



## A new fossil of *Ceratophrys* Wied-Neuwied (Ceratophryidae: Anura) from Southeastern Brazil

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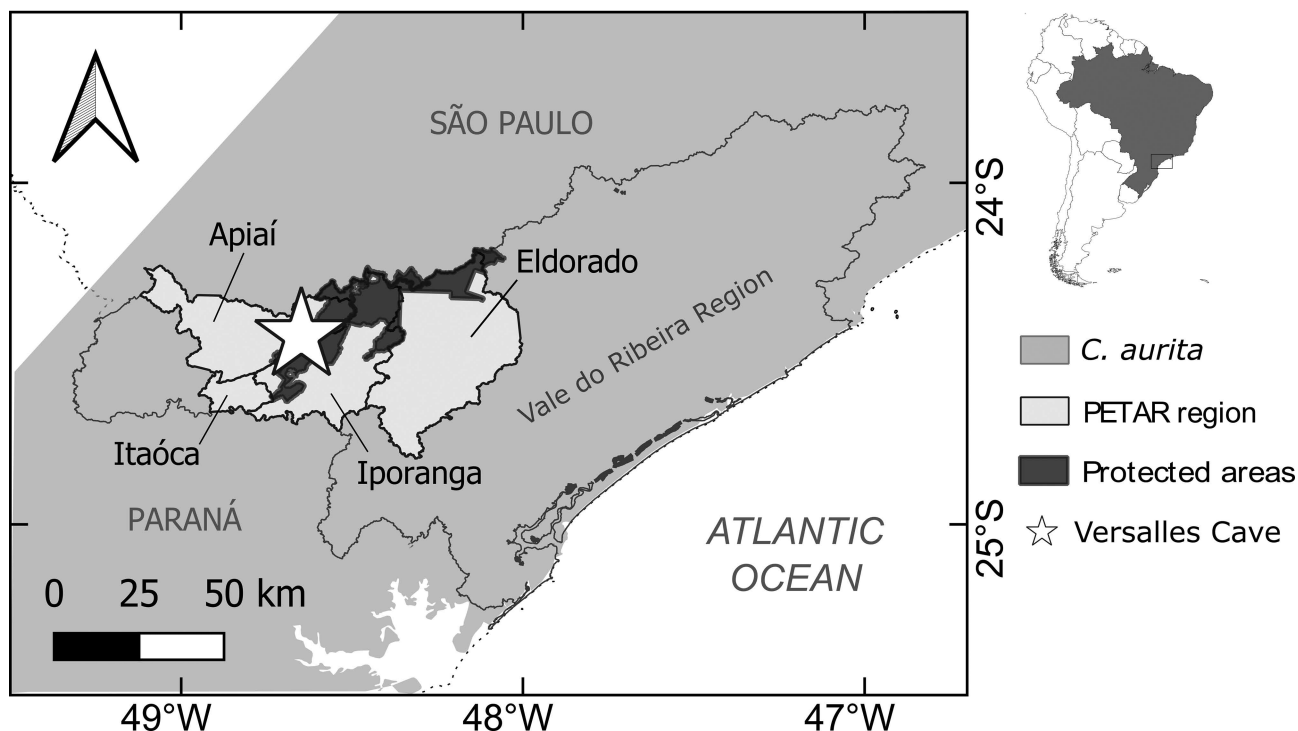
The South American horned-frog *Ceratophrys* Wied-Neuwied (Ceratophryidae) represents a monophyletic genus (Fabrezi 2006; Fabrezi & Quinzio 2008; Faivovich *et al.* 2014; Gómez & Turazzini 2021), presenting the combination of diagnostic characters: nasal with robust, bar-shaped maxillary process, and squamosal and frontoparietal in broad contact forming a postorbital fenestra (Nicoli 2019). The eight living species of *Ceratophrys* are divided in two species groups or clades: *C. aurita* species group—*C. aurita* (Raddi), *C. cranwelli* Barrio, *C. joazeirensis* Mercadal de Barrio, and *C. ornata* (Bell) corresponding to the southeastern clade of Nicoli (2019); and *C. cornuta* species group—*C. calcarata* Boulenger, *C. cornuta* (Linnaeus), *C. stolzmanni* Steindachner, and *C. testudo* Andersson, corresponding to the northwestern clade of Nicoli (2019) (Lynch 1982; Faivovich *et al.* 2014).

