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The distribution of *Cteniloricaria* (Siluriformes: Loricariidae): known and new records in Brazil suggest headwater captures as drivers of disjoint distribution

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Cteniloricaria is a genus of Neotropical armored catfishes belonging to the Loricariinae, currently including two valid species: *C. platystoma* and *C. napova*. *Cteniloricaria platystoma* is presently recorded across the main coastal drainages of the Guiana Shield, from the Sinnamary River, French Guiana, to the Essequibo River basin, Guyana, and is considered to be restricted to the region. *Cteniloricaria napova* is only known from its type locality at the headwaters of the Paru de Oeste River, Amazon basin, Sipaliwini Savannah, Trio Amerindian territory in Suriname, close to the Brazilian border. Based on a specimen of *C. napova*, captured in the Cuminapanema River, a tributary to the Curuá River, within Brazilian territory, the geographic distribution of the species and the genus is extended, representing the first record of *Cteniloricaria* in Brazil. The genus shows a disjoint distribution, and divergence between populations in the north-flowing coastal rivers of the Guianas and the south-flowing Amazon tributaries, and more recent headwater capture between south-flowing Amazon tributaries, may have played a key role in shaping its current distribution. Illustrations, diagnostic characters, morphometrics, description of the habitat where the new specimen was captured, extinction risk assessment, and a discussion of the distribution of the genus are provided.

Keywords: Amazon basin, Armored catfish, Cuminapanema, Loricariinae, Range extension.

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Cteniloricaria é um gênero de cascudos neotropicais pertencente à Loricariinae, atualmente incluindo duas espécies válidas*:* *C. platystoma* e *C. napova*. Atualmente, *C. platystoma* é registrada nas principais drenagens costeiras do Escudo das Guianas, desde o rio Sinnamary, na Guiana Francesa, até a bacia do rio Essequibo, Guyana, sendo considerada restrita à região. *Cteniloricaria napova* é conhecida unicamente por sua localidade-tipo nas cabeceiras do rio Paru de Oeste, bacia Amazônica, Savana Sipaliwini, território indígena de Trio, no Suriname, próximo à fronteira com o Brasil. Com base em um espécime de *C. napova*, capturado no rio Cuminapanema, afluente do rio Curuá, em território brasileiro, a distribuição geográfica da espécie e do gênero se estende até a bacia do rio Curuá, representando o primeiro registro de *Ctenilоricaria* no Brasil. O gênero apresenta uma distribuição disjunta e, eventos como divergência entre as populações dos rios costeiros das Guianas e nos afluentes do Amazonas, e mais recente captura de cabeceiras entre os afluentes do Amazonas, podem ter desempenhado um papel fundamental em sua distribuição atual. São fornecidos ilustrações, caracteres diagnósticos, morfometria, descrição do habitat onde o novo espécime foi capturado, avaliação do risco de extinção e uma discussão sobre a distribuição do gênero.

Palavras-chave: Bacia Amazônica, Cascudo, Cuminapanema, Extensão de distribuição, Loricariinae.

INTRODUCTION

One of the main components of the order Siluriformes is the family Loricariidae, which currently includes more than 1,000 species and comprises six subfamilies: Delturinae, Hypoptopomatinae, Hypostominae, Lithogeninae, Loricariinae, and Rhinelepinae (Van der Laan *et al*., 2021). Species belonging to the family are recognized by having the body covered in ossified dermal plates, integumentary teeth known as odontodes (Garg *et al*., 2010), and a ventral oral disk that facilitates surface attachment and feeding (Geerinckx *et al*., 2011). Fishes belonging to Loricariidae are commonly known as cascudos or acaris (Brazil), corronchos or cuchas (Colombia, Venezuela), carachamas (Peru), or viejas (Argentina, Paraguay, and Uruguay).

Loricariinae currently includes 255 valid species, classified in 31 genera (Van der Laan *et al*., 2021), distributed from the La Plata River basin in Argentina to southern Central America (Ferraris, 2003). Species in this subfamily are characterized by a long and depressed caudal peduncle and absence of an adipose fin. They usually live on the substrate and present marked variations in body shape due to the different habitats, from lotic to lentic systems, over organic or inorganic substrates such as rocks, fallen tree trunks, or soft substrate (Covain *et al*., 2008).

Isbrücker, Nijssen (in Isbrücker, 1979) described *Ctenilоricaria*, designating *Loricaria platystoma* Günther, 1868 as the type species, along with *Oxyloricaria fowleri* Pellegrin, 1908 (=*Harttia fowleri*), and *Parasturisoma maculata* Boeseman, 1971 (=*Ctenilоricaria platystoma*). The authors compared the new genus to *Harttia* Steindachner, 1877 and diagnosed the former by having the abdomen completely covered by plates (*vs*.

variable covering of abdominal plates), and a more slender body (*vs*. robust body; see Identification for a diagnosis of *Cteniloricaria* from *Harttia*).

