Article

Discovery of an additional piece of the large gymnophthalmid puzzle: a new genus and species of stream spiny lizard (Squamata: Gymnophthalmidae: Cercosaurinae) from the western Guiana Shield in Venezuela

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Abstract

Gymnophthalmids are a highly diverse group of Neotropical lizards and its species richness is still in process of discovery. The incorporation of molecular evidence and a noticeable increase in taxon and geographic sampling in systematic studies has led to the description of numerous new genera and species of gymnophthalmids (particularly in Cercosaurinae) in recent years. Herein we describe a new genus and species of cercosaurine lizard with crocodile-like morphology, from the Venezuelan Guiana Shield on the basis of molecular phylogenetic and morphological evidence. *Kataphraktosaurus* **gen. nov.** can be readily distinguished from all other genera of Cercosaurinae by a unique combination of morphological characters that includes heterogeneous dorsal scalation with enlarged and strongly keeled scales forming two paravertebral rows, ventral and subcaudal scales imbricated and strongly keeled, large and symmetrical cephalic scales, absence of postmental scale, palpebral disc translucent and divided, tail slightly compressed, all digits clawed, and only six femoral pores (three at each hindlimb) inserted in a clump of small scales. This genus is described as monotypic and only contains *Kataphraktosaurus ungerhamiltoni* **sp. nov.**, which is known from one specimen and diagnosed by the same set of aforementioned characters. The secretive habits of this species and the remoteness of the locality may explain its singleton situation. Following the International Union for Conservation of Nature's criteria, we categorized the new species as Data Deficient.

Key words: Amazonia, biodiversity, Neotropics, Orinoco basin, phylogeny, reptile, systematics, taxonomy

Resumen

Gymnophthalmidae es un grupo de lagartos neotropicales muy diverso y su riqueza de especies aún está en proceso de descubrimiento. La incorporación de evidencia molecular y un incremento notable en el muestreo taxonómico y geográfico en estudios sobre su sistemática han resultado en la descripción de un gran número de géneros y especies nuevas de gymnoftálmidos (particularmente en Cercosaurinae) en años recientes. Aquí describimos un nuevo género y especie de lagarto cercosaurino con fenotipo cocodriloide, del Escudo Guayanés venezolano, a partir de análisis filogenéticos moleculares y caracteres morfológicos. *Kataphraktosaurus* **gen. nov.** se distingue de todos los demás géneros de Cercosaurinae por su combinación única de caracteres morfológicos que incluye un patrón de folidosis dorsal heterogéneo, con escamas agrandadas y fuertemente aquilladas formando dos filas paravertebrales, escamas ventrales y subcaudales imbricadas y fuertemente aquilladas, escamas cefálicas grandes y simétricas, ausencia de escama postmental,

disco palpebral translúcido y dividido, cola ligeramente comprimida, todos los dedos con uñas, y solo seis poros femorales (tres en cada muslo) insertos en medio de una agrupación de pequeñas escamas. Este género, descrito como monotípico, solo incluye a *Kataphraktosaurus ungerhamiltoni* **sp. nov.**, conocida por un espécimen y cuya diagnosis consta del mismo conjunto de caracteres mencionados para el género. Los hábitos crípticos de esta especie y lo remoto de la localidad tipo pueden explicar el hecho de que sólo se conozca un ejemplar. Siguiendo los criterios de la Unión Internacional para la Conservación de la Naturaleza, asignamos a la nueva especie la categoría de Datos Insuficientes.

Palabras clave: Amazonia, biodiversidad, cuenca del Orinoco, filogenia, Neotrópico, reptil, sistemática, taxonomía

Introduction

The lizard family Gymnophthalmidae includes 267 extant species from 52 genera distributed throughout the Neotropics (Uetz *et al*. 2020). Convergence of many morphological characters in different gymnophthalmid lineages, the rarity of some taxa in museum collections, and the lack of sampling in large geographical areas have resulted in a rather complicated and unstable taxonomy. Most of the original taxonomic arrangements within Gymnophthalmidae, which were only based on morphology (*e.g.*, Burt & Burt 1931; Ruibal 1952; Uzzel 1966) changed dramatically in the last two decades. The pioneer molecular phylogeny of Pellegrino *et al*. (2001) represents the beginning of a new age in Gymnophthalmidae systematics. This is characterized by a constant increase in taxon and geographic sampling that have led to taxonomic revisions and rearrangements to accommodate newly discovered species and phylogenetic relationships, while ensuring a monophyletic taxonomy (*e.g.*, Castoe *et al*. 2004; Doan and Castoe 2005; Goicoechea *et al*. 2012; Pyron *et al*. 2013; Kok 2015; Torres-Carvajal *et al*. 2015, 2016; Goicoechea *et al*. 2016; Marques-Souza *et al*. 2018; Moravec *et al*. 2018; Pellegrino *et al*. 2018; Sánchez-Pacheco *et al*. 2018; Fang *et al*. 2020; Lehr *et al*. 2020; Vásquez-Restrepo *et al*. 2020).

Gymnophthalmidae is subdivided into subfamilies—sometimes considered as tribes (Pellegrino *et al*. 2001; Goicoechea *et al*. 2016)—of which Cercosaurinae is the most species-rich, with about half of all recognized gymnophthalmid species. Currently, the more than 150 Cercosaurinae species are grouped in 21 genera (Torres-Carvajal *et al*. 2016; Moravec *et al*. 2018; Sánchez-Pacheco *et al*. 2018; Lehr *et al*. 2019, 2020; Fang *et al*. 2020; Mamani *et al*. 2020; Parra *et al*. 2020; Torres-Carvajal *et al*. 2020; Vásquez-Restrepo *et al*. 2020). Within this rich subfamily, some linages have evolved a striking phenotype, presumably adapted to aquatic or semi-aquatic life. It includes a streamlined body with pointed snout, compressed tail, heterogeneous dorsal and lateral scalation, sometimes with enlarged tubercles, and strongly keeled scales forming crests on body and tail (*i.e.*, crocodile-like morphology, hereafter CLM as in Marques-Souza *et al*. 2018). This combination of morphological characters is present in members of the genera *Echinosaura*, *Gelanesaurus*, *Magdalenasaura*, *Neusticurus*, *Potamites* (Uzzell 1965; 1966; Doan and Castoe 2005; Torres-Carvajal *et al*. 2016; Marques-Souza *et al*. 2018; Fang *et al*. 2020), and the two monotypic genera *Centrosaura* and *Rheosaurus*, which were recently erected by Vásquez-Restrepo *et al*. (2020) to remedy the polyphyly of *Echinosaura*. This CLM phenotype has evolved at least four independent times in the evolutionary history of Cercosaurinae, is apparently modulated by ecological and environmental selective pressures, and may be linked to the development of the Pebas Lake in western Amazonia during the Miocene (Marques-Souza *et al*. 2018). In this study, we report our discovery of a new CLM gymnophthalmid from the western Guiana Shield in Venezuela. The results of our detailed morphological and genetic comparisons, including phylogenetic analysis, indicate that the specimen corresponds to a new stream lizard species, which is not nested within any of the current described Cercosaurinae genera. To maintain a monophyletic taxonomy, while preserving phenotypic diagnosis of current genera within the subfamily, we create a new genus for this new species.

Material and methods

Fieldwork. The only specimen collected and its associated data resulted from our fieldwork between 13 and 16 July 2010, in a rainforest area on the northwestern foothill of the Serranía del Cuao, Amazonas state, Venezuela (Fig. 1). At this location, we (CLBA, FJMRR, and SCF) performed diurnal and nocturnal visual surveys for herpetofauna and georeferenced the collection sites using a GPS receiver Garmin 60CSX with datum WGS 84. The specimen was captured manually and transported to an improvised laboratory in the field, where it was photographed in life (we

used these photographs to describe its coloration). After photographed, it was anesthetized and euthanized with an overdose of topical benzocaine solution (50 mg/g), fixed in a 10 % formalin solution, and preserved in 70 % ethanol. We dissected a sample of muscular tissue from the right thigh prior to fixation and preserved it in 95 % ethanol for molecular analyses.
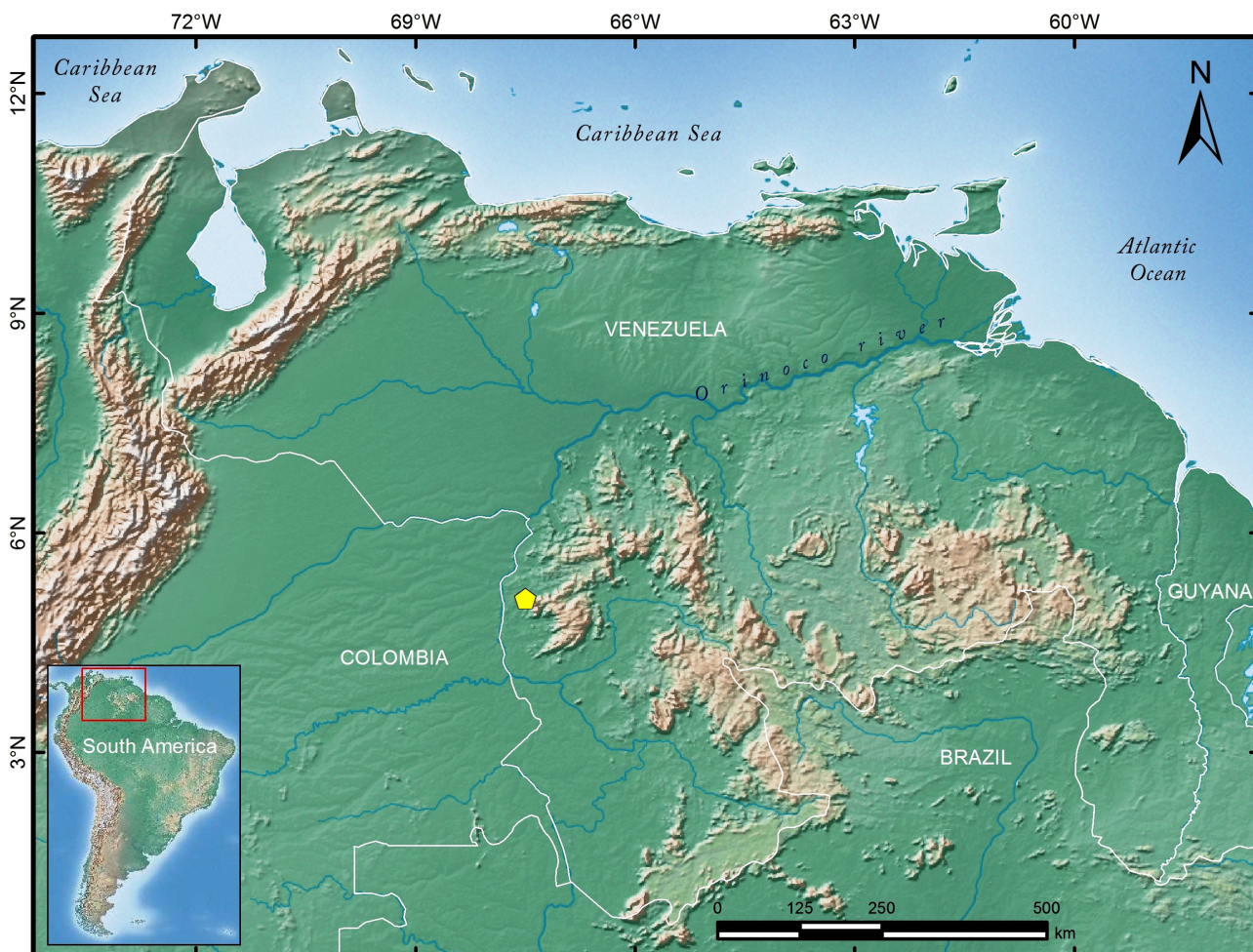