*Ceratophrys* present a copious fossil record with nearly 40 fossil specimens and two species known exclusively from fossils (Nicoli 2019; Barcelos *et al.* 2020): *Ceratophrys ameghinorum* Fernicola, and *Ceratophrys sagoni* Barcelos, Almeida-Silva, Santos & Verdade. The fossil record of Ceratophryidae ranges from the Late Miocene to the Late Pleistocene (Nicoli *et al.* 2017). Nicoli (2019) reviewed most of these fossils and proposed that the great majority of fossil species determinations in Ceratophryidae lack supportive characters, and should be determined only to the genus level (Nicoli 2019). Later, many of the known fossil specimens representatives of Ceratophryidae were included in the phylogenetic analyses of Gómez & Turazzini (2021), but only a single record from Brazilian territory was included in the analyses. We present a summary of data available from Ceratophryidae fossils found in Brazil and describe a new specimen.

There are only three fossil specimens attributed to *Ceratophrys* registered in Brazil: two of them (i.e. BMNH 18895/6) determined as *C. aurita* from Pleistocene of Lagoa Santa, state of Minas Gerais (Günther 1859; Barcelos *et al.* 2020; Gómez & Turazzini 2021) and one specimen of the exclusively extinct species *Ceratophrys sagoni* from Late Pleistocene–Early Holocene of Versalles Cave, Apiaí, state of São Paulo (Barcelos *et al.* 2020). The new specimen we describe here (ZUFABC 038), an almost complete skull, is also from Versalles Cave fossiliferous locality.

We compared the skull morphology of the fossil ZUFABC 038 to  $\mu$ CT-scanned specimens and museum specimens of all living and fossil species of Ceratophryidae (Appendix I). Photos of the fossil specimens were taken with a LGK10 cell phone 13 MP, f/2.2, AF (LTE model). The osteological nomenclature follows Lynch (1971) and Nicoli (2019). The Versalles Cave (Fig. 1) is located approximately 16 km northeast of the city of Apiaí, state of São Paulo UTM 22J 737457/7294530, 715m (Datum WGS). The area belongs to the Alto do Ribeira Area fossiliferous locality, part of the austral portion of Ribeira Belt (de Almeida *et al.* 1973), one of the geotectonic provinces that border San Francisco Craton (de Almeida *et al.* 1973). The specimen ZUFABC 038 was collected by Alessandro Marques de Oliveira and the EGRIC–Espeleo Grupo de Rio Claro in September 2014. Its age is unknown, however, *Nothrotherium maquinense* (Lund) was found in the cave during the same paleontological expedition and dated between 13,037 and 12,790 BP (before present; Oliveira 2018). Therefore, the cave sediments are tentatively assessed as Late Pleistocene–Early Holocene in age.

**Institutional Abbreviations**—**BMNH** British Museum of Natural History; **Cas-herp**, California Academy of Sciences—Herpetology; **KU** University of Kansas; **MLP** Museo de La Plata; **MZUSP** Museu de Zoologia da Universidade de São Paulo; **ZUFABC** Coleção Zoológica da Universidade Federal do ABC.



**FIGURE 1.** Map showing the location (white star) of the Versalles Cave, Apiaí municipality, state of São Paulo, Southeastern Brazil (UTM 22J 737457/7294530, 715m [Datum WGS]) and the current distribution of *Ceratophrys aurita*.

## Systematic paleontology

### Anura Duméril

### Neobatrachia Reig

### Ceratophryidae Tschudi

### *Ceratophrys* Wied-Neuwied

(Fig. 2)

**Type Species.** *Ceratophrys varius* Wied-Neuwied (currently *C. aurita* [Raddi]). Extant taxon, Neotropical distribution.