Cteniloricaria historically has been treated either as a synonym of *Harttia* (Oyakawa, 1993; Rapp Py-Daniel, 1997; Rapp Py-Daniel, Oliveira, 2001; Provenzano *et al*., 2005; Covain *et al*., 2006; Covain, Fisch-Muller, 2007; Provenzano, 2011) or as a valid genus (Isbrücker, 1980, 1981, 2001; Ferraris, 2003, 2007; Covain *et al*., 2012, 2016; Oyakawa *et al*., 2013; Londoño-Burbano, Reis, 2019, 2021). Covain, Fisch-Muller (in Covain *et al*., 2012) described the second species included in *Cteniloricaria*, *C. napova*, diagnosing the new species from *C. platystoma* by its distinctly spotted color pattern, more numerous premaxillary teeth, and body and head proportional measurements (Covain *et al*., 2012:136).

Cteniloricaria napova is currently known by the type series, 12 specimens from the type locality at the headwaters of the Paru de Oeste River, Sipaliwini Savannah, Trio Amerindian territory, Four Brothers Mountains, Suriname. This species has recently been recorded from the Brazilian territory in Pará State from a different, despite contiguous, river basin than the type locality. Dutra *et al*. (2020), in a rapid assessment of the ichthyofauna of the southern Guiana Shield tributaries of the Amazon River in Pará, listed *C. napova* along seven other species recorded as the first record for the Brazilian territory, but did not include the species as a novelty for the region. Here we describe the specimen of *C. napova* comprising that first record of the genus and the species to Brazil, from the Cuminapanema River, Curuá River basin, northern Brazil. The type species, *C. platystoma*, is more widely distributed in coastal rivers of the Guianas from the Essequibo in Guyana to the Sinnamary in French Guiana and is here compared to *C. napova*.

MATERIAL AND METHODS

Study area. The broadest amount of protected areas in the world is located at the left bank of the Amazon River, the so-called Northern Pará Drainage System - NPDS (Dutra *et al*., 2020), with approximately 22 million ha (SEMA, 2010). In 2011 the State Environmental Agency of Pará (SEMA) established a partnership with Conservation International (CI) and Institute of Man and Environment of the Amazon (IMAZON) to develop management plans for the protected areas of the NPDS based, in part, on the field expeditions for ichthyofaunal studies accomplished by the Museu Paraense Emilio Goeldi (MPEG) in 2008 and 2009 (SEMA, 2011). The Trombetas State Forest (FLOTA Trombetas), one of the seven protected areas, represents 14% (almost 3.2 million ha) of the NPDS and is mainly drained by the Trombetas, Cuminá, and Cuminapanema rivers (Fig. 1) (SEMA, 2011).

Fieldwork. In April 2008, the Cuminapanema River and 13 tributary streams were sampled inside the FLOTA Trombetas. During this expedition, one specimen of *Cteniloricaria napova* (MPEG 34190) was collected from the Cuminapanema River basin, Óbidos, Pará State, Brazil (Tab. 1; Fig. 2). As stated by Dutra *et al*. (2020), that research was authorized by the Brazilian System of Biodiversity Information and Authorization (SISBIO), license number 4681–1. It was also approved by the Ethics Committee on the Use of Animals in Research of the Federal University of Pará, process CEUA 8293020418.

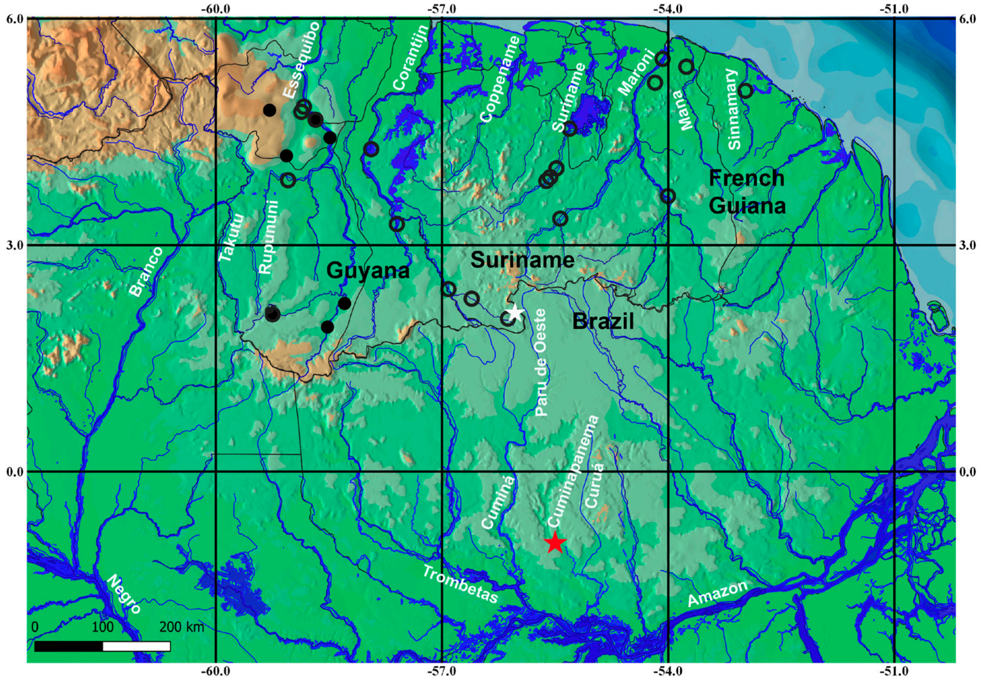

FIGURE 1 | Distribution of *Ctenilоricaria* in the Guiana Shield. Circles = *C. platystoma* according to Covain *et al.* (2012); black dots = *C. platystoma*, examined specimens. White star, type locality of *C. napova*; red star, new locality of *C. napova*. Each symbol can cover more than one lot or locality.

TABLE 1 | Descriptive morphometrics and meristic data of *Ctenilоricaria napova* from the Cuminapanema River. Asterisk = broken spine.

	MPEG 34190 (n=1)
Standard length (SL)	117.4
Percentages of standard length	
Head length (HL)	21.1
Predorsal length	31.4
Postdorsal length	57.9
Caudal-peduncle length	48.5
Cleithral width	18.1
Abdominal length	16.7
Thoracic length	15.0
Pectoral-fin unbranched ray length	22.5
Pelvic-fin unbranched ray length	19.4
Dorsal-fin unbranched ray length	*
Anal-fin unbranched ray length	16.5
Anus to pelvic-fin origin length	10.3
Anus to pectoral-fin origin length	24.6
Anus to anal-fin origin length	8.4
Anus to tip of snout length	39.0
Body width at dorsal-fin origin	15.3

TABLE 1 | (Continued)

	MPEG 34190 (n=1)
Body width at anal-fin origin	13.1
Body width at eighth postdorsal plate	13.0
Body width at fourteenth postdorsal plate	8.6
Body depth at dorsal-fin origin	10.6
Minimum caudal peduncle depth	1.7
Percentages of head length	
Snout length	51.4
Nostril to tip of snout length	36.0
Distal end of operculum to tip of snout length	75.6
Maximum orbital diameter	17.7
Interorbital width	24.2
Head depth	49.4
Head depth at internostril	22.3
Meristic data	
Number of premaxillary teeth	45
Number of dentary teeth	31
Number of plates before coalescence	20
Number of plates after coalescence	9
Number of plates in the lateral series	29
Number of plates of lateral abdominal plates	6
Pectoral-fin rays	i.6
Dorsal-fin rays	i.7
Pelvic-fin rays	i.5
Anal-fin rays	i.5
Caudal-fin rays	i.11.i

Laboratory work. The specimen was identified following Covain *et al*. (2012) and deposited in the fish collection of the MPEG, Belém, Pará (MPEG 34190). Institutional acronyms follow Sabaj (2020).

RESULTS

Identification. *Cteniloricaria* can be diagnosed (besides characters mentioned above) from *Harttia* by having a dark transverse, half-moon shaped band on the caudal-fin base, occupying the base of all rays on upper and lower lobes (*vs*. dark blotch at caudal-fin base); tip of snout covered with plates (*vs*. tip of snout naked, devoid of plates); and abdominal plates shaped as medium-sized polygonal plates completely covering the abdomen (*vs*. abdominal plates absent or present as small platelets, partially or entirely covering the abdomen) (Londoño-Burbano, Reis, 2021). *Ctenilloricaria napova* was initially diagnosed by Covain, Fisch-Muller (in Covain *et al*., 2012) from its only congener, *C. platystoma*, by having a distinctly spotted color pattern (our specimen, Fig. 2; *vs*. indistinctly marbled without spots, Fig. 3) and from its molecular barcode.

FIGURE 2 | *Cteniloricaria napova*, MPEG 34190, 117.4 mm SL, Brazil, Pará State, Óbidos municipality, unnamed creek tributary to Cuminapanema River, Curuá River basin (approx. 0°57'S 55°30'W).

Besides, the authors listed five proportional measurements and one count that supposedly distinguish the two species, but these were presented as mean, standard deviation, and P values. When looking at the range for each of those variables and the entire table of comparative measurements, all ranges extensively overlap, not being actually diagnostic. The Brazilian specimen was identified as *Cteniloricaria napova* based on the color pattern, its locality, morphometric measurements, and meristic counts obtained as additional information (Tab. 1).

Conservation status. *Cteniloricaria napova* is known from the headwaters of the Paru de Oeste River in southern Suriname and the middle Cuminapanema River in Brazil, both draining to the Amazon basin in the southern border of the Guiana Shield (Fig. 1). Both river basins are mostly unexplored, and the species is likely to occur in other localities within these basins. The two known collecting sites are located inside conservation areas, the Trio Amerindian territory in Sipaliwini District, Suriname, and the Trombetas State Forest in Brazil. Despite gold mining and moderate deforestation in the region, rivers and forests are mostly well preserved, and no specific threats to the species were identified. For these reasons, *C. napova* is preliminarily assessed as Least Concern (LC) according to the IUCN criteria and categories (IUCN Standards and Petitions Committee, 2019).

FIGURE 3 | *Loricaria platystoma*, BMNH 1866.8.14.124, lectotype, 171.5 mm SL, Suriname. Photo by Mark Allen (WAM; ACSI Images Database).

DISCUSSION

The Guianas Region is a significant Neotropical area of endemism across most taxonomic groups (Cardoso, Montoya-Burgos, 2009). Rivers in the Guianas Region drain towards the Atlantic Ocean and are separated from the Amazon basin by a series of old mountains in the northern border of Brazil, markedly isolating the hydrological systems of the Guianas Region (Cardoso, Montoya-Burgos, 2009). The relative isolation of the Guianese hydrological systems, along with the possibility that this region was a Pleistocene humid refuge, may explain its high level of endemic freshwater fishes and other organisms (Cardoso, Montoya-Burgos, 2009). However, the authors stated that this hypothesis has been difficult to conciliate with freshwater fish diversification at the temporal scale because most of the diversity predates the Pleistocene; contrary to what Miller *et al*. (2005) suggested, in that significant and periodic sea-level fluctuations have persisted throughout the last six million years, with an accelerated rhythm during the Pleistocene. On the other hand, Rocha, Kaefer (2019) discussed that the Amazonian diversity appears to be the result of multiple factors with contribution of both allopatric and parapatric diversification mechanisms across different taxa, in addition to vicariant processes (see also Noonan, Gaucher, 2005; Whinnett *et al*., 2005; Antonelli *et al*., 2010). Even though the Pleistocene humid refuge remains to be accepted as one of the primary process in diversification of freshwater fishes in the region (Weitzman, Weitzman, 1982), low sea-level periods might have allowed river interconnections at their lower section, enhancing freshwater taxa dispersal from one basin to another. In contrast, high sea level periods would have fragmented populations into newly isolated river basins thus promoting allopatric differentiation (Cardoso, Montoya-Burgos, 2009).

Cteniloricaria napova was considered an endemic species of the Sipaliwini region in southern Suriname, southern Guiana Shield with altitudes varying from 100 to 500 m above sea level, including areas of both Amazon rainforest and savanna vegetation (Vari *et al*., 2009). Nevertheless, the fish fauna of the Guianas is among the best known in South America due to a series of intensive investigations and inventories, particularly in French Guiana, and new species are being found by every expedition conducted in that region (see Lemopoulos, Covain, 2018). Several fishes appear to have dispersed north-south across this watershed divide, rising evidence for the southern Guiana Shield slope being a north-south dispersal region (Lujan *et al*., 2020).

River capture is potentially a key geomorphological driver of range expansion and cladogenesis in freshwater limited taxa (Cardoso, Montoya-Burgos, 2009; Albert, Reis, 2011). River capture is characterized by the transference of a river (or a segment of a river) between basins caused by erosion and/or tectonic processes and, as a result, the biodiversity associated with the diverted river (*i.e*., species and genetic diversity) will then be present in the receiver basin (Albert, Reis, 2011; Souza *et al*., 2020). Considering the current distribution of the two species of *Cteniloricaria*, two main stream capture events may have played a key role in shaping their current distributions.

The first event might have caused the divergence between *Cteniloricaria platystoma*, distributed in the north-flowing coastal rivers of the Guianas from the Essequibo in Guyana to the Sinnamary in French Guiana, and *C. napova*, occurring in the south-flowing Amazon tributaries Paru de Oeste and Curuá (Fig. 1). Headwaters of the Corantijn River are separated from the headwaters of above Amazon tributaries by two mountain chains: the Grens and the Acarai mountains, although these highlands are supposedly semi-permeable to fish dispersal because of headwater interdigitations (Lujan, Armbruster, 2011). A possible connection already hypothesized by Nijssen (1970) is located in the Sipaliwini Savannah, connecting the Paru de Oeste River (a tributary to the Trombetas River and type locality of *C. napova*) to the Sipaliwini River (a tributary to the Corantijn River). Nijssen (1970) described several potential headwater corridors that might have provided dispersal routes for fishes between the north-flowing Corantijn and south-flowing Paru de Oeste rivers across the Grens and Acarai Mountains, which form the drainage divide. However, a parsimony analysis of endemism in fish communities across the eastern Guiana Shield by Lemopoulos, Covain (2018) raised doubts for Nijssen's (1970) corridor hypothesis, given the distinctiveness of the fish samples between headwaters of Paru de Oeste and Corantijn rivers; thus the authors hypothesized vicariant assemblages for such region.

The second event that may have played an essential role in shaping the distribution of *Cteniloricaria napova* is a possible, more recent headwater capture between south-flowing Amazon tributaries, namely the Paru de Oeste and the Cuminapanema rivers, leading to the presence of the species in both parallel basins (Fig. 1). The alternative scenario of *C. napova* passing between these two basins through the Amazon River is less probable considering the alluvial environment of the Amazon main channel.

There are other examples within the Loricarioidea about disjoint distribution of taxa, such as the reported here for *Ctenuloricaria*. One of them is related to the poorly known but unique genus *Lithogenes* Eigenmann, 1909. *Lithogenes villosus* Eigenmann, 1909 (Potaro-Essequibo) and *L. wahari* Schaefer & Provenzano, 2008 (Cuao-Orinoco) are found in the Guiana Shield, and a third species, *L. valencia* Provenzano, Schaefer, Baskin & Royero, 2003, is thought to be from the Lago Valencia drainage in the coastal mountains of northern Venezuela (Lujan, Armbruster, 2011). Dispersal via headwater capture seems a likely avenue for *Lithogenes*, as well as for *Ctenuloricaria*, which live in clear, swift-flowing streams (Schaefer, Provenzano, 2008). The type of habitat described for *Lithogenes* is the same as for *Ctenuloricaria* regarding water conditions and type of current, although the latter is also found on sandy bottom (see Londoño-Burbano *et al*., 2014, 2020; Lujan *et al*., 2018, 2020 for additional examples of disjoint distribution within Loricariidae and Loricariinae).

Most distributions within the Guiana Shield can be explained by current watershed boundaries, stream capture events in the uplands of larger systems, and/or ancient river systems such as the proto-Berbice (Lujan, Armbruster, 2011); stream capture events seems to be more suitable regarding *Ctenuloricaria*. River captures can contribute both to a range expansion, allowing species to reach new basins, and to a secondary contact between populations of species previously present in neighboring basins (Souza *et al*., 2020); ideally, both geological and biological evidence converge when inferring drainage rearrangement events (Waters *et al*., 2001, 2006). However, geological evidence is not always available or is generally based on controversial morphological features (*e.g*., ‘capture elbows’; Souza *et al*., 2020). Therefore, in many cases, it is necessary to rely on biological data, particularly species distribution and genetics, for supporting cases of drainage rearrangements (Souza *et al*., 2020).

As stated above, even though several scenarios for the disjoint distribution of *C. napova* are possible, river capture seems to be the more appropriate for the distribution area and adaptations shown by the species (*i.e*., types of substrate, fast currents, water quality). Nevertheless, further studies within and between populations of *Ctenuloricaria* using molecular evidence to test genetic distances, haplotype diversity, niche partitions, and phylogeographic analyses, encompassing the entire distribution of the genus, are necessary to offer a more robust hypothesis for the origin of the distribution of this group across the Guiana and Brazilian shields.

Material examined: *Ctenuloricaria napova*: MHNG 2704.030, 6, 71.0–128.7 mm SL, paratypes, Suriname, Sipaliwini District, Savannah in Trio Amerindian territory at the Suriname-Brazil border, Four Brothers Mountains in an unnamed tributary creek of the Paru de Oeste River, collected and donated by the Trio tribe in Sipaliwini. MPEG 34190, 1, 117.4 mm SL, Brazil, Pará State, Óbidos municