOGY

Class AMPHIBIA Linnaeus, 1758

Order ANURA Duméril, 1805

Family CERATOPHRYIDAE Tschudi, 1838

Genus *CERATOPHRYNS* Wied-Neuwied, 1824

Type Species—*Ceratophrys varius* Wied-Neuwied, 1824 (currently *C. aurita* [Raddi, 1823]).

Extant Taxon—Neotropical distribution.

CERATOPHRYNS SAGANI, sp. nov.

(Figs. 1, 2)

Holotype—ZUFABC 037, a nearly complete skull, lacking the right premaxilla and right columella. It is well preserved with no signs of deformation.

Etymology—The specific epithet *sagani*, in genitive singular, is in honor of the eminent North American astronomer Carl Sagan (1934–1996), whose passion for the communication of science continues to inspire.

Type Locality—Versalles Cave, municipality of Apiaí, state of São Paulo, Brazil UTM 22J 737457/7294530, 715 m (Datum WGS) (Oliveira, 2015). ZUFABC 037 was collected in Versalles Cave, located within an area privately owned by Purical Mining Company, ca. 16 km northeast of the municipality of Apiaí, state of São Paulo (Fig. 3B). The area belongs to the Alto do Ribeiro region, which is part of the austral portion of the Ribeira Belt (de Almeida et al., 1973), one of the three geotectonic provinces that border the San Francisco Craton, of the Brazilian Atlantic Shield (Theodorovicz, 2014). The area possesses typical geomorphological and speleological features, with high speleomorphological variety (more than 200 recognized caves) and represents important Quaternary paleontological sites (Karmann and Ferrari, 2002). The caves of the region are estimated to age between 2–1.7 million BP (Karmann and Ferrari, 2002). The sediments found in these caves present evidence of reworking of the stratigraphic horizon, due to floods (Dias Neto et al., 1984). The sediments are of low maturity and possess a low degree of selection, with several sizes of granulometry in consonance with decomposing organic matter, blackish coloration and carbonate cementation at some levels (Dias Neto et al., 1984). The fossils found in those caves are usually disjointed and highly fragmented due to the high degree of reworking (Ghilardi et al., 2011).

Distribution—Known only from the type locality.

Diagnosis—Attributed to Ceratophryidae by the presence of the following characters: (1) cranial exostosis; (2) frontoparietal–squamosal arc; (3) otic ramus of squamosal expansive and overlapping the otoccipital; (4) zygomatic ramus of squamosal sutured to the maxilla; (5) teeth monocuspid; (6) teeth non-pedicellate. Attributed to *Ceratophrys* by the combination of the following characters: (1) palatal shelf of premaxilla lacking; (2) facial lobe of premaxillae deep; (3) palatal shelf of maxilla not evident anteriorly, posteriorly forming a large pterygoid process fused to the pterygoid; (4) nasals large, fused medially; (5) nasal fused to maxilla, nasal–pterygoid relationship not evident; (6) nasals broadly fused to frontoparietals; (7) temporal arcade forming supratemporal fenestrae, (8) temporal arcade notched posteriorly; (8) epiotic eminences prominent, concealed dorsally by the temporal arcade; and (9) cristae paroticae narrow and long. Attributed to the *C. aurita* group of species by the presence of a subquadrangular otic plate. Distinguished as a new species within the genus by the following autapomorphies: (1) two fenestrae formed by the suture of sphenethmoid with vomer in ventral view; (2) epiotic eminences of exoccipital with a cotyloid concavity; and (3) columella footplate with three curved crests.

DESCRIPTION

Description of ZUFABC 037

The holotype specimen ZUFABC 037 of *Ceratophrys sagani* sp. nov. seems to be an adult based on the hyperossification of the skull, with synostosis of skull bones (except for the articulation of the vomer and its adjacent bones). The skull bears markedly dermostosed bones (i.e., frontoparietal, nasal, squamosal, maxilla, and premaxilla) with a tuberculated ornamentation on its dorsal surface. The nasals are flat, wide, and symmetrical paired bones, that taper anteriorly with dermostosis on their dorsal surface. The nasals articulate synostotically with each other medially. Each possesses a bar-shaped maxillary process laterally, which sutures with the pars facialis of the maxilla and the zygomatic ramus of the squamosal. Posteriorly, the nasals articulate with the anterior edge of their respective frontoparietal. There is a discrete groove following the axis of the suture between the nasals at the posterior extremity. The anterior portions of the nasals overlap the sphenethmoid along a suture that is poorly ossified. The posterior edges of the nasals form infralocular flanges, which suture with the zygomatic ramus of their respective squamosal to generate a pronounced oblique groove that lacks dermostosis. The groove links the orbits to the choanae. The choanae aperture is oblong and directed medially. It is formed anteriorly by contact between the pars facialis of the maxillae and the anterior portion of the sphenethmoid, posteriorly by contact between the maxillary process of the nasal and the zygomatic ramus of the squamosal, and laterally and posteriorly by the pars facialis of the maxilla, and the nasal. The bones forming each choanae aperture are well ossified and synostotically fused, except for the visible suture between the nasals and the sphenethmoid.