FIGURE 1. Map of Venezuela indicating the geographic position of Caño Bejuco (yellow pentagon), near Tobogán del Cuao, Autana municipality, Amazonas state, Venezuela, type locality of *Kataphraktosaurus ungerhamiltoni* **gen. nov., sp. nov.**

Morphology. The holotype was deposited at the Museo de Historia Natural La Salle (MHNLS), Caracas, Venezuela. For comparisons with all other genera of crocodile-like gymnophthalmids, we used morphological descriptions from the literature (Boulenger 1890, 1911; Barbour 1924; Uzzell 1965, 1966; Fritts & Smith 1969; Fritts *et al.* 2002; Köhler *et al.* 2004; Donnelly *et al.* 2006; Lotzkat *et al.* 2012; Fang *et al.* 2020; Vásquez-Restrepo *et al.* 2020). We followed Kok *et al.* (2018) and Vásquez-Restrepo *et al.* (2020) for morphological description format, pholidotic nomenclature, and scale counts. Scale counts and measurements were made by the first author under a stereomicroscope; bilateral meristic and qualitative characters were recorded from both sides and are presented as left/right. Morphometric measurements were taken with a caliper to the nearest 0.1 mm, except limbs and tail that were measured with a piece of string and a ruler. Measurements were taken as follows: snout-vent length (SVL), from snout tip to anterior margin of vent; neck length (NL), from posterior margin of tympanum to anterior insertion of forelimb; axilla-groin distance (AGD), from posterior border of arm insertion to anterior border of leg insertion; tail length (TL), from posterior margin of vent to tail tip; head length (HL), from tip of snout to posterior margin of tympanum; head width (HW), at the maximum width of the head; head depth (HD), at the maximum depth of the head; snout length (SL), from snout tip to anterior corner of eye; forelimb length (FL), from axilla to tip of 4th finger claw; hind limb length (HiL), from groin to tip of 4th toe claw.

Molecular and taxon sampling. Following previous molecular studies on gymnophthalmid systematics (*e.g.*, Pellegrino *et al.* 2001; Torres-Carvajal *et al.* 2016; Vásquez-Restrepo *et al.* 2020), we selected four gene fragments for

our phylogenetic analysis: three mitochondrial (mtDNA; 12S and 16S rRNAs, and ND4) and one nuclear (nuDNA; C-MOS). In addition to the new sequences generated in this study from our new species, we obtained from GenBank (http://www.ncbi.nlm.nih.gov/genbank) sequences of these four markers for 77 terminals representing 20 genera of Cercosaurinae, and eight species of the other five subfamilies of Gymnophthalmidae (Bachiinae, Ecpleopodinae, Gymnophthalminae, Rhachisaurinae, and Riolaminae). We used *Alopoglossus viridiceps* (Alopoglossidae) to root all trees.

DNA extraction, amplification, and sequencing. We extracted genomic DNA from a 95 % ethanol-preserved tissue sample of thigh muscle using the Wizard® Genomic DNA Purification Kit (Promega Corporation) and following the manufacturer's protocol. Polymerase chain reactions (PCR) for DNA amplification were performed in a final volume of 25 μL, using 2 μL extracted DNA, 1.25 μL of each forward and reverse primers, 8 μL of MasterMix, and 12.5 μL H_2O. Negative controls were run on all amplifications to check for contamination. Primers and reaction conditions used to amplify the four DNA markers are presented in the Table 1. PCR products were inspected in 1 % agarose gels by horizontal electrophoresis. Cycle sequencing reactions were performed by Macrogen Labs (Macrogen Inc., Korea). All PCR products were sequenced in both forward and reverse directions, to check for potential errors. We assembled contigs and inspected chromatograms using Sequencher 4.8 (GeneCodes, Ann Arbor, MI, USA). Finally, we performed BLAST queries (https://blast.ncbi.nlm.nih.gov/Blast.cgi) of the new sequences to verify their identity and to discard contaminations or mislabeling errors. GenBank accession codes of all analyzed sequences (including newly generated ones) are in Appendix 1.

TABLE 1. Primers and PCR conditions used to amplify the four gene fragments (three mitochondrial and one nuclear) used in this study.

Gene	Primer name, sequence, and source (forward/reverse)	PCR conditions
12S	**12SA-L** (Palumbi *et al*. 1991) AAACTGGGATTAGATACCCCACTAT	95 ℃/15 s; 35 x (95 ℃/30 s, 50 ℃/30 s, 72 ℃/1 min); 72 ℃/10 min
	12SB-H (Palumbi *et al*. 1991) GAGGGTGACGGGCGGTGTGT	
16S	**16Sar-5'** (Palumbi *et al*. 1991) CGCCTGTTTATCAAAAACAT	95 ℃/15 s; 35 x (95 ℃/30 s, 50 ℃/30 s, 72 ℃/1 min); 72 ℃/10 min
	16Sbr-3' (Palumbi *et al*. 1996) CCGGTCTGAACTCAGATCACGT	
ND4	**ND4** (Arévalo *et al*. 1994) CACCTATGACTACCAAAAGCTCATGTAGAAGC	94 ℃/3 min; 35 x (94 ℃/45 s, 50 ℃/45 s, 72 ℃/1 min); 72 ℃/6 min
	LEU (Arévalo *et al*. 1994) CATTACTTTTACTTGGATTTGCACCA	
C-MOS	**G73** (Saint *et al*. 1998) GCGGTAAAGCAGGTGAAGAAA	94 ℃/2 min; 35 x (94 ℃/1 min, 56 ℃/45 s, 72 ℃/1 min); 72 ℃/7 min
	G74 (Saint *et al*. 1998) TGAGCATCCAAAGTCTCCAATC	

Phylogenetic analyses. We used MUSCLE (Edgar 2004) under default settings as implemented in AliView 1.14 (Larsson 2014) to generate multiple sequence alignments of each marker separately. These alignments were concatenated with SequenceMatrix 1.7.8 (Vaidya *et al*. 2011). The best-fit partition scheme and corresponding models of nucleotide substitution for each partition were simultaneously assessed in PartitionFinder2 (Lanfear *et al*. 2017) according to the corrected Akaike Information Criterion (AICc). For this, we considered branch lengths as linked and evaluated three partition schemes: 1) all four markers combined; 2) mtDNA and nuDNA; and 3) each marker independently. We performed maximum likelihood (ML) tree searches implementing the optimal partition scheme and substitution models in Garli 2.01 (Zwickl 2006). To increase the exhaustiveness of tree searches, we

performed 500 independent tree searches, each with 175 attachments per branch (twice the number of terminals of the dataset, plus one), run termination threshold of 10,000 generations without significant improvement in likelihood, and maximum SPR distance of six branches away from original location. Other settings were set on default values. We also computed bootstrap support (BS) in Garli 2.01 via 1,000 pseudoreplicates under the same settings used for the tree searches. Clade frequencies of bootstrap pseudoreplicates were plotted onto the most likely tree with SumTrees 4.3.0 in DendroPy 4.3.0 (Sukumaran & Holder 2010, 2017). We performed all searches in the CIPRES Science Gateway (Miller *et al*. 2010). In addition to phylogenetic analysis, we estimated uncorrected pairwise genetic distances of 16S using uniform rates and default parameters in MEGA 7.0.14 (Kumar *et al*. 2016). We used this molecular marker because it is the best represented in our dataset (Appendix 1) and also the most commonly used to assess genetic divergence among lizards.

Results

Phylogenetic reconstruction and relationships. Our final concatenated dataset consists of a total of 1,926 bp. The best-fit partition scheme and optimal evolution models (lnL = -36,980.84; AICc = 74,438.40) for our dataset includes four subsets, each one corresponding to a single gene, with GTR+I+G as the optimal nucleotide substitution model for 12S, 16S, and ND4, and TVM+G for C-MOS. The most likely inferred topology (Fig. 2; lnL = -36,728.47) is well resolved. Within a monophyletic Cercosaurinae (BS = 92 %), all sampled genera with more than one species are monophyletic and with BS > 75 %. The exception is *Proctoporus*, which is paraphyletic with respect to *Cercosaura*, *Dendrosauridion*, *Potamites*, and *Selvasaura*. Most deeper nodes have BS < 70 %. Our specimen (MHNLS 19960) is nested within Cercosaurinae (BS = 92 %) as sister of all cercosaurines except *Placosoma* and *Neusticurus* (BS = 58 %; Fig. 2). Uncorrected pairwise 16S distances between our specimen and all other cercosaurins sampled in the phylogeny range between 8.8–15.1 %.

Morphology. The specimen MHNLS 19960 shows a unique combination of morphological characters that sets it apart from all other species and genera of Cercosaurinae. The main diagnostic characters are (Figs. 4–7): heterogeneous dorsal scalation with enlarged and strongly keeled scales, ventral and subcaudal scales slightly imbricated and strongly keeled, large and symmetrical cephalic scales, absence of postmental scale, palpebral disc translucent and divided, tail slightly compressed, all digits clawed, and only six femoral pores (three at each hindlimb) inserted in a clump of small scales. To avoid repetition, detailed morphological descriptions of qualitative and quantitative characters and comparisons with relevant taxa are provided below.

Data integration. The best explanation for the phylogenetic relationships and pattern of phenotypic variation of MHNLS 19960 is that this specimen belongs to a previously unknown species that is not nested within or sister of any of the currently recognized genera of Cercosaurinae. To formalize our discovery and to preserve a monophyletic taxonomy, we describe and name, according to the rules of the ICZN (1999), a new species and genus.

Taxonomy

Kataphraktosaurus gen. nov.

Type species: *Kataphraktosaurus ungerhamiltoni* **sp. nov.**

Definition. This new genus is defined by the unique combination of the following characters: (1) Dorsal scales heterogeneous, with large, longitudinally keeled scales intercalated by small irregular, granular to flat scales; (2) dorsal surface of head with large, weakly keeled, symmetrical scales; (3) two subtriangular internasals, each one as long as wide; (4) two large pentagonal frontonasals, more than two times longer than wide; (5) prefrontals absent; (6) frontal scale single, hexagonal, double-keeled; (7) two pentagonal frontoparietals, single-keeled; (8) interparietal large, subpentagonal, well-differentiated; (9) parietals large, polygonal, paired, flanking interparietal; (10) occipitals not differentiated; (11) temporal scales not differentiated; (12) lower eyelid developed, with palpebral disc divided into several unpigmented scales; (13) postmental absent; (14) three pairs of enlarged chin shields; (15) ventral scales pentagonal, keeled, mucronate, imbricated; (16) tail slightly compressed; (17) forelimbs and hind limbs pentadactyl; (18) digits clawed; (19) femoral pores inserted in a clump of 4–5 scales.
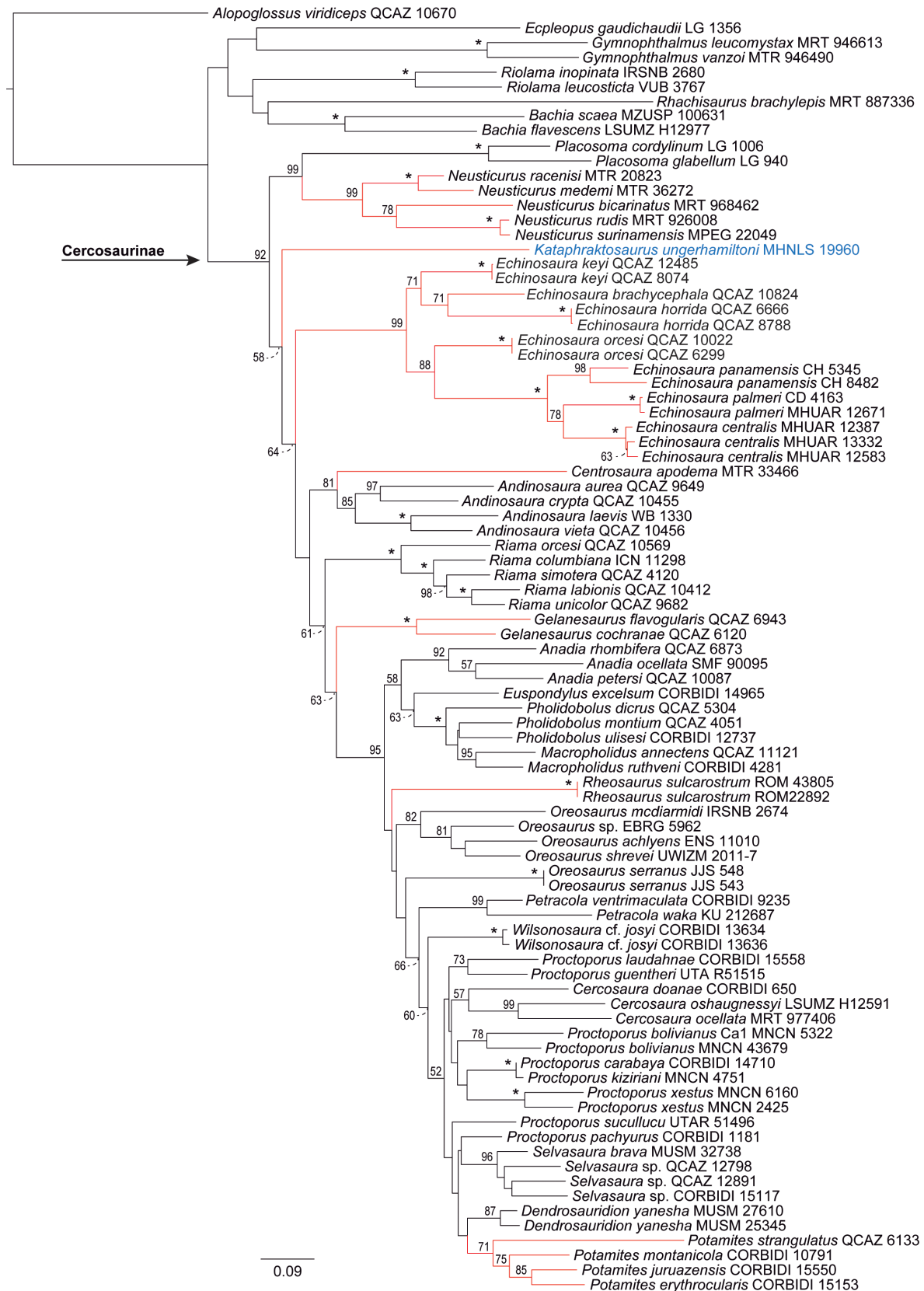
FIGURE 2. Maximum likelihood tree (lnL = -36,728.472) inferred from an aligned concatenated matrix of 1,926 bp including gene fragments of 12S, 16S, ND4 and C-MOS, depicting the phylogenetic relationships of *Kataphraktosaurus ungerhamiltoni* **gen. nov., sp. nov.** (in blue font) within Cercosaurinae. Branches in red indicate species with crocodile-like morphology. Numbers above nodes represent bootstrap support values inferred from 1,000 pseudoreplicates; values below 50 % are not included; asterisks represent 100 % bootstrap support.
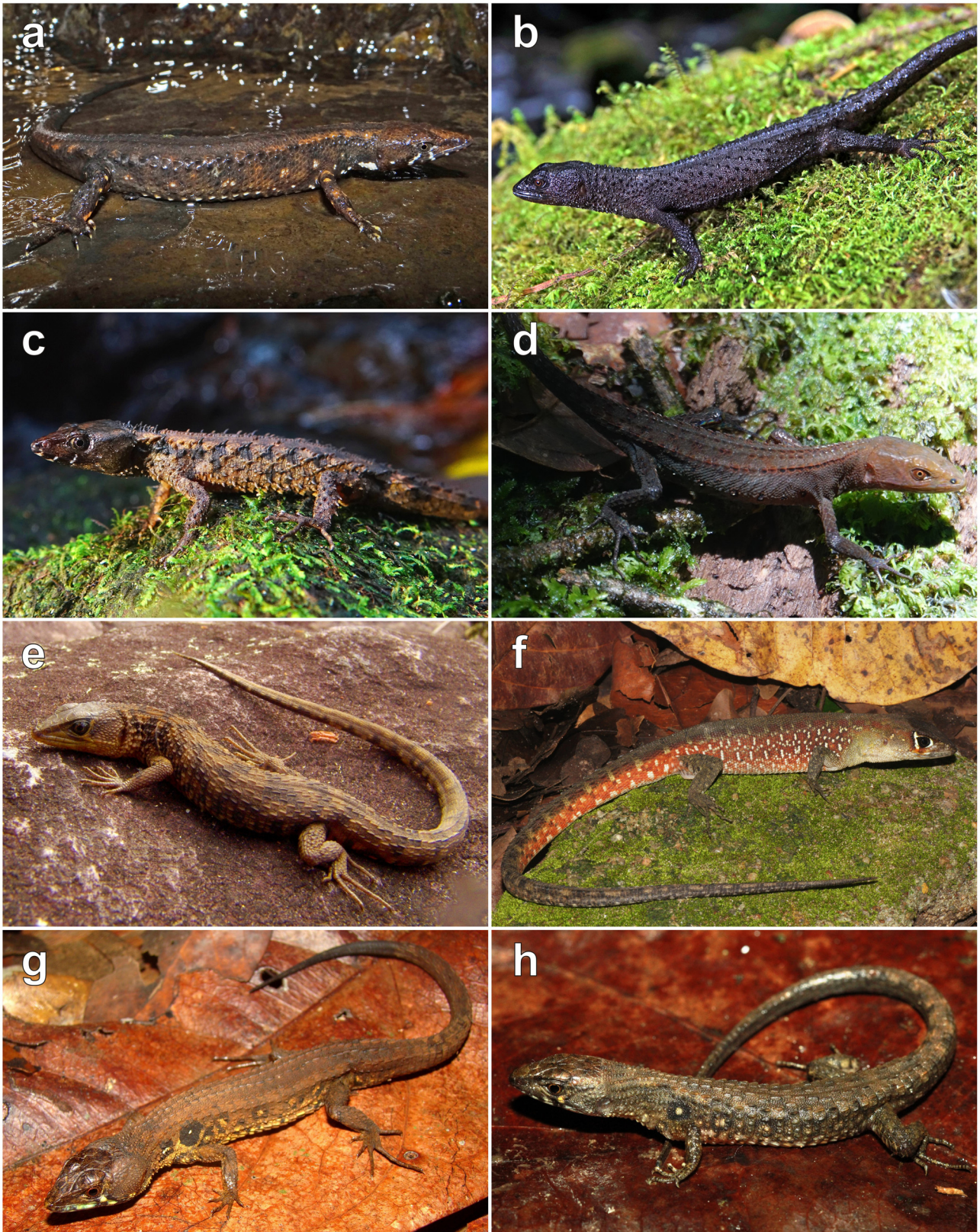
FIGURE 3. Some Cercosaurinae lizards with crocodile-like morphology: (a) *Centrosaura apodema*, from La Alfombra, Pérez Zeledón, Costa Rica; (b) *Echinosaura brachycephala*, from Mindo, Pichincha, Ecuador; (c) *Echinosaura horrida*, from Puerto Quito, Pichincha, Ecuador; (d) *Gelanesaurus flavogularis*, from Archidona, Napo, Ecuador; (e) *Neusticurus arekuna*, from Chivatón, Bolívar, Venezuela; (f) *Neusticurus medemi*, from Las Pavas, Amazonas, Venezuela; (g) *Potamites ecpleopus*, from Juami river, Amazonas, Brazil; (h) *Potamites erythrocularis*, from Inambari, Madre de Dios, Peru. Photos: C.L. Barrio-Amorós (a–f), F.J.M. Rojas-Runjaic (g), and G. Chávez (h).

Diagnosis. Apart from the new genus described herein, Cercosaurinae includes 21 genera: *Anadia, Andinosaura, Centrosaura, Cercosaura, Dendrosauridion, Echinosaura, Euspondylus, Gelanesaurus, Macropholidus, Magdalenasaura, Neusticurus, Oreosaurus, Petracola, Pholidobolus, Placosoma, Potamites, Proctoporus, Rheosaurus, Riama, Selvasaura*, and *Wilsonosaura* (Torres-Carvajal *et al.* 2016; Moravec *et al.* 2018; Sánchez-Pacheco *et al.* 2018; Lehr *et al.* 2019, 2020; Fang *et al.* 2020; Vásquez-Restrepo *et al.* 2020). Among them, only *Centrosaura, Echinosaura, Gelanesaurus, Magdalenasaura, Neusticurus, Potamites* and *Rheosaurus* have heterogeneous dorsal scalation (*i.e.*, presence of enlarged dorsal tubercular, spine-like, or keeled scales intermixed with small flat or granular scales; Fig. 3). Therefore, we restrict our comparisons to these seven genera.

Kataphraktosaurus is readily distinguished from *Centrosaura, Echinosaura, Gelanesaurus, Magdalenasaura, Neusticurus*, and *Potamites* by lacking a postmental scale (present in all the species of these genera, except in *E. brachycephala*, where it can be absent or reduced); having pentagonal, mucronate, strongly keeled, imbricate ventral scales (squared or rounded squares, usually flat, and not imbricated; only keeled in *E. brachycephala, E. centralis,* and *E. horrida*); and six femoral pores (total count) in males (≥ 6 in *Echinosaura*, ≥ 10 in *Potamites*, ≥ 20 in *Centrosaura* and *Magdalenasaura*, and > 30 in *Gelanesaurus* and *Neusticurus*). In addition, *Kataphraktosaurus* differs from *Centrosaura* by having symmetrical paired intersanals (not paired and asymmetrical), paired frontonasals (several small irregular scales in the frontonasal region), prefrontals absent (paired), a single frontal (divided), and femoral pores inserted in a clump of scales (in the center of a single scale). From *Echinosaura*, it differs by its smaller SVL (adult male 49 mm *vs*. > 70 mm in *Echinosaura*) and by having large and well-defined interparietal and parietals (several irregular and small scales on the parietal region), three pairs of chin shields (usually one pair), two ventral scales per tail verticil (three or more scales), and femoral pores inserted in a clump of scales (in the center of a single scale). From *Gelanesaurus* by having homogeneous brown coloration around the nostril (a conspicuous blackish spot surrounding nostril), two continuous longitudinal ridges on dorsum (four), heterogeneous scales on the flanks of the body, with enlarged keeled scales (scales homogeneous, not tuberculated), gular scales keeled and juxtaposed (smooth and imbricated), and tail scales arranged in verticils (not arranged in verticils). From *Magdalenasaura*, it differs by having weakly keeled and wrinkled dorsal scales on head (smooth), small asymmetrical occipitals (large, paired, and symmetrical), enlarged strongly keeled dorsal scales (smooth to weakly keeled, not tuberculated), gular scales keeled and juxtaposed (smooth and imbricated), and femoral pores inserted in a clump of scales (in the center of a single scale). From *Neusticurus*, it can be distinguished by lacking prefrontals (present) and having paired internasals (absent) and a slightly compressed tail (strongly compressed). From *Potamites*, it differs by lacking prefrontals (present), having internasals (absent), palpebral disc divided into several scales (undivided), and by its acuminate and moderately long snout (blunt and short snout). *Kataphraktosaurus* shares with *Rheosaurus* the absence of postmental scale and the presence of strongly keeled ventral and subcaudal scales. However, it can be readily distinguished from the later by lacking prefrontal scales (present) and by having: a pair of frontonasals (three); small, irregular and not differentiated occipitals (large and symmetrical); rostral and mental scales smooth (grooved); six infralabials (four); supra and infralabials smooth (supralabials keeled and infralabials with central striation); two continuous longitudinal ridges on dorsum (four); cloacal plate with four large smooth scales (six, keeled); six femoral pores in adult males (14–15 femoral pores); and femoral pores inserted in a clump of 4–5 scales (in clumps of 3–4 scales).

Content: Monotypic. The only known species in this genus is *Kataphraktosaurus ungerhamiltoni* **sp. nov.**, which is described below.

Geographic distribution: Western Guiana Shield region, in the western foothills of the Serranía del Cuao, Amazonas state, Venezuela.

Etymology: The generic name *Kataphraktosaurus* (gender masculine) is derived from the combination of the Greek word κατάφρακτος ("*katáphraktos*"), which means completely enclosed, covered or armored, and the Neo-Latin -*saurus*—derived from the ancient Greek σαῦρος ("*saûros*")—, which means lizard. This name highlights the "armored" condition of this lizard as a result of the strongly keeled, tuberculated, and pointed scales that cover its body.

Kataphraktosaurus ungerhamiltoni **sp. nov.**
(Figures 4–7)
Suggested common name in English: Cuao's stream spiny lizard
Suggested common name in Spanish: Lagartija espinosa del Cuao

Holotype. Adult male, MHNLS 19960 (field number AJC 3014), from Caño Bejuco, near Tobogán del Cuao, Autana municipality, Amazonas state, Venezuela (5°05'58"N, 67°29'54"W; elevation 124 m), collected on 14 July 2010, by C.L. Barrio-Amorós, F.J.M. Rojas-Runjaic, and S. Castroviejo-Fisher.

Definition. This species is defined by the same character states listed for the genus, in combination with the following characteristics: (1) small body size (49 mm SVL; female unknown); (2) snout acuminate, moderately long; (3) palpebral disc with five to seven large palpebral scales; (4) six supralabials; (5) six infralabials; (6) paravertebral rows of enlarged scales continuous; (7) collar distinct, containing six enlarged scales; (8) ventral scales arranged in 20 transverse and eight longitudinal rows; (9) six femoral pores (three on each side) in males (female unknown); (10) tail with six pairs of longitudinal ridges around it (two dorsal submedian, two dorsolateral, two median laterals, two lower lateral, two ventrolateral, and two ventral submedian); (11) two subcaudal scales by verticil; (12) three keeled scales on the dorsal submedian ridge by verticil; (13) subdigital lamellae on fourth finger 15–16; (14) subdigital lamellae on fourth toe 21–22.

Description of holotype. Adult male in a good state of preservation (Figs. 4–7), with a piece of muscle removed from its right thigh for molecular analyses, and with the following measurements: SVL: 49 mm; HL: 13.6 mm; HW: 8.9 mm; HD: 6.3 mm; SL: 4.7 mm; NL: 9.7 mm; AGD: 21.1 mm; TL: 84.9 mm; FL: 15.6 mm; HLL: 24.8 mm. Head longer than wide (HL/HW: 1.5), depressed (HD/HW: 0.7). Snout acuminate in dorsal view and profile, moderately long (SL/HL: 0.4), gently sloping toward top of head (Fig. 4a–d). Tongue deeply bifid, tips smooth, dorsal surface posterior to cleft covered by scale-like papillae. Rostral (Fig. 4a) barely visible from above, smooth, wider than long (tape-like), slightly higher than adjacent supralabials, in contact with internasals dorsally, and with nasals and first pair of supralabials laterally. Internasals two, subtriangular, as long as wide, with weak marginal keels; both scales broadly in contact medially, each one in contact with rostral anteriolaterally, with nasals lateroposteriorly, and with frontonasals posteriorly (Fig. 4a). Frontonasals two, pentagonal, more than two times longer than wide, with some weakly raised sinuous keels longitudinally oriented; both scales broadly in contact medially, with their posterior edges posterolaterally divergent, forming an obtuse angle; each frontonasal is in contact with internasals anteriorly, with nasals and loreals laterally, with pre-supraoculars posterolaterally, and with frontal posteromedially (Fig. 4a). Frontal single, hexagonal, wider anteriorly, with anteromedial and posteromedial vertices convex; its surface with two weakly raised sinuous keels longitudinally oriented; frontal in contact with frontonasals anteriorly, with some small pre-supraoculars anterolateraly, with 1st and 2nd supraoculars posterolaterally, and with frontoparietals posteriorly (Fig. 4a). Supraoculars four, weakly ornamented with sinuous marginal keels; all supraoculars laterally bordered by two–three rows of keeled supraciliars; 1st supraocular subtriangular, in contact with two/three small granular pre-supraoculars anteriorly; 2nd supraocular the largest, subtrapezoidal, medially in contact with frontal, frontoparietal and parietal; 3rd and 4th supraocular the smallest, tubercular, subquadrangular to nearly circular at their base, in contact with parietal (Fig. 4a). Frontoparietals two, pentagonal, wider posteriorly, each one medially crossed by a keel (which comes from the frontal) ended in a rounded tubercle at its posterolateral margin. Interparietal large, almost flat, subpentagonal, with parallel lateral margins and near semicircular posterior margin, projecting farther posteriorly than the parietals; interparietal in contact with frontoparietals anteriorly, parietals laterally, and with numerous small irregular occipital scales posteriorly (Fig. 4a). Parietals two, large, about as wide as interparietal, polygonal (nearly circular), flat, slightly wrinkled, each one in contact with frontoparietal, with 3rd and 4th supraoculars anteriorly, with interparietal medially and with four medium-sized scales laterally and posteriorly (Fig. 4a). Occipital and temporal regions covered by juxtaposed small and medium-sized polygonal keeled scales, being larger and more strongly keeled those aligned behind the eye (Fig. 4a).

Nasal elliptical, wider than high; the one on the left side vertically divided; that on the right side complete; anterior half of nasal smooth, about three times larger than the posterior half; posterior half irregularly wrinkled; nostril completely located on the anterior half, not protruded, furrowed around its anterior margin, slightly directed posterolaterally, barely visible from above (Fig. 4b, d). Loreal region slightly concave, almost vertical. Loreal scale large, polygonal, higher posteriorly, almost flat; loreal in contact with frontonasal dorsally, with nasal anteriorly, with 1st–3rd supralabial ventrally, and with one preciliar and two/one suboculars posteriorly (Fig. 4b, d). Eyes protuberant;

pupil round. Palpebral disc translucent, with five to seven large palpebral scales. Suboculars six/five, arranged in a row above supralabials; 1st subocular almost as high as wide, all the posterior ones about two times wider than high. Supralabials six/six, infralabials six/six; supra- and infralabials smooth and tape-shaped. Tympanum slightly recessed (Fig. 4b, d).

Mental smooth, wider than long, rounded anteriorly, concave posteromedially; in contact with 1st pair of infralabials posterolaterally, and with 1st pair of geneials posteromedially. Postmental scale absent (Fig. 4c). Three pairs of large smooth geneials (Fig. 4c), 1st and 2nd pair similar in size, 3rd pair about half the size of the 1st and 2nd; 1st pair longer than wide, both broadly in contact medially, laterally in contact with 1st and 2nd infralabials; 2nd pair of geneials longer (left) or slightly longer (right) than wide, medially separated by three small scales, laterally in contact with 2nd and 3rd infralabials; 3rd pair of geneials about as long as wide, medially separated by two rows of small scales, laterally separated from infralabials by one row of small weakly keeled scales. Gular scales keeled, longer than wide, being smaller and weakly keeled those located on the anterior and anteromedial portions of the gular region; progressively larger and stronger keeled laterally and posteriorly; becoming nearly circular, spine-like, and spaced by small granules on the mid-third of the gular region (Fig. 4c); nearly hexagonal, juxtaposed, strongly keeled, and arranged in three transverse rows at the posterior end of that region. Collar distinct, containing six enlarged scales; collar fold naked and conspicuous (Fig. 5b).

Dorsal and lateral surfaces of neck and body covered with heterogeneous scales. Large, strongly keeled and posteriorly pointed scales juxtaposed forming two continuous paravertebral rows, not completely aligned, from occiput to tail base (Fig. 5a). Numerous oblique rows of similar enlarged scales extending posterolaterally from each paravertebral row and through the flanks, to the border of ventral scales. Enlarged scales on these diagonal rows becoming slightly smaller lateroposteriorly, separate from each other in the same row and from enlarged scales of neighboring rows by about two–five small flat or granular scales (Fig. 5a, c).

Ventral scales pentagonal, keeled, mucronate, slightly imbricate, arranged in 20 transverse and eight longitudinal rows; progressively increasing in size from chest to belly; those in the most lateral rows heavily keeled (Fig. 5b). Cloacal plate elliptical, mostly covered by four large smooth scales symmetrically arranged; two medial (anterior and posterior), similar in size, roughly triangular, barely in contact with each other at the center of the plate, and two larger lateral scales, pentagonal, separated from each other by the medial scales (Fig. 5d); anterior margin of the plate delineated by eight small rounded to subtriangular scales. Six femoral pores (three at each hindlimb), in a row separated medially by the two anteriormost scales of the precloacal plate (Fig. 5d). Each femoral pore surrounded by 4–5 small bulging scales, giving it a flower-like appearance (Fig. 5d).

Tail complete (not regenerated), slightly compressed; dorsal and lateral surfaces covered with heterogeneous scales mainly juxtaposed (Fig. 5e–f); ventral surface with homogeneous enlarged subcaudals, keeled, imbricate, pentagonals (longer than wide), with convex posterior margin (Fig. 5g). Tail with twelve longitudinal ridges around it: two dorsal submedian (paravertebral), two dorsolateral, two median laterals, two lower lateral, two ventrolateral, and two ventral submedian (Fig. 5e–g). Dorsal submedian ridges continuous with paravertebral ones coming from occiput (Fig. 5a); dorsolateral ridges originating above the thighs; all the remaining ridges starting from the base of the tail. Dorsal submedian, dorsolateral, median lateral, and lower lateral ridges formed by a series of increasing-in-size scales from the anterior margin of each caudal verticil (Fig. 5e–f), each verticil corresponding to two subcaudal scales (Fig. 5g) and containing three transverse rows of keeled scales at the dorsal submedian ridges; distal scale of dorsal median and dorsolateral ridges of each verticil distinctly overlapping the next verticil (Fig. 5e).

Scales on dorsal surface of forelimbs large, similar in size, strongly keeled, mucronate, slightly imbricate, forming longitudinal rows (Fig. 5a); scales on dorsal surface of hand keeled, forming five rows that individually extend to the tip of each of the five fingers (Fig. 6b). Scales becoming rounded and weakly keeled towards the ventral surface of the forearm; small, flat, polygonal to rounded, and juxtaposed on the palm. Subdigital lamellae on fingers entire, rectangular, much wider than long. Subdigital lamellae on fourth finger 15/16 (Fig. 6a). Scales on dorsal surface of hind limbs heterogeneous, strongly keeled, lanceolate to mucronate, slightly imbricate, forming longitudinal rows (Fig. 5a); scales on dorsal surface of foot keeled, forming five rows, individually extending to the tip of each of the five fingers (Fig. 6d). Scales becoming weakly keeled towards the ventral surface of the thigh and shank; small, flat, polygonal to rounded, and juxtaposed on the sole. Subdigital lamellae on toes generally divided on the proximal half, entire on the distal half, rectangular, wider than long. Subdigital lamellae on fourth toe 21/22 (Fig. 6c). All digits clawed.
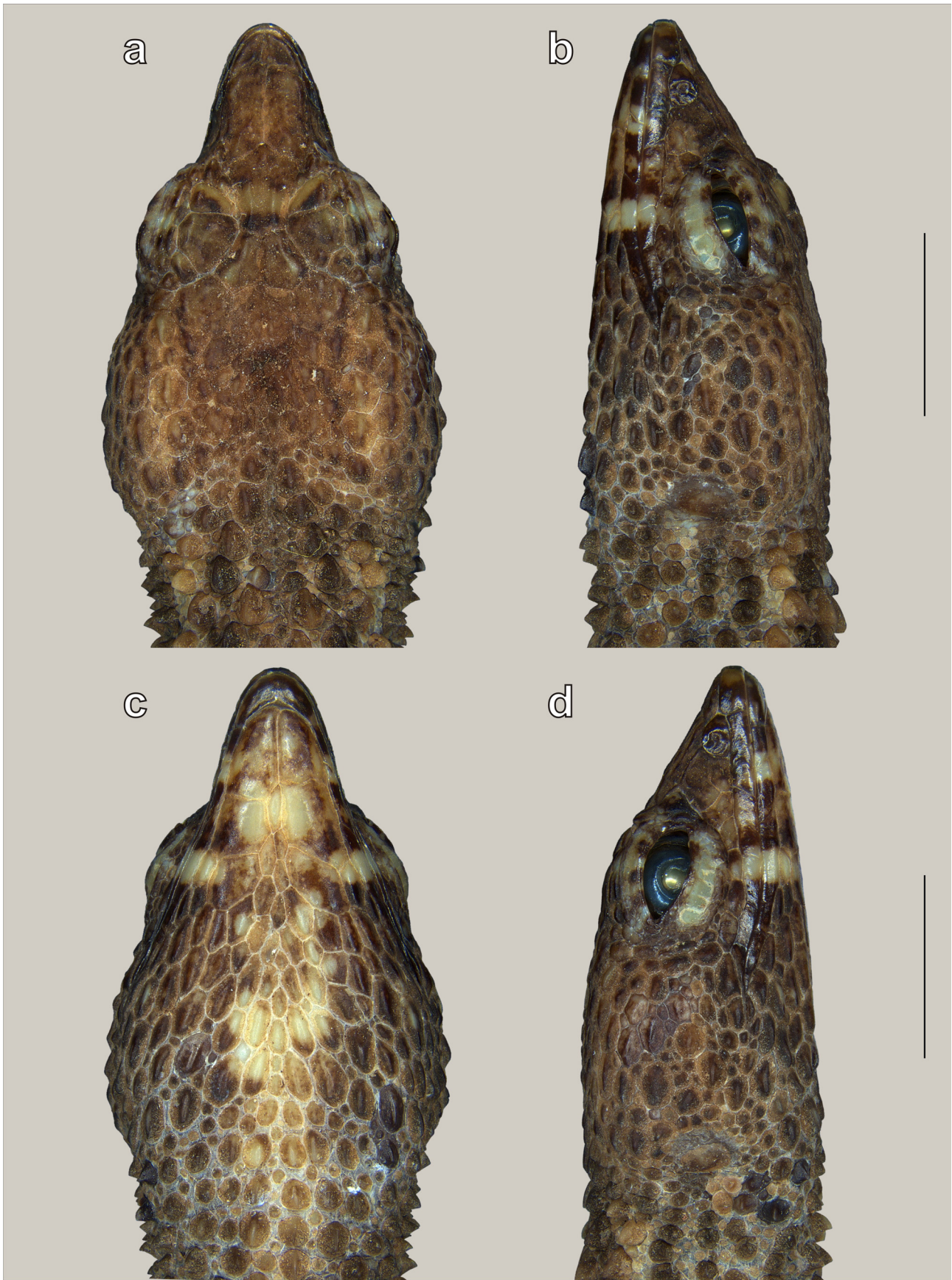
FIGURE 4. Male holotype of *Kataphraktosaurus ungerhamiltoni* **gen. nov., sp. nov.** (MHNLS 19960) in preservative. Dorsal (a), left lateral (b), ventral (c), and right lateral (d) views of the head. Scale bars represent 5 mm. Photos: F.J.M. Rojas-Runjaic.
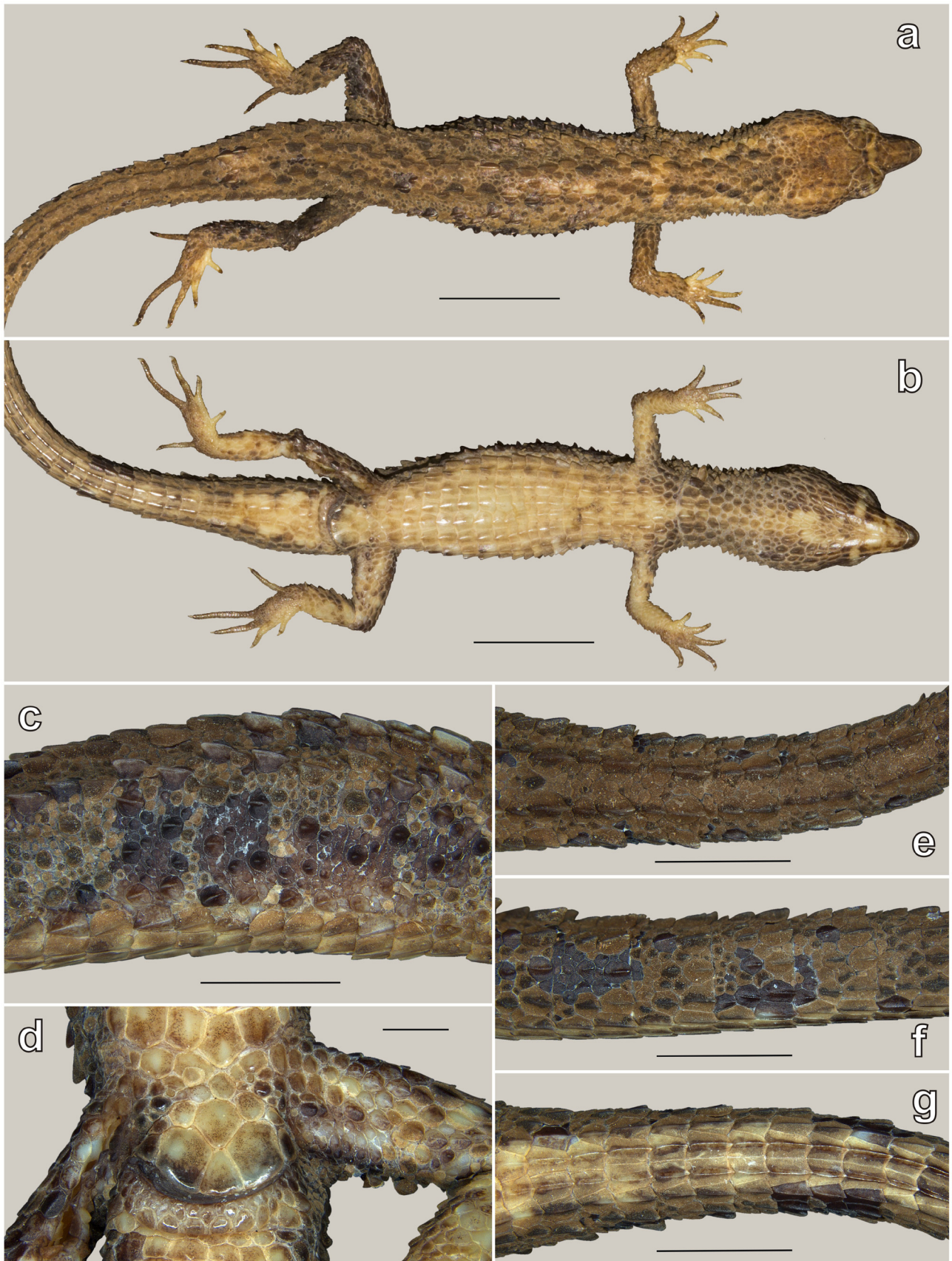
FIGURE 5. Male holotype of *Kataphraktosaurus ungerhamiltoni* **gen. nov., sp. nov.** (MHNLS 19960) in preservative. Dorsal (a) and ventral (b) views of the body; lateral view of the trunk (c); cloacal plate and undersurface of thighs (d); dorsal (e), lateral (f), and ventral (g) views of the tail. Scale bars represent 10 mm (a–b), 5 mm (c, e–g), and 2 mm (d). Photos: L.Y. Echevarría (a–b) and F.J.M. Rojas-Runjaic (c–g).

FIGURE 6. Male holotype of *Kataphraktosaurus ungerhamiltoni* **gen. nov., sp. nov.** (MHNLS 19960) in preservative. Ventral (a) and dorsal (b) views of the right hand; ventral (c) and dorsal (d) views of the right foot. Scale bars represent 1 mm. Photos: F.J.M. Rojas-Runjaic.

Coloration of holotype in life and preservative. In life (Fig. 7a), dorsal background reddish-brown, with some poorly defined, irregular, dark brown, and light brown blotches. Head with a well-defined light brown interocular stripe, finely bordered with dark brown. An ill-defined light brown dorsolateral stripe on each side extending from the posterodorsal corner of the eye to the neck. Supra and infralabial scales darker, with four–five pale vertical stripes; the most posterior the largest, dorsally reaching the eye and ventrally the geneials. Palpebral disc translucent. Iris copper. Ventrally, with some small irregular white spots on the geneials and an irregular ocher spot medially extending from the gular region to the chest; rest of the gular region dark brown. Chest, belly, undersurface of forearms, cloacal plate and anterior portion of tail dirty ocher; ventral surface of thighs and shanks variegate, with pale ocher and dark brown. First and second digits of hands and feet pale yellow. Palms and soles grayish brown. In preservative (after nine years preserved in ethanol 70 %; Figs. 4–6), the general color pattern is quite similar; the reddish brown background has faded into light brown; the irregular dark brown blotches maintain a similar intensity but turned slightly more contrasting with the background color; light brown blotches turned yellowish white. Ventral surfaces ocher colored in life, turned dirty white.

FIGURE 7. Male holotype of *Kataphraktosaurus ungerhamiltoni* **gen. nov., sp. nov.** (MHNLS 19960) in life (a). Western slope of Serranía del Cuao seen from the Cuao River (b) and Tobogán del Cuao in Caño Bejuco (c), Amazonas state, Venezuela. Photos: F.J.M. Rojas-Runjaic.

Distribution and natural history. *Kataphraktosaurus ungerhamiltoni* is only known from its type locality near Tobogán del Cuao, in the foothills of Serranía del Cuao, northwestern Amazonas state, Venezuela, at 124 m asl (Figs. 1, 7b–c). However, it is likely that its distribution extends through similar habitats across the slopes of the Cuao-Sipapo mountain system in northern Amazonas state. We found the only known specimen during the night, sleeping among the leaf litter accumulated next to a pool of a fast-flowing rocky stream in a pristine tropical humid

forest. We presume it is a diurnal and semi-aquatic species that inhabits in the leaf litter of the forests adjacent to black water streams.

Etymology. This species is named in honor of Mr. Felix Unger-Hamilton, in recognition of his support and interest in the study and conservation of Venezuelan biodiversity and the description of new species.

Discussion

Kataphraktosaurus is the twenty-second genus of Cercosaurinae and the eighth with CLM. CLM has been interpreted as a series of morphological changes related to aquatic or semiaquatic lifestyles (Uzzell 1966; Donnelly *et al.* 2006; Marques-Souza *et al.* 2018). It has been hypothesized that this phenotype evolved at least four times within Cercosaurinae (Marques-Souza *et al.* 2018). These last authors further argued that a compressed tail, a double tail crest, and vertically enlarged tubercle-like scales on dorsum may improve locomotion in water by maximizing effort through undulatory movements to swim. However, according to the literature (Uzzell 1966; Altamirano-Benavides *et al.* 2013; Fang *et al.* 2020) and our own field experience, some species exhibiting CLM phenotype do not appear to have a semi-aquatic life style (for example, some *Echinosaura* and all the specie of *Gelanesaurus* and *Magdalenasaura*), as they are often found dwelling into the forest—on leaf litter or rotten logs—or in rocky areas next to streams and creeks, but not directly in them. We suggest that future research should evaluate whether there is a causal connection between aquatic behavior and characters potentially associated with it (*e.g.*, compressed tail, double tail crest) by independently reconstructing the evolution of those characters (Wenzel & Carpenter 1994). Furthermore, it also seems necessary to evaluate the definition and categories of aquatic and semi-aquatic habits in these lizards through quantitative studies of locomotory performance.

A related issue is that since the seminal work of Pellegrino *et al.* (2001), attempts to infer Gymnophthalmidae evolutionary history mostly relay on the same four markers used in this study (approximately 2,000 aligned bp). This amount of data seems insufficient to satisfactorily resolve a radiation of nearly 300 species, which is illustrated by the low support values of most internal nodes and the conflicting topologies among different studies (*e.g.*, Goicoechea *et al.* 2012, 2016; Pyron *et al.* 2013; Kok 2015; Torres-Carvajal *et al.* 2015, 2016; this study). We suggest that studies addressing Gymnophthalmidae systematics and evolution would strongly benefit from an increase in character sampling.

Lizards with a semi-aquatic and secretive mode of life are very difficult to locate and collect, and most times finding them is a matter of luck. Therefore, securing samples requires large sampling efforts. Although only a few herpetological surveys had been carried out in the Cuao-Sipapo massif and surrounding areas (Gorzula & Señaris 1999; Barrio-Amorós *et al.* 2004; Rojas-Runjaic *et al.* 2013), this locality is only ~ 62 km from Puerto Ayacucho—the capital of the Venezuelan Amazonas state—, which in comparison to the Cuao-Sipapo massif has been extensively explored by naturalists. The fact that only one specimen of *Kataphraktosaurus ungerhamiltoni* is known, suggests that this is a rather secretive and/or rare lizard, with a geographic distribution restricted to the Cuao-Sipapo massif. Given that the western Guiana Shield lowland herpetofauna is predominantly represented by widely distributed Guianan-Amazonian taxa (Rojas-Runjaic & Señaris 2019; Señaris & Rojas-Runjaic 2020), the absence of reports of this lizard from relatively well-sampled localities in the lowlands of western Guiana Shield leads us to suspect that its type locality is in the lower limit of its altitudinal range, which probably extends towards the uplands of the Cuao-Sipapo massif.

Limited sample sizes in systematics are a problematic reality (Castroviejo-Fisher *et al.* 2011; Lim *et al.* 2012). The description of a new species on the basis of one specimen, singletons (Lim *et al.* 2012), represents the most extreme example because variation cannot be taken into account. This challenging situation can be somehow overcome if variation of putative diagnostic characters is well-understood within the other comparative units, there is congruence among different datasets, the singleton is well-preserved so diagnostic characters are very unlikely to result from preservation artifacts, and the singleton type locality data is detailed and precise to allow potential future collections (Köhler & Padial 2016; Guayasamin *et al.* 2018). Our description of *Kataphraktosaurus ungerhamiltoni* is supported by molecular and morphological characters, its type locality is described with accuracy, and the specimen is well-preserved. However, the knowledge of the variation of diagnostic characters within CLM gymnophthalmids is limited because several species are only known from a handful of specimens, such as *Neusticurus tatei* (Burt & Burt, 1931) and *Rheosaurus sulcarostrum*. The solution is theoretically simple but complicated to execute: only an

increase of character and specimen sampling can improve the situation. Despite this uncertainty regarding variation, we argue that explaining the data at hand as the product of other known mechanisms responsible for organism variation (*e.g.*, development, sexual dimorphism, intraspecies variation, and preservation artifacts) would require further assumptions and complicated scenarios.

We suggest to categorize *Kataphraktosaurus ungerhamiltoni* as "Data Deficient" (DD) according to the IUCN Red List (2019) because it is only known from one locality and a single specimen, with no additional information about its ecology, population status, and potential threats. Although there is some tourist activity in the Tobogán del Cuao and surroundings, the forests of that region are well-preserved, and above 500 m asl they are protected by the "Macizo Cuao-Sipapo y Cerro Moriche" Natural Monument.

Acknowledgements

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Taxon	Code	Locality	12S	16S	ND4	C-MOS	References
Alopoglossidae							
Alopoglossus viridiceps	QCAZ 10670	Ecuador: Pichincha: Nanegal, Santa Lucía Cloud Forest Reserve	KP874789	KP874841	KJ705316	KP874899	Torres-Carvajal *et al.* (2015); Torres-Carvajal and Lobos (2014)
Gymnophthalmidae							
Bachiinae							
Bachia flavescens	LSUMZ H12977	Brazil: Pará: Santarém: Agropecuária Treviso	AF420705	AF420753	AF420869	AF420859	Pellegrino *et al.* (2001)
Bachia scaea	MZUSP 100631	Brazil: Rondonia, Porto Velho	KC597257	KC597260	-	KC597263	Teixeira et. al. (2013)
Ecpleopodinae							
Ecpleopus gaudichaudii	LG 1356	Brazil: São Paulo: Boissucanga	AF420660	AF420738	AF420901	AF420855	Pellegrino *et al.* (2001)
Gymnophthalminae							
Gymnophthalmus leuco-mystax	MRT 946613	Brazil: Roraima: Fazenda Salvamento	AF420675	AF420715	AF420906	AF420824	Pellegrino *et al.* (2001)
Gymnophthalmus vanzoi	MTR 946490	Brazil: Roraima: Boa Vista	MH732650	MH732701	-	-	Recoder *et al.* (2018)
Rhachisaurinae							
Rhachisaurus brachylepis	MRT 887336	Brazil: Minas Gerais: Serra do Cipó	AF420665	AF420737	AF420877	AF420853	Pellegrino *et al.* (2001)
Riolaminae							
Riolama leucosticta	VUB 3767	Venezuela: Bolivar: Yuruani-tepui	-	JQ742254	KP283396	KP283389	Kok *et al.* (2012); Kok (2015)
Riolama inopinata	IRSNB 2680	Venezuela: Bolívar: Murisipán-tepui	-	KP283384	KP283395	KP283388	Kok (2015)
Cercosaurinae							
Anadia ocellata	SMF90095	Panama: Chiriqui: Santa Clara	MH579588	MH579625	-	-	Moravec *et al.* (2018)
Anadia petersi	QCAZ 10087	Ecuador: Morona-Santiago: Nuevo Israel	KU902130	KU902211	KU902286	KU902050	Torres-Carvajal *et al.* (2016)
Anadia rhombifera	QCAZ 6873	Ecuador: Esmeraldas: Bilsa Biological Station	KU902129	KU902210	KU902285	KU902049	Torres-Carvajal *et al.* (2016)
Andinosaura aurea	QCAZ 9649	Ecuador: El Oro: El Panecillo	KY670682	KY681100	KY710831	KY670647	Sánchez-Pacheco *et al.* (2018)

Taxon	Code	Locality	12S	16S	ND4	C-MOS	References
Andinosaura crypta	QCAZ 10455	Ecuador: Cotopaxi: Naranjito, Bosque Integral Otonga (BIO	KY670684	KY681102	KY710833	KY670649	Sánchez-Pacheco *et al.* (2018)
Andinosaura laevis	WB 1330	?	KY670690	KY681108	KY799165	KY670654	Sánchez-Pacheco *et al.* (2018)
Andinosaura vieta	QCAZ 10456	Ecuador: Cotopaxi: Naranjito, Reserva de Bosque Integral Otonga (BIO)	KY670695	KY681113	KY710841	KY670659	Sánchez-Pacheco *et al.* (2018)
Centrosaura apodema	MTR 33466	Costa Rica: San José, Tinamastes	MG896665	MG896701	-	MG963840	Marques-Sousa *et al.* (2018)
Cercosaura doanae	CORBIDI 650	Peru: San Martín: Mariscal Cáceres: Laguna Negra	KP874773	KP874825	KP874935	KP874875	Torres-Carvajal *et al.* (2015)
Cercosaura ocellata	MRT 977406	Brazil: Mato Grosso: Aripuanã	AF420677	AF420731	AF420883	AF420834	Pellegrino *et al.* (2001)
Cercosaura oshaugnessyi	LSUMZ H12591	Ecuador: Sucumbíos: Cuyabeno Wildlife Production Reserve	AF420698	AF420751	AF420896	AF420838	Pellegrino *et al.* (2001), Torres-Carvajal *et al.* (2016)
Dendrosauridion yanesha	MUSM 27610	Peru: Cusco: Alfamayo	MH579623	-	-	-	Moravec *et al.* (2018)
Dendrosauridion yanesha	MUSM 25345	Peru: Pasco: N.P. Yanachaga Chemillen	MH579624	MH579658	-	-	Moravec *et al.* (2018)
Echinosaura brachycephala	QCAZ 10824	Ecuador: Pichincha: Nanegal, Santa Lucía Cloud Forest Reserve	KU902137	KU902218	KU902293	KU902055	Torres-Carvajal *et al.* (2016)
Echinosaura centralis	MHUAR 12387	Colombia: Antioquia: Briceño, vereda el Anime, quebrada el Chorrillo	MN275473	MN275481	MN606049	MN606045	Vásquez-Restrepo *et al.* (2020)
Echinosaura centralis	MHUAR 12583	Colombia: Bolívar: Norosí, Casa de Barro	MN275474	MN275482	MN606050	MN606046	Vásquez-Restrepo *et al.* (2020)
Echinosaura centralis	MHUAR 13332	Colombia	MN275475	MN275483	MN606051	MN606047	Vásquez-Restrepo *et al.* (2020)
Echinosaura horrida	QCAZ 6666	Ecuador: Esmeraldas: Alto Tambo, El Placer-La Carolina	KU902138	KU902219	KU902294	KU902056	Torres-Carvajal *et al.* (2016)
Echinosaura horrida	QCAZ 8788	Ecuador: Esmeraldas: Alto Tambo, El Placer	KU902139	KU902220	KU902295	KU902057	Torres-Carvajal *et al.* (2016)
Echinosaura keyi	QCAZ 8074	Ecuador: Esmeraldas: 5 km on road Alto Tambo-El Placer, Otokiki Reserve	KU902140	KU902221	KU902296	KU902058	Torres-Carvajal *et al.* (2016)

Taxon	Code	Locality	12S	16S	ND4	C-MOS	References
Echinosaura keyi	QCAZ 12485	Ecuador: Esmeraldas: Chuchubí, on path above Chuchubí Resort	KU902141	KU902222	KU902297	KU902059	Torres-Carvajal *et al.* (2016)
Echinosaura orcesi	QCAZ 6299	Ecuador: Esmeraldas: Alto Tambo, El Placer	KU902142	KU902223	KU902298	KU902060	Torres-Carvajal *et al.* (2016)
Echinosaura orcesi	QCAZ 10022	Ecuador: Esmeraldas: Alto Tambo, Otokiki Reserve	KU902143	KU902224	KU902299	KU902061	Torres-Carvajal *et al.* (2016)
Echinosaura palmeri	CD 4163	Colombia: Valle del Cauca: Dagua, El Cauchal	MN275476	MN275484	MN606052	-	Vásquez-Restrepo *et al.* (2020)
Echinosaura palmeri	MHUAR 12671	Colombia: Valle del Cauca: Buenaventura, Isla Palma	MN275477	MN275485	MN606053	MN606048	Vásquez-Restrepo *et al.* (2020)
Echinosaura panamensis	CH 5345	Panamá: Coclé: El Cántaro, nacimiento Río Indio	-	MH140720	MN606054	-	Vásquez-Restrepo *et al.* (2020)
Echinosaura panamensis	CH 8482	Panamá: Panamá: Cerro Brewster, estación Guagaral	-	MH140722	MN606055	-	Vásquez-Restrepo *et al.* (2020)
Euspondylus excelsum	CORBIDI 14965	Peru: Huánuco: Huánuco: Santa Clara	KU902198	KU902273	KU902354	KU902117	Torres-Carvajal *et al.* (2016)
Gelanesaurus cochranae	QCAZ 6120	Ecuador: Napo: Río Hollín, Jondachi-Loreto road	KU902145	KU902226	KU902301	KU902063	Torres-Carvajal *et al.* (2016)
Gelanesaurus flavogularis	QCAZ 6943	Ecuador: Tungurahua: Machay River, Baños-Puyo road	KU902147	KU902228	KU902303	KU902065	Torres-Carvajal *et al.* (2016)
Kataphraktosaurus ungerhamiltoni **gen. nov., sp. nov.**	MHNLS 19960	Venezuela: Amazonas: Autana: Caño Bejuco, near Tobogán del Cuao	**MW493235**	**MW493236**	**MW512829**	**MW512828**	This study
Macropholidus annectens	QCAZ 11121	Ecuador: Loja: 15 km E Loja	KC894342	KC894356	KC894370	KP874877	Torres-Carvajal and Mafla-Endara (2013), Torres-Carvajal *et al.* (2015)
Macropholidus ruthveni	CORBIDI 4281	Peru: Lambayeque: El Totoral	KC894354	KC894368	KC894382	-	Torres-Carvajal and Mafla-Endara (2013)
Neusticurus bicarinatus	MRT 968462	Brazil: Mato Grosso: Apiacás	AF420671	AF420708	-	AF420816	Pellegrino *et al.* (2001)
Neusticurus medemi	MTR 36272	Brazil: Amazonas: Rio Içá, Comunidade Cachoeirinha,	MG896655	MG896690	MG920209	-	Marques-Sousa *et al.* (2018)
Neusticurus racenisi	MTR 20823	Brazil: Roraima: Serra do Tepequém	MG896658	MG896693	MG920187	MG963830	Marques-Sousa *et al.* (2018)

Taxon	Code	Locality	12S	16S	ND4	C-MOS	References
Neusticurus rudis	MRT 926008	Brazil: Amapá: Serra do Navio	AF420689	AF420709	AF420905	-	Pellegrino *et al.* (2001)
Neusticurus surinamensis	MPEG 22049	Brazil: Pará: município de Almeirim, Estação, SW Área do Jari 112	MG896659	MG896694	-	MG963831	Marques-Sousa *et al.* (2018)
Oreosaurus achlyens	ENS 11010	Venezuela:	KY670697	KY681115	KY799160	-	Sánchez-Pacheco *et al.* (2018)
Oreosaurus mcdiarmidi	IRSNB 2674	Venezuela: Bolívar: Abakapá-tepui	-	JQ742263	KP283392	KP283385	Kok *et al.* (2012); Kok (2015)
Oreosaurus shrevei	UWIZM 2011.7	Trinidad and Tobago: Trinidad island, Aripo Northern Range	KY670700	KY681118	-	KY670663	Sánchez-Pacheco *et al.* (2018)
Oreosaurus sp.	EBRG 5962	Venezuela: Anzoátegui: Macizo de Turimiquire, Cerro El Guamal	KY670701	KY681119	KY799161	-	Sánchez-Pacheco *et al.* (2018)
Oreosaurus serranus	JJS 543	Colombia: Sierra Nevada de Santa Marta	KY670698	KY681116	KY799163	KY670661	Sánchez-Pacheco *et al.* (2018)
Oreosaurus serranus	ROM 53608	Colombia: Magdalena: headwaters of the Río Guachacos, Corregimiento de Minca, finca Vista Hermosa	KY670699	KY681117	KY799164	KY670662	Sánchez-Pacheco *et al.* (2018)
Petracola ventrimaculata	CORBIDI 9235	Peru: Cajamarca	KJ948193	KJ948144	KJ948145	KJ948220	Aguirre-Peñafiel *et al.* (2014)
Petracola waka	KU 212687	Peru: Cajamarca: Celendin: E slope Abra Gelic, 20 km E Celendin	AY507864	AY507876	-	AY507903	Castoe *et al.* (2004)
Pholidobolus dicrus	QCAZ 5304	Ecuador: Morona-Santiago: Guarumales	KP874776	KP874828	KP874938	KP874885	Torres-Carvajal *et al.* (2015)
Pholidobolus montium	QCAZ 4051	Ecuador: Pichincha: Quito	KC894346	KC894360	KC894374	KP874890	Torres-Carvajal *et al.* (2015), Torres-Carvajal and Mafla-Endara (2013)
Pholidobolus ulisesi	CORBIDI 12737	Peru: Cajamarca	KP874788	KP874840	KP874949	KP874898	Torres-Carvajal *et al.* (2016)
Placosoma cordylinum	LG 1006	Brazil: Rio de Janeiro: Teresópolis	AF420673	AF420734	AF420879	AF420823	Pellegrino *et al.* (2001)
Placosoma glabellum	LG 940	Brazil: São Paulo: Iguape	AF420674	AF420742	AF420907	AF420833	Pellegrino *et al.* (2001)
Potamites erythrocularis	CORBIDI 15153	Peru: Madre de Dios: Tambopata: Manu-Tambopata Corridor	KU902152	KU902233	KU902308	KU902070	Torres-Carvajal *et al.* (2016)

Taxon	Code	Locality	12S	16S	ND4	C-MOS	References
Potamites juruazensis	CORBIDI 15550	Peru: Huánuco: Leoncio Prado: Tingo María National Park	KU902156	KU902238	KU902313	KU902075	Torres-Carvajal *et al.* (2016)
Potamites montanicola	CORBIDI 10791	Peru: Ayacucho: La Mar: Pampa Aurora	KU902158	KU902240	KU902315	KU902077	Pellegrino *et al.* (2001)
Potamites strangulatus	QCAZ 6133	Ecuador: Napo: Archidona	KU902159	KU902241	KU902316	KU902078	Torres-Carvajal *et al.* (2016)
Proctoporus bolivianus	MNCN 43679	Bolivia: La Paz: Sorata Valley	JX435943	JX435997	JX436069	JX436043	Goicoechea *et al.* (2012)
Proctoporus bolivianus Ca1	MHNC 5322	Peru: Puno: between Trapiche and Sina	JX435945	JX435988	-	JX436045	Goicoechea *et al.* (2012)
Proctoporus carabaya	CORBIDI 14710	Peru: Cusco: Quispicanchis: Capire	KU902164	KU902245	KU902321	KU902083	Torres-Carvajal *et al.* (2016)
Proctoporus kiziriani	MNCN 4751	Peru: Cusco: Marcapata Valley	JX435904	JX435977	JX436097	JX436048	Goicoechea *et al.* (2012)
Proctoporus guentheri	UTA R-51515	Peru: Cusco: Chocalloc	AY507849	AY507872	AY225185	AY507900	Goicoechea *et al.* (2012)
Proctoporus laudahnae	CORBIDI 15558	Peru: Huánuco: Leoncio Prado: La Garganta camp-Tingo María, National Park	KU902172	KU902251	KU902329	KU902091	Torres-Carvajal *et al.* (2016)
Proctoporus pachyurus	CORBIDI 11811	Peru: Junin: Tarma: Palca District (Anexo Huandunga	KU902178	KU902255	KU902335	KU902097	Torres-Carvajal *et al.* (2016)
Proctoporus sucullucu	UTAR 51496	Peru: Cusco: Kusilluchayoc	AY507857	AY507878	AY225171	AY507905	Doan and Castoe (2003); Castoe *et al.* (2004)
Proctoporus xestus	MNCN 2425	Bolivia: La Paz: between Lambate and Totoral	JX435899	JX436001	JX436100	JX436007	Goicoechea *et al.* (2012)
Proctoporus xestus	MNCN 6160	Bolivia: Cochabamba: Cochabamba	JX435898	JX436002	JX436101	-	Goicoechea *et al.* (2012)
Rheosaurus sulcarostrum	ROM 22892	Guyana: Baramita, approximately 1 km S airstrip	AF206584	AF206584	-	-	Fu (2000)
Rheosaurus sulcarostrum	ROM 43805	Guyana: Baramita, approximately 1 km S airstrip	MN275478	MN275486	MN606056	-	Vásquez-Restrepo *et al.* (2020)
Riama columbiana	ICN 11298	Colombia: Caldas: municipio de Villa María, vereda Montaño, Bosques de la CHEC, predio La Mesa,	KY670706	KY681124	KY710847	KY670668	Sánchez-Pacheco *et al.* (2018)
Riama labionis	QCAZ 10412	Ecuador: Cotopaxi: Naranjito, Reserva de Bosque Integral Otonga (BIO)	KJ948172	KJ948121	KJ948148	KJ948207	Aguirre-Penafiel *et al.* (2014)

APPENDIX 1. (Continued)

Taxon	Code	Locality	12S	16S	ND4	C-MOS	References
Riama orcesi	QCAZ 10569	Ecuador: Napo: Antisana Ecological Reserve, Virgen de Guacamayos	KU902197	KU902272	KU902353	KU902116	Torres-Carvajal *et al.* (2016)
Riama simotera	QCAZ 4120	Ecuador: Carchi: Reserva Ecológica El Ángel	KY670716	KY681134	KY710854	KY670676	Sánchez-Pacheco *et al.* (2018)
Riama unicolor	QCAZ 9682	Ecuador, Imbabura: Cotacachi-Cayapas Ecological reserve, trail near Cuicocha Lake	KJ948188	KJ948138	KJ948157	KJ948205	Aguirre-Peñafiel *et al.* (2014)
Selvasaura brava	MUSM 32738	Peru: Junin: B.P. Pui Pui, Rio Bravo	MH579612	MH579648	-	MH579703	Moravec *et al.* (2018)
Selvasaura sp.	QCAZ 12798	Ecuador; Napo: Wildsumaco Wildlife Sanctuary, Wildsumaco Lodge	KU902206	KU902281	KU902362	KU902125	Moravec *et al.* (2018)
Selvasaura sp.	CORBIDI 15117	Peru: San Martín: Mariscal Cáceres: Laurel	KU902203	KU902278	KU902359	KU902122	Torres-Carvajal *et al.* (2016)
Selvasaura sp.	QCAZ 12891	Ecuador: Zamora-Chinchipe: El Pangui, Wawayme River Basin, Concession ECSA-viewpoint	KU902207	KU902282	KU902363	KU902126	Torres-Carvajal *et al.* (2016)
Wilsonosaura cf. *josyi*	CORBIDI 13634	Peru: Huancavelica: Tayacaja: Colcabamba-Quintao District	KU902201	KU902276	KU902357	KU902120	Torres-Carvajal *et al.* (2016)
Wilsonosaura cf. *josyi*	CORBIDI 13636	Peru: Huancavelica Tayacaja: Colcabamba-Quintao District	KU902202	KU902277	KU902358	KU902121	Torres-Carvajal *et al.* (2016)