*Ceratophrys aurita* Raddi

**Referred Specimen.** ZUFABC 038, partial skull.

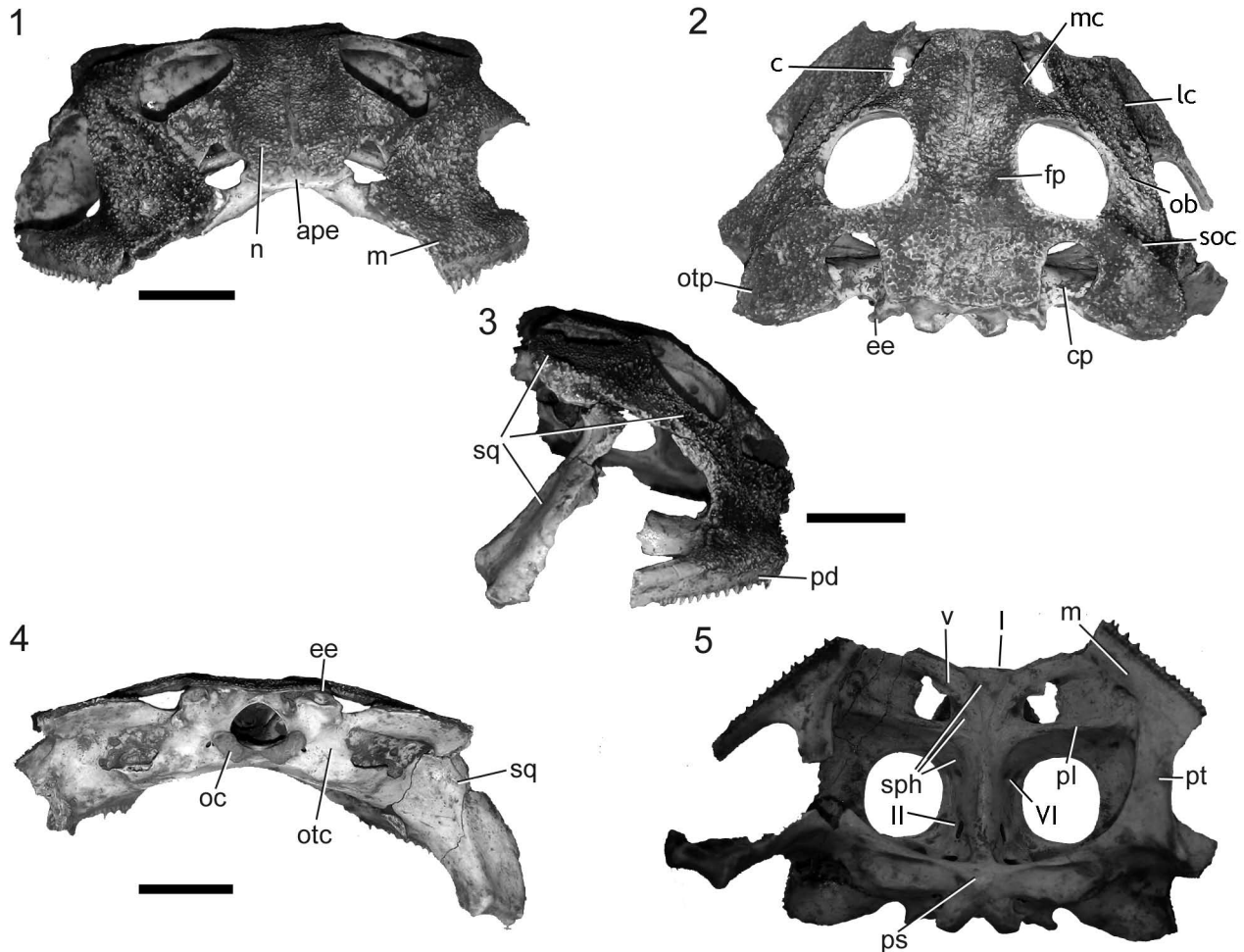
**Locality and Age.** Versalles Cave, Apiaí municipality, state of São Paulo, Brazil, Late Pleistocene–Early Holocene.

**Distribution.** The extant species distribution ranges from states of Minas Gerais and Bahia to Rio Grande do Sul, Brazil (Frost 2021). The paleodistribution is restricted to one locality in the state of Minas Gerais (Günther 1859 [Barcelos *et al.* 2020]) and one locality in the state of São Paulo, Brazil.

**Description.** The specimen ZUFABC 038 consists of a skull partially preserved and five fragments that were glued together. The left ventral ramus of squamosal, posteriormost and anteriormost portions of maxilla, premaxillae, left quadratojugal, septomaxillae and columellae are not preserved. The larger fragment consisted of the main parts of the skull. The hyperossification of the skull, with synostosis of skull bones are indicative of an adult specimen. The right maxilla is broken in three fragments from the skull, a cranial portion of the right pars facialis, including a fragment of the palatine and a fragment of the maxilla from region of the pterygoid process, with non-pedicellated fang-like teeth preserved. The right ventral ramus of squamosal synostosed to the quadratojugal constitute other two fragments. Those fragments were glued together (Fig. 2), and allowed the estimation of the approximate maximum cranium height (25 mm). We measured the width of the skull-half (from right quadrate to the jugular foramen = 30 mm) and mirrored it to infer the approximate maximum width (60 mm).

The nasals are paired bones that are flat, symmetrical and wide (Fig. 2.1). The nasals articulate synostotically with each other medially and bear exostosis in its dorsal surface, except throughout the axis of the suture between the nasals. The minimum-interorbital width is 9 mm, the maximum bi-orbital width is 29 mm, and the diameter of anteroposterior

orbit is 10 mm. The nasals articulate synostotically with each frontoparietal posteriorly. The maxillary process of the nasals is bar-shaped and bear a medial crest on its proximal portion (Fig. 2.2). It articulates with each zygomatic ramus of the squamosal laterally, forming the infraorbital flange. The nasals, maxilla, and zygomatic ramus of the squamosal participates in the formation of the choanae aperture, which is oblong and directed medially. Frontoparietals are paired, symmetrical, dorsally exostosed bones, synostotically fused to each other throughout their contact. Each frontoparietal sutures laterally with the squamosal through a parieto-squamosal arch, forming a postorbital fenestra (diameter = 4 mm) (Nicoli 2019).



**FIGURE 2.** Skull of the fossil *Ceratophrys aurita* ZUFABC038. Skull in 1, frontal view; 2, dorsal view; 3, lateral view; 4, posterior view; 5, ventral view. Abbreviations: c, choana; cp, crista parotica; ee, epiotic eminence; fp, frontoparietal; lc, lateral crest; m, maxilla; mc, medial crest; n, nasal; ob, oblique crest; oc, occipital condyles; otp, otic plate; otc, otoccipital; ape, anterior projection of sphenethmoid; pl, palatine; ps, parasphenoid; pd, pars dentalis; pt, pterygoid; sph, sphenethmoid; sq, squamosal; v, vomer. Scale bars equal 10 mm.

Squamosals are paired, triradiate bones that bear exostosis on its dorsal surface. The three rami of the squamosal are: the ventral ramus, otic ramus, and zygomatic ramus. The squamosal otic ramus is exostosed dorsally and bear a subquad-rangular otic plate. This otic plate is dorsolaterally curved and presents a dorsal concavity. The otic plate extends posteriorly beyond the level of the occipital condyles. The lateral portion of the otic plate also bears a lateral process ventrally projected. The maximum width between otic plates is 44 mm. The squamosal zygomatic ramus articulates with the pars facialis of the maxilla, with the maxillary process of the nasal and with the anterior ramus of the pterygoid. The ventral and zygomatic rami articulate with the maxilla and contribute to the formation of the subtemporal fenestra (Fig. 2.3). Two crests originate from the contact of the zygomatic ramus with adjacent bones: the lateral crest (that extends throughout the subtemporal fenestrae edge) and the oblique crest (that extends through the anterior-most edge of the orbit to the lateral process of otic plate). The squamosal ventral ramus constituted two fragments. It is an elongate element, ventrally directed, which sutures the quadrate and the pterygoid (Fig. 2.4).

Pterygoids are paired, triradiate bones. The anterior and posterior rami of the right pterygoid is heavily fragmented. The anterior and medial rami of left pterygoid are well preserved. The pterygoid anterior ramus sutures to the respective maxilla and palatine forming the lateral edge of the interpterygoid vacuity. The maximum inter-ptyergoids distance is 22 mm. The pterygoid medial ramus sutures the parasphenoid and the otoccipital (Fig. 2.5). The posterior ramus sutures the ventral ramus of the squamosal and the quadrate. Only the right quadrate is preserved. The maxilla is preserved only between the vomer and the interpterygoid vacuity. The pars facialis of the right maxilla was split into three fragments. The pars dentalis of the maxilla bear fang-like non-pedicellate teeth (15 on the right and 6 on the left maxilla).

The sphenethmoid sutures the cultriform process of the parasphenoid posteriorly, the vomer and the palatine medially, and the nasals anteriorly. The anterior portion of sphenethmoid is a wide and truncated projection that bears two olfactory nerve foramina (CN I). A well-developed abducens nerve foramen (CN VI) is placed at the medial portion of sphenethmoid, on the suture with the cultriform process of parasphenoid. At the posterior portion, the sphenethmoid meets the otoccipital and the cultriform process of parasphenoid and forms the optic nerve foramen (CN II). The vomers are paired bones sutured to the sphenethmoid, and the maxilla. Vomers present vomerine teeth. The palatines are elongated paired bones. The parasphenoid is a T-shaped bone. The cultriform process of the parasphenoid does not reach the level of the planum antorbitale. The otoccipital sutures synostotically to the parasphenoid, the sphenethmoid, the frontoparietal, the squamosal, and the pterygoid. The otoccipital bears epiotic eminences flat in posterior view and slender in dorsal view. The epiotic eminences are partially overlapped by the processus posterior of the frontoparietal, forming the posttemporal fenestra. The posterior portion of otoccipital bears juxtaposed occipital condyles.

The specimen ZUFABC038 is attributed to *Ceratophryidae* on the basis of the following synapomorphies: exostosed skull, parieto-squamosal arch present, zygomatic ramus of squamosal in contact with the maxilla, non-pedicellate and fang-like teeth, parieto-squamosal arch present, and the otic ramus of squamosal expanded and overlapping the prootics (Lynch 1971, 1982; Fabrezi 2006; Fabrezi & Quinzio 2008; Nicoli 2019). ZUFABC038 is assigned to *Ceratophrys* by nasal with robust bar-shaped maxillary processes, parieto-squamosal arch forming a postorbital fenestra, absence of pars palatina (and palatine process) on the anterior half of the maxilla (Nicoli 2019), the presence of posterior margin of dermocranium indented, and synostosis of most skull bones into an akinetic unit (Wild 1997; Lynch 1982).

The specimen ZUFABC038 can be assigned to the [*C. aurita*–*C. joazeirensis*] clade by the presence of a medial crest on the nasal, presence of vomerine teeth, and lateral crests on the zygomatic ramus of squamosal and maxilla (Nicoli 2019). Unfortunately, other characters diagnosing the [*C. aurita*–*C. joazeirensis*] and the southeastern clade (i.e. *C. aurita* species group) as a bony dorsal shield (Nicoli 2019) are not preserved in the specimen ZUFABC038. Our comparative study on specimens character variation within *Ceratophrys* (Appendix 1) show that it is possible to diagnose the specimen ZUFABC038 as a fossil representative of *C. aurita* by sharing with other exemplars of this species the combination of characters: zygomatic ramus of the squamosal wide (narrow-shaped in *C. joazeirensis*; Barcelos *et al.* 2020); three crests and two depressions on zygomatic ramus of squamosal and maxilla (Fig. 2.2) (absent in *C. cranwelli* and *C. ornata*), the otic plate of the squamosal dorsally concave (convex in *C. joazeirensis*, *C. cranwelli* and *C. ornata*); anterior-most portion of sphenethmoid forming a wide and truncated projection (Fig. 2.1) (short and rounded in *C. joazeirensis*), and nasal and maxilla forming choanae aperture oblong-shaped (Fig. 2.1; Barcelos *et al.* 2020) (rounded in *C. joazeirensis*, *C. cranwelli*, and *C. ornata*).

We are aware Nicoli (2019) hypothesizes *C. aurita* and *C. joazeirensis* may represent variations within a same species based on osteology. The author compared one specimen of *C. aurita* (MLP 1280) to two cleared and stained specimens of *C. joazeirensis* (MZUSP 56463, 126203) and claimed ontogenetic variation. Our sample includes eight *C. aurita*, and one specimen of *C. joazeirensis*, but despite observing some intraspecific variation in *C. aurita*, it is still possible to diagnose specimens as indicated above. Following our observations, we interpret the figures in Nicoli (2019) as follows: the morphology of the large specimen (MZUSP 56463) agrees with that diagnostic for *C. aurita* (i.e. three crests and two depressions on zygomatic ramus of squamosal and maxilla, anterior-most portion of sphenethmoid forming a wide and truncated projection, and nasal and maxilla forming choanae aperture oblong-shaped). The smaller specimen (MZUSP 126203) presented a rounded otic plate and zygomatic ramus of squamosal and maxilla without crests or depressions in its posterior edges, characters not congruent to [*C. aurita*–*C. joazeirensis*] clade, but it could be ontogenetic variation if it is a juvenile as Nicoli (2019) proposed.

Misidentification concerning *C. aurita* and *C. joazeirensis* are reported in literature (Maciel *et al.* 2013), so it would be important to check for Nicoli's specimens identities. Unfortunately, the information on locality or identity assertion of these exemplars are missing in Nicoli (2019). These specimens were not at MZUSP during our visit, and when we asked the collection manager for the data associated to MZUSP 56463 and MZUSP 126203, the answer was that the record of



MZUSP 56463 was not available in the system, and that MZUSP 126203 was associated to a hyloid originally from Werner Bokermann collection (WCAB). As the specimens studied by Nicoli (2019) are clearly *Ceratophrys*, it is something worth to check in the future.

We noted three polymorphic characters in the skull of *C. aurita* species based in our sample, but that not overlap with the characters observed in *C. joazeirensis* (under brackets): the ornamentation of the projection of the anterior portion of sphenethmoid can be wide and truncated (e.g. MZUSP 31367), or wide and rounded (e.g. KU 223818) (narrow and rounded); a concavity/scar on the suture between the vomer and the anterior portion of sphenethmoid may be present (e.g. cas:herp:84998) or absent (e.g. MZUSP 61114-2) (absent); *Ceratophrys aurita* ZUFABC038 enlarges the range of skull-ratio for the clade [*C. aurita*–*C. joazeirensis*] from 41% (in *C. aurita* ZUFABC038) to 50% (former skull-ratio proposed by Nicoli 2019) (50% in *C. joazeirensis*). The intraspecific variation in the osteology of *Ceratophrys* species is unexplored, as for most anurans, and may highlight the discussion on paleodiversity and paleoclimatic changes in South America (e.g. Simon *et al.* 2016).

In contrast to the much better approached paleofauna of Ceratophryidae in Argentina, there is a hidden paleodiversity of Ceratophryidae in Brazil, with only four specimens registered (including the one in this paper). *Ceratophrys aurita* ZUFABC 038 is the third record of *C. aurita* and fourth record of Ceratophryidae for the Brazilian territory. The fossiliferous locality of Versalles Cave is located in the current distribution range of *C. aurita* (Fig. 1; Araújo *et al.* 2010). Still, the distribution of *C. aurita* during the last glacial maximum was potentially broader than the current one (Vieira *et al.* 2018), considering the expansion of southeastern forests to the interior of the country. The record of the specimens *Ceratophrys aurita* BMNH 18895/6 from Lagoa Santa–MG is congruent to this more continental paleodistribution. Lastly, *Ceratophrys aurita* ZUFABC038 states the extant species occurs in the southeastern of Brazil for at least the Late Pleistocene.

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## APPENDIX 1

**Specimens Examined.** Acronyms are: CM-HERPS (Carnegie Museum of Natural History—Herpetology) Cas-herp (California Academy of Sciences—Herpetology); DNPM-MP (Departamento de Produção Mineral—Museu de Paleontologia); KU (University of Kansas—Herpetology); MACN (Museo de Ciencias Naturales de Buenos Aires “Bernardino Rivadavia”); MCZ:Herp (Museum of Comparative Zoology, Harvard University); MLF (Miguel Lillo Foundation); MLP (Museo de Ciencias Naturales de La Plata); MZUSP (Museu de Zoologia da Universidade de São Paulo); UF-H (Florida Museum of Natural History—Herpetology); USNM (National Museum of Natural History, Smithsonian Institution).

Dry skeletons: *Ceratophrys aurita* MZUSP 22976\* MZUSP 61114(2); DNPM-MP 1-AR; KU 98129; KU 223818; *Ceratophrys cornuta* KU 222113; *Ceratophrys cranwelli* KU 211317; FML 5471.

Cleaned and stained: *Chacophrys pierottii* MZUSP 16274.

Fossils: *Ceratophrys*† MLP 86-viii-1-4, 86-viii-1-5, 86-viii-1-6; *C. ameghinorum*† MACN 14317 (paratype), 14318, 19731 (paratype); *C. prisca*† MACN 14323, *C. rusconii*† MACN 19744; *Ceratophrys* sp.† MACN 14328.

Specimens examined through  $\mu$ CT-scanned 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; *C. joazeirensis* MZUSP 142284; *C. ornata* MZUSP 70791; *C. stolzmanni* USNM 160970; *Chacophrys pierottii* KU191932, MZUSP 99329; *Lepidobatrachus asper* MZUSP 94595; *L. laevis* MZUSP 94681; UF-H-12347; *L. llanensis* MZUSP 74347; *Telmatobius thompsoni* UF-H-39734.