The frontoparietals are paired, symmetrical, wide, and heavily ossified bones fused to each other throughout their contact. There is tuberculated ornamentation on their dorsal surfaces. Dorsally, there is an interocular crest along the suture of the frontoparietals, which becomes clearer between the medial portion of the interocular region and the anterior edge of the frontoparietals, where they articulate with the posterior portion of nasals. The articulation between the frontoparietals and the nasals forms part of the infraocular flanges. The posterior portion of each frontoparietal invests the otic ramus of their respective squamosal dorsally, forming supraorbital flanges. The posterior-most portions of the frontoparietals invest their respective exoccipital and partially cover the epiotic eminence; the frontoparietal process has acute edges at this posterior portion. The posterior-most portion of each frontoparietal articulates synostotically with the otic ramus of their respective squamosal, forming the crista parotica, which is the posterior flange of supratemporal fenestrae. Ventrolaterally, the lamina perpendicularis is present in the dorsolateral region of the braincase along the entire length of the frontoparietal. The trochlear nerve foramen (cranial nerve [CN] IV) is present in ventral view, between the orbits and the optic nerve foramen (CN II).

The squamosals are paired, well-developed bones, exhibiting dermostosis on the dorsal surface. The squamosal has three rami. The ventral ramus of the squamosal is wide, elongated and flat anteroposteriorly, oriented posterolaterally and it is concave anteriorly. It articulates synostotically with the posterior ramus of the pterygoid, with the quadrate and the maxilla. Anteriorly, the otic ramus of the squamosal articulates with the lateral edge of the frontoparietal forming the anterior edge of the supratemporal fenestra. The otic ramus has a medially directed projection, which articulates with the otoccipital forming the crista parotica. Ventrally, this projection participates in the configuration of the auditory capsule. The otic ramus of the squamosal also bears the otic plate (sensu Lynch, 1971), a subquadrangular bony projection, which is directed posterolaterally and is well

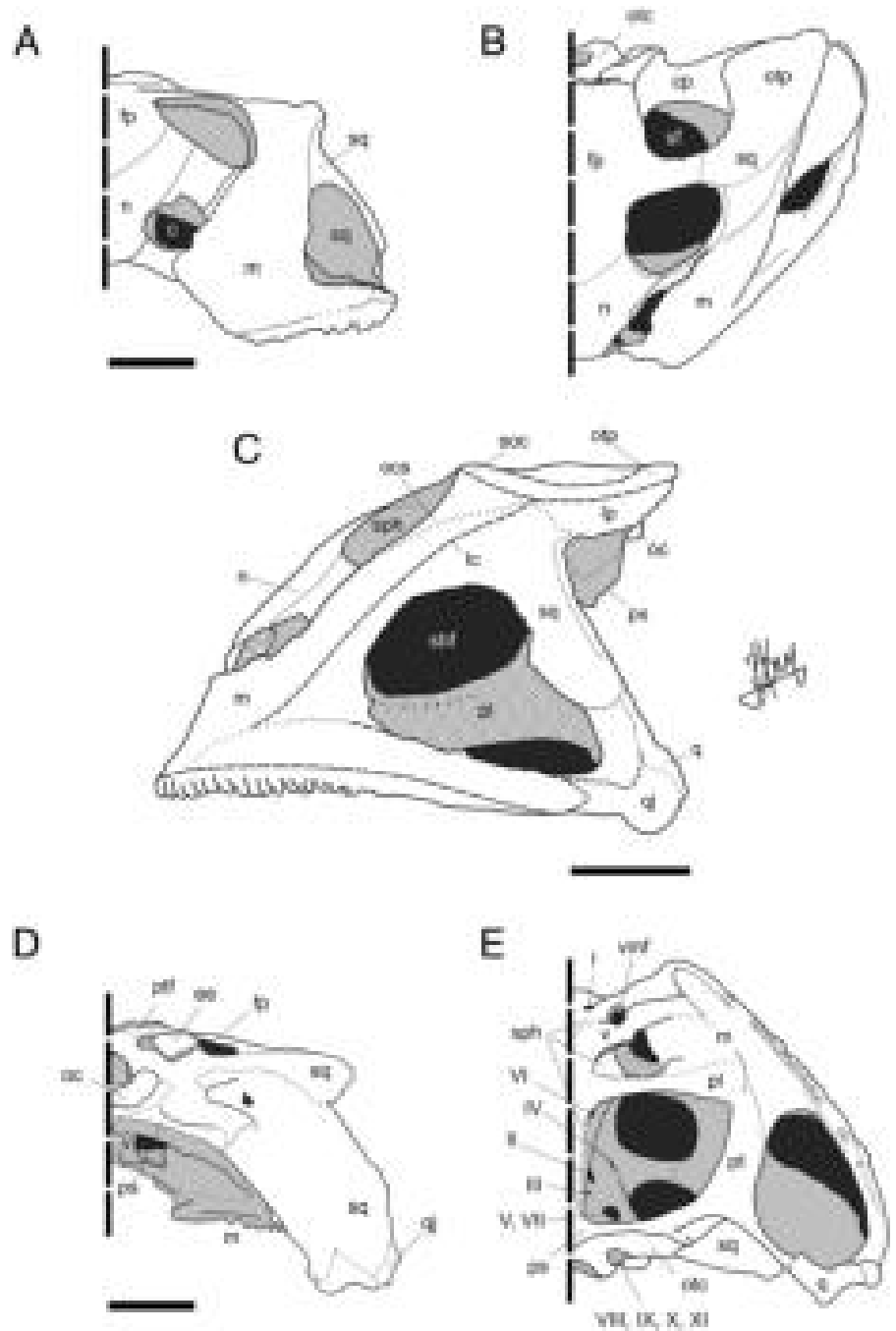


FIGURE 1. *Ceratophrys sagani*, sp. nov., interpretive drawings of skull in **A**, frontal, **B**, dorsal, **C**, lateral, **D**, posterior, and **E**, ventral views. **Abbreviations:** I–XI, cranial nerve foramina; **c**, choana; **cp**, crista parotica; **ee**, epiotic eminence; **fp**, frontoparietal; **lc**, lateral crest; **lp**, lateral plate; **m**, maxilla; **n**, nasal; **oc**, occipital condyles; **ocs**, oblique crest of squamosal; **otc**, otoccipital; **otp**, otic plate; **pl**, palatine; **ps**, parasphenoid; **pt**, pterygoid; **ptf**, posttemporal fenestra; **q**, quadrate; **qj**, quadratojugal; **sbf**, subtemporal fenestra; **sf**, supratemporal fenestra; **soc**, supraorbital crest; **sph**, sphenethmoid; **sq**, squamosal; **v**, vomer; **vmf**, ventromedial fenestra. Scale bars equal 10 mm.

expanded and tapering in dorsolateral view, following the axis of three convergent crests of the squamosals. The otic plate is highly curved dorsolaterally and presents a dorsal concavity.

The zygomatic ramus of the squamosal articulates with the pars facialis of the maxilla, and with the anterior ramus of the pterygoid. Medially, it articulates with the nasals and with the pars facialis of the maxillae. From these contacts, two well-developed crests are formed. The anterior-most crest, called the lateral crest, results from the contact among the bifurcated anterior ramus of pterygoid, the pars facialis of the maxilla, and the anterior edge of the zygomatic ramus of the squamosal. The other crest, termed the oblique crest, is formed by the contact between the zygomatic ramus of the squamosal and the nasal.

The oblique crest begins at the anterolateral flange of the orbit and extends, diagonally oriented, until it connects with the lateral crest. The medial portion of the otic ramus of the squamosal articulates with the frontoparietal and forms the supraorbital flange. At the contact between the otic ramus of the squamosal and the frontoparietal another well-developed crest arises, the supraorbital crest. The supraorbital crest is laterally oriented and meets the other crests of the zygomatic ramus of squamosals at its distal portion and extends through the axis of the lateral edge of the otic plate of otic ramus of squamosal. There are two depressions in the orbital arch between the crests of the zygomatic ramus.

The pterygoids are paired, triradiate, laminate, and symmetrical bones. The pterygoid has three well-developed processes:

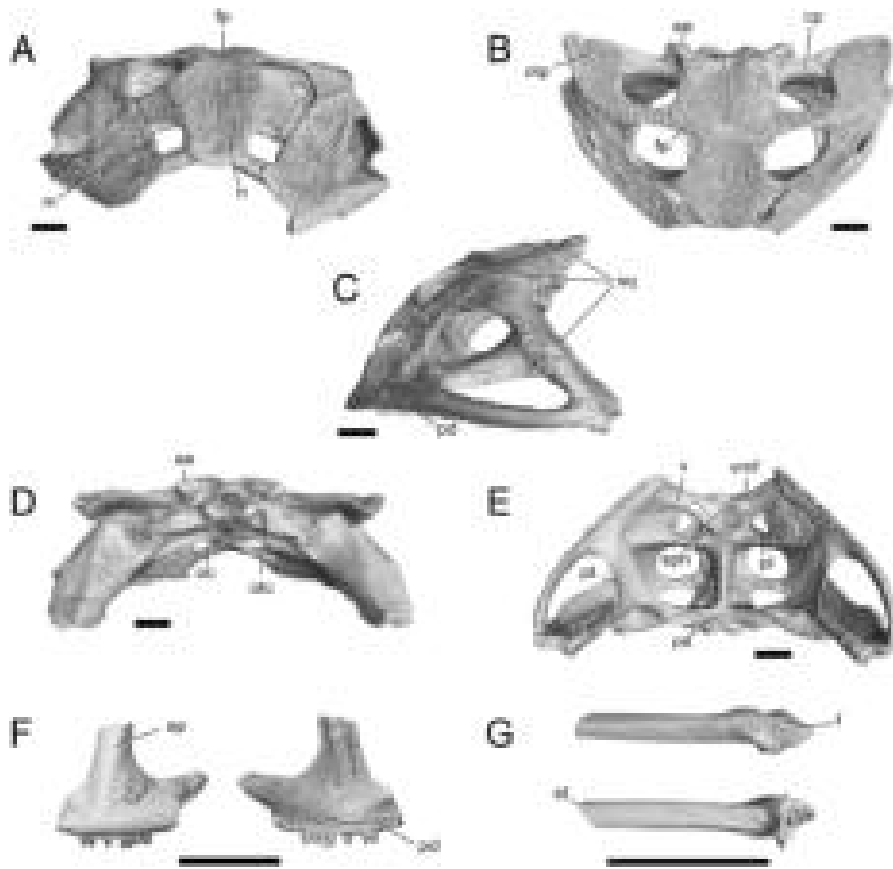


FIGURE 2. *Ceratophrys sagani*, sp. nov., ZUFABC037, holotype. **A–E**, digital renderings of skull in **A**, frontal, **B**, dorsal, **C**, lateral, **D**, posterior, and **E**, ventral views. **F**, the left premaxilla in posterior (right) and frontal (left) views. **G**, the left columella in posterior (upper) and frontal (lower) views. **Abbreviations:** **ap**, alary process; **cp**, crista parotica; **ee**, epiotic eminence; **f**, footplate; **fp**, frontoparietal; **m**, maxilla; **n**, nasal; **oc**, occipital condyles; **otc**, otoccipital; **otp**, otic plate; **pd**, pars dentalis; **pl**, palatine; **ps**, parasphenoid; **pt**, pterygoid; **sph**, sphenethmoid; **sq**, squamosal; **st**, stylus; **v**, vomer; **vmf**, ventromedial fenestra. Scale bars equal 10 mm.

anterior, medial, and posterior ramus. The anterior ramus laterally articulates extensively with the pterygoid process of the maxilla, and, medially, with the distal edge of the palatine and the sphenethmoid. The anterior ramus forms the lateral edge of the interpterygoid vacuity. The medial portion of the anterior ramus of the pterygoid is tilted dorsoventrally and obliquely arranged along its length, which is flattened at its distal edge. The medial ramus of the pterygoid is a tapering portion that articulates diagonally with the distal edge of the ala of the parasphenoid and with the ventrolateral edge of the otoccipital, forming the posterior edge of interpterygoid vacuity. The posterior ramus of the pterygoid is a posterolaterally curved portion, which articulates laterally with the medial edge of the ventral ramus of the squamosal and posteroventrally with the pars articularis of the quadrate.

The quadrate is a discrete bone, constricted medially and expanded laterally. It is heavily synostosed with the quadratojugals, the posterior ramus of the pterygoid and the ventral ramus of the squamosal, the articulations are obscured by synostosis. There is a condyle at the medial portion of the quadrate, result of the articulation with the posterior ramus of the pterygoid and posterolaterally with the ventral ramus of the squamosals. The sutures between the posterior portion of the pars palatina and the pars facialis of the maxilla, quadratojugal, ventral and zygomatic rami of the squamosal form the subtemporal fenestra, which is an ellipsoidal opening lateral to the cranium. The quadratojugals are paired, massive, and ‘V’-shaped bones in lateral view. The anterior portion of each is cylindrical and articulates anteriorly with the pars dentalis and the pars palatina of the maxilla and its posterior portion articulates with the quadrate and the squamosal.

The premaxillae are paired bones. Only the left premaxilla is preserved in the fossil (Fig. 2F). The pars dentalis of the

premaxilla has ten non-pedicellate teeth, but only seven are well preserved. The base of the alary process of premaxilla bears dermostosis on its dorsal surface. The alary process of the premaxilla is roughly perpendicular to the long axis of the pars dentalis of the premaxilla, but slightly divergent laterally. The alary process of the premaxilla articulates ventrally with the anterior portion of the sphenethmoid. The distal edge of the alary process is not preserved in the fossil. The maxillary ramus of the premaxilla is long, ‘V’-shaped in lateral view, and articulates ventrally with the pars palatina of the maxilla. The septomaxillae should be in the olfactory capsule, but they are not preserved in the fossil.

The maxillae have three portions: pars dentalis, pars palatina, and pars facialis. The pars dentalis is compact and bears small hollows internally, corresponding to the pulp cavity and the teeth. The teeth are not well preserved; based on the preserved roots, the paired maxillae could bear at least 40 teeth. Most teeth are worn and deteriorated, except eight and nine teeth from the right and left maxilla, respectively, are preserved in good condition. Those teeth are non-pedicellate and fang-like. The distal edge of the pars dentalis of the maxilla is ‘V’-shaped in lateral view and overlaps the anterior part of the quadratojugal. The pars palatina of the maxilla is reduced, investing dorsally, the pars facialis, and exhibits an internal hollow along its entire length. The pars facialis of the maxilla has dermostosis on its dorsal surface. It articulates dorsally with the nasal and with the zygomatic ramus of the squamosal; and ventrally with the anterior portion of sphenethmoid and the lateral edges of the vomer, the palatine, and the pterygoid.

The sphenethmoid is at the central cranium axis, it is not exostosed and has three portions, that articulate conspicuously with adjacent bones. The anterior portion is a wide, rounded, and

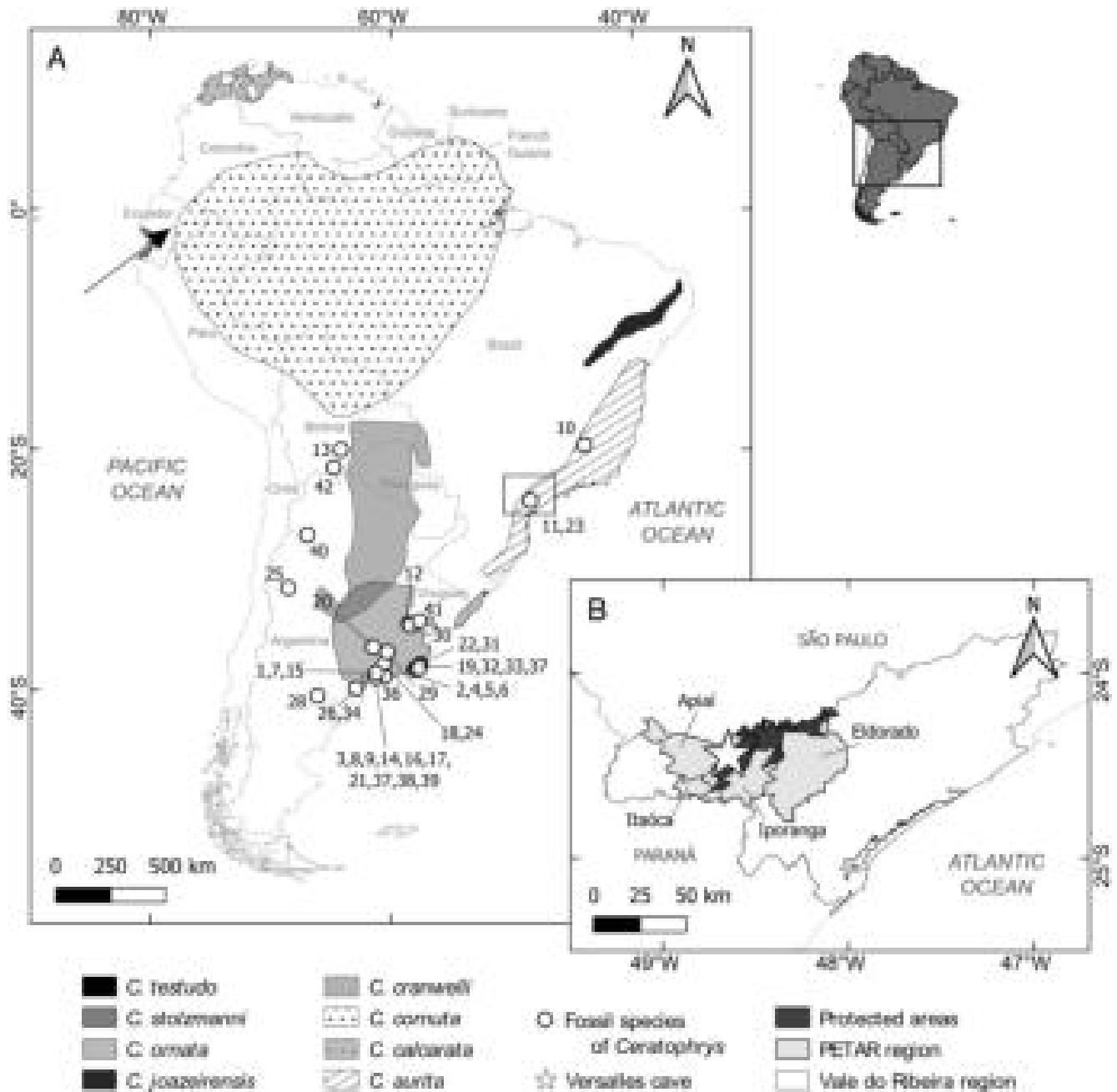


FIGURE 3. Distribution of extant and fossil species of *Ceratophrys*. **A**, geographical distribution of extant species of *Ceratophrys* and several fossil specimens of *Ceratophrys*, after the data in Table 1. Many fossil specimens share the same fossil locality. The area in the black rectangular frame is enlarged and shown in detail. The black arrow indicates the type locality of *C. testudo*, known only from the holotype. **B**, location (white star) of the Versalles Cave, Apiaí municipality, state of São Paulo, southeastern Brazil (UTM 22J 737457/7294530, 715 m [Datum WGS]).

anteriorly directed projection (Fig. 2A); below this projection are two olfactory nerve foramina (CN I). The anterior portion articulates dorsally with the anterior edge of the nasals. The dorsum of the sphenethmoid articulates laterally with the pars facialis of the maxilla. The sphenethmoid articulates with anterior edge of the vomer, forming a fenestra that we propose to call the ventromedial fenestra (Figs. 1B, 2B). The medial portion of the sphenethmoid is reduced, triangular, and slightly concave in ventral view. It articulates synostotically with the vomer anteriorly and laterally, and the palatine posteriorly at the level of the planum antorbitale. The posterior portion of the sphenethmoid is bifurcated, with broad

laminae. The anterior portion of the laminae bears an abducens nerve foramen (CN VI), whereas the posterior portion of the laminae bears an optic nerve foramen (CN II). The posterior portion of the sphenethmoid articulates anteriorly with the proximal portion of the palatine, laterally with the lamina perpendicularis of the frontoparietals, and posteriorly with the otoccipital. Laterally it articulates with the anterior edge of the cultriform process of parasphenoid. All sutures are obscured by extensive synostosis. There is no dorsal exposure of the sphenethmoid.

The vomers are anterolaterally oriented paired bones, each with an anterior and a posterior portion. The anterior portion

of each vomer articulates with the sphenethmoid throughout its entire width. This suture is not heavily ossified in contrast to all the other sutures of the vomers. A foramen penetrates the suture between the anterior portion of the sphenethmoid and the vomer. To our knowledge, this foramen is unique among anurans. The distal edge of each vomer invests the pars facialis of the respective maxillae. The posterior portion of each vomer presents a laterally directed lamina near the pars odontoides, the postchoanal process, initiating medially and extending for two-thirds of the length of the vomer. The extremities of the postchoanal process are not preserved in the fossil, preventing further description and comparison. The posterior portion of each vomer articulates medially with its respective palatine, the anterior edge of the cultriform process of the parasphenoid, and the medial portion of the sphenethmoid. The articulations are obscured by synostosis. Vomerine teeth and dental ridges are not preserved.

The palatines are elongated, laterally oriented, and do not meet each other medially. The proximal edge of each palatine articulates anteriorly with the sphenethmoid and the vomer with a high degree of synostosis. The distal edge of each palatine expands and invests the pars facialis of the respective maxilla ventrally and articulates with the pterygoid dorsally.

The parasphenoid is a 'T'-shaped bone formed by two symmetrical, laterally oriented alae, and a single, anteriorly oriented cultriform process. Each ala articulates broadly anteriorly and posteriorly with the otoccipital and anterolaterally with the pterygoid. The alae are well developed and possess a crest along their anterior edge resulting from contact with the medial ramus of the pterygoid. Each ala has an anteroventrally-curved flange with the concavity directed posteriorly, resulting from the articulation with the posterior portion of otoccipital, where the auditory nerve foramen (CN VIII) is located on the right concavity and the jugular nerve foramen (CN IX-XI) on the left concavity. A protuberance is present at the distal edge of each ala resulting from contact with the otoccipital and medial ramus of pterygoid. The cultriform process of the parasphenoid articulates laterally with the lamina perpendicularis of each frontoparietal, and the medial portion of the sphenethmoid and otoccipital. The articulation between the parasphenoid and the otoccipital forms two foramina—the optic nerve foramen (CN II), anteriorly and the oculomotor nerve foramen (CN III) posteriorly. The sutures are not clear because of the high degree of synostosis.

The prootics and the exoccipitals are continuous and indistinguishable as the otoccipital (Lynch, 1971). The internal structure of this compound element is dominated by its spongy component with only a thin lamellar wall. Ventrally, the otoccipital articulates with the parasphenoid alae and the medial rami of the pterygoids. Dorsally, it articulates with the lamina perpendicularis of the frontoparietal. Anteriorly, the prootics articulate with the posterior portion of sphenethmoid, where the foramina for the CN II are formed. The sutures between those bones are obscured by synostosis. The posterior portion of otoccipital forms the posteromedial parts of the auditory capsules and the occipital condyles, which are juxtaposed (Type II; Lynch 1971), massive, and lacking a constricted base, with rounded and ventromedially-to-dorsolaterally angled articular surfaces. The jugular and auditory nerve foramina (CN VIII) are located above the occipital condyle. The epiotic eminences are located above the foramen magnum, and are triangular protuberances in dorsal view, partially covered by the processus posterior of frontoparietals and with a cotyloid concavity, in posterior view.

The plectral apparatus, also known as the columella, is a slender, cylindrical bone, that is enlarged at its proximal edge. It is located in the middle ear, below the otic ramus of the squamosal and associated with the fenestra ovalis of the otoccipital. Three portions are recognized from proximal to distal end: footplate, stylus, and distal cartilaginous elements that connect to the external ear. The columella footplate is composed of a complex

trochanter or apophysis, which has a concave ventral surface, and three curved crests (Fig. 2G). One crest is dorsal, initiating at the posteromedial portion of footplate and extending to the anterodorsal end; the second crest is ventral, following the same conformation of the dorsal crest, but forming one of the axes that structure the concavity; the third crest extends through the posteromedial portion of columella footplate until the ventral axis structuring the concavity, forming an accentuated curve. The stylus is not entirely preserved in the fossil.

Comparison with Extant Species of *Ceratophrys*

Ceratophrys sagani, sp. nov. differs from all other living and fossil species of Ceratophryidae by bearing two fenestrae on the suture between the anterior portion of the sphenethmoid and the anterior edge of the vomer. Our comparison indicates that it is an autapomorphy. We noted a concavity in living specimens of *C. joazeirensis* (MZUSP 142284) and a discrete crest in *C. aurita* (cas:herp:84998) specimen topologically congruent to the ventromedial fenestrae of *C. sagani*. The new taxon differs from all other extant species of Ceratophryidae by presenting three crests on the footplate of the columella (two ventral and one dorsal; Fig. 2G). We also observed a columella only with a ventral crest in *Ceratophrys joazeirensis*, whereas other species of *Ceratophrys* bear two plectral apophyses on columella (Peri, 1993). In posterior view, the posterior-most surface of epiotic eminences of all extant and extinct species of *Ceratophrys* species are flat, and there are dorsolateral protuberances, recorded here in *C. calcarata* and *C. cornuta* of the *C. cornuta* group and in *C. aurita* and *C. joazeirensis*, of the *C. aurita* group. In *Ceratophrys sagani* sp. nov. the dorsolateral protuberances are absent, and this fossil species is autapomorphic in having a concavity on the posterior surface of epiotic eminences.

Ceratophrys sagani has a wide and rounded projection on the anterior-most portion of the sphenethmoid, differing from *C. joazeirensis*, *C. cranwelli* (narrow and rounded), and from *C. cornuta* (narrow and truncated). In *C. aurita*, this projection is consistently wide, but polymorphic in being either truncated or rounded.

Ceratophrys sagani exhibits a subquadrangular otic plate, which is a diagnostic character of the *C. aurita* species group. Further, *C. sagani* and *C. aurita* present the otic plate curved dorsally, whereas other species within the group bear a ventrally curved otic plate. *Ceratophrys sagani* and *C. aurita* are unique in having a zygomatic ramus of the squamosal that is wide and bears a crest on its dorsal surface, differing from the narrow zygomatic ramus of *C. ornata* and *C. joazeirensis* (Figs. 1B, 2B). Additionally, *C. aurita* and *C. sagani* share the presence of two depressions at the orbital arch between the crests of the zygomatic ramus of the squamosal. In dorsal view, the epiotic eminences of *C. sagani* resemble the slender structures of *C. aurita* and differ from the elliptical eminences of *C. joazeirensis* (Vieira et al., 2006).

The alary process of the premaxilla (Fig. 2F) in *Ceratophrys sagani* is not as narrow as in *C. joazeirensis*, resembling that in *C. aurita* and *C. cranwelli*. There is a rounded dermostosis at the external surface of the alary process of the premaxilla (near the base of the alary process) in *C. sagani* sp. nov., and such a similar dermostosis is polymorphic in *C. aurita* specimens (see Gayer 1984).

Comparison with Fossils of Ceratophryidae

Ceratophrys sagani is the second largest (skull width = 70 mm) of the known fossil Ceratophryidae, being only slightly smaller than *C. ameghinorum* (skull width = 72 mm; MACN 14318; Fig. S1). In addition to its overall size, the skull of the new species differs proportionately from those of other fossil taxa.

The maximum bi-narial diameter is 6.9% larger than in *C. ameghinorum*, and so are the maximum bi-premaxillary diameter (3.04% larger), minimum interorbital diameter (10% larger), height of premaxillary alary process (9.16% larger), maximum cranium height (5% larger), and diameter of supratemporal fenestrae (18.75% larger). *Ceratophrys sagani* also has a curved posterior edge of the otic plate, differing from that of *C. ameghinorum* where the posterior edge of the otic plate is straight, well-developed, and dorsally projected.

Both *C. sagani* and *C. rusconii* (MACN 19744; Fig. S2) have supratemporal and subtemporal fenestrae, with the epiotic eminences partially covered by the processus posterior of the frontoparietal and the subquadrangular otic plate of the squamosal. However, the projection of the anterior portion of the sphenethmoid is well-developed in *C. sagani*, whereas it is short and rounded in *C. rusconii*. The otic plate of *C. sagani* is curved dorsally at its distal edge but ventrally concave in *C. rusconii* (the latter resembling *C. ornata*).

Ceratophrys sagani resembles the fossil specimens (NHMUK 18895/6) of *Ceratophrys* from the Pleistocene of Lagoa Santa (Minas Gerais, Brazil). These specimens were originally classified by Günther (1859) as *C. cornuta*. They were subsequently identified as *C. aurita* without justification (Lynch, 1971; Báez and Gasparini, 1977) and proposed as closely related to the [*C. aurita*-*C. joazeirensis*] clade (Faivovich et al., 2014). The fossil classified by Günther (1859) requires revision. It resembles *C. aurita* in the presence of posterior margin of dermocranium indented, supratemporal fenestrae, subquadrate otic plate of squamosal, three crests on the squamosal and the maxilla, and truncated and flat anterior portion of sphenethmoid. Herein, it is referred to as *Ceratophrys* cf. *C. aurita* (NHMUK 18895/6), in the lack of a review of characters and phylogenetic proposal.

In sum, *Ceratophrys sagani* differs from *Ceratophrys* cf. *C. aurita* (NHMUK 18895/6), *C. ameghinorum*, *C. rusconii* and all other *Ceratophrys* fossil species based on the presence of epiotic eminences with concave surface in posterior view (Figs. 1D, 2D); columella footplate with three curved crests; and ventromedial fenestra along the vomer-sphenethmoid contact.

DISCUSSION

Ceratophrys sagani is a new species of *Ceratophrys* that bears a subquadrangular otic plate indicative of close relation to the *C. aurita* species group. The new species is autapomorphic among the ceratophryids in having: (1) two fenestrae formed on the suture between sphenethmoid and vomer, as observed in ventral view; (2) epiotic eminences of otoccipital with a cotyloid concavity; (3) columellar footplate with three curved crests. The recent recovery of *Baurubatrachus pricei* phylogenetically outside Ceratophryidae (Nicoli et al., 2016; Báez and Gómez, 2018), makes *Ceratophrys sagani* the single extinct species of Ceratophryidae discovered from the fossil record of Brazil (the third ceratophryid fossil from Brazil), and one of the northern-most records for the group.

Contribution to Character Variation in Ceratophryidae

Although the ceratophryid skull has been extensively studied, many of its characters remain poorly understood. The anterior portion of the sphenethmoid was recognized as present by Gayer (1976) and Perí (1994) but was deemed absent in Wild (1997b), who recognized the anterior portion of the sphenethmoid as part of the vomer (Fig. 1B). Perí (1994) considered that this anterior portion is well developed in *Ceratophrys* and *Lepidobatrachus*, perhaps the result of a densely ossified skull (Gayer, 1976). The sphenethmoid and the vomer are fused in Ceratophryidae, and we observed ornamentation on this region in the specimen (*C. joazeirensis* MZUSP 142284) that is not mentioned in

the literature. By analyzing the anatomical axes of the μ CT-scan images of the *Ceratophrys* specimens under analyses, we noted that the region of contact between the sphenethmoid and the vomer in *C. aurita*, *C. joazeirensis*, and *C. cornuta* (specifically in the portion of the ventromedial fenestra of *C. sagani*) exhibits a thin and compact layer of bone, whereas in other species of *Ceratophrys* the bone in this portion is spongy. The origin of the ventromedial fenestra is unknown, and could be the retention of a larval character (e.g., an accessory nerve foramen).

The epiotic eminences of the otoccipital probably provide a bony surface for muscle insertion (Gayer, 1984). The variation of these structures is not well explored, although Vieira et al. (2006) noted shape differences between *C. joazeirensis* (elliptical) and *C. aurita* (slender) in dorsal view. We observed *C. aurita*, *C. calcarata*, *C. cornuta*, and *C. joazeirensis* have dorsolateral protuberances in the epiotic eminences of the otoccipital, and, in posterior view, the epiotic eminences surfaces are flat in the living and fossil species of Ceratophryidae, except for the new species *C. sagani* (epiotic eminence with a concavity on the posterior surface, Fig. 2D).

The columellar footplate of Ceratophryidae is generally concave/globous, without any ornamentation (e.g., *Lepidobatrachus* and *Chacophrys*), with an anterior and posterior pletral apophysis (e.g., *C. cranwelli* and *C. ornata*) or a ventral crest (e.g., *C. joazeirensis*). The development of these apophyses is ontogenetically variable and sexually dimorphic (Perí, 1993). *Ceratophrys sagani* sp. nov. is unique among species of Ceratophryidae in having the footplate of the columella ornamented with three curved crests (Fig. 2G).

Geographic Distribution of Ceratophryidae

Ceratophrys sagani, sp. nov. represents the third formally described record of a fossil of Ceratophryidae from Brazil and one of the most northern records for the group (Table 1; Fig. 3A). The great majority of Ceratophryidae fossils are located in southern South America. There are two possible explanations for this paleodistribution: (1) the ancient distribution of *Ceratophrys* species was concentrated in the south and subsequently expanded northward to the recent distribution of the group; or (2) the group has a deep history in the north but the fossil evidence is hindered by the poor preservational potential of northern environments (e.g., Amazonian and Atlantic Forests). It is certainly possible that the prevalence of material in southern South America simply reflects the strong fossil collection efforts of anuran species in Argentina.

The majority of the fossils belonging to *Ceratophrys* are found within the geographical distribution range of living species of the genus, the *C. aurita* group in particular (Fig. 3). However, there are some outliers: the specimens *Ceratophrys* sp. (PVSJ 284, upper Miocene of Ullum Valley, San Juan), *Ceratophrys* sp. (FMNH-P.14402, upper Miocene-lower Pliocene of Corral Quemado, Catamarca), *Ceratophrys* sp. and *Ceratophrys ornata* (MNHN unnumbered specimens; Vergnaud-Grazzini 1968, Pleistocene of Tarija and Chuquisaca, respectively), located west of the distribution of the living species *Ceratophrys cranwelli*, and *Ceratophrys* sp. (MD-CH-06-165 upper Miocene of Arroyo Chasicó) located south of the distribution of *C. ornata*.

The distribution of all *Lepidobatrachus* fossil specimens, i.e., *Lepidobatrachus* sp. (IANIGLA-PV 112, upper Miocene), *Lepidobatrachus australis* (MMH FMH 85-12-2a, Pliocene) and *Lepidobatrachus* sp. (GHUNL-Pam 8633, upper Miocene) are more than 250 km south to the southern limit of the distribution range of extant species (Fig. S3).

Vieira et al. (2018) hypothesized that the species of *Ceratophrys* and *L. asper* had a wider distribution during the Last Glacial Maximum (~21,500 BP). The actual distribution of fossils can corroborate this assertion indicating that, since the

late Miocene, the paleodistribution of some species of Ceratophryidae expanded to areas west and south of the current distribution.

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ORCID

Lucas A. Barcelos  <http://orcid.org/0000-0003-4911-1695>
 Diego Almeida-Silva  <http://orcid.org/0000-0002-9186-4685>
 Charles M. D. Santos  <http://orcid.org/0000-0001-5577-0799>
 Vanessa K. Verdade  <http://orcid.org/0000-0001-8990-0571>

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APPENDIX 1. Examined specimens

Dry Skeletons

Ceratophrys aurita MZUSP 22976; MZUSP 61114(2); DNPMP-1-AR; KU223818; KU98129.

Cleaned and Stained

Chacophrys pierottii MZUSP 16274.

Fossils

†*Ceratophrys ameghinorum* MACN 14317, 14318, 19731;
†*C. ornata* MLP 86-viii-1-4; †*C. prisca* MACN 14323,
†*C. rusconii* MACN 19744; †*Ceratophrys* sp. MLP 86-viii-1-5/6;
Ceratophrys sp.† MACN 14328; †*Ceratophrys cornuta* NHMUK
18895/6.

μCT-scanned and X-radiograph (*) Images

Alsodes nodosus CM-HERPS-68395; *Ceratophrys aurita*
MZUSP 31367; and Cas-herp-84998; *C. calcarata* MZUSP
99657; *C. cornuta* MZUSP 70548; uf:herp:63162; MCZ: Herp:
A-17499; *C. cranwelli* MZUSP 99320; MCZ: Herp: A-35360.

Ceratophrys joazeirensis MZUSP 142284; *C. ornata* MZUSP
70791; *C. stolzmanni* USNM 160970; *C. testudo* NRM 1912*; *Cha-*
cophrys pierottii KU191932, MZUSP 99329; *Lepidobatrachus*
asper MZUSP 94595; *L. laevis* MZUSP 94681; UF-H-12347;
L. llanensis MZUSP 74347; *Telmatobius thompsoni* UF-H-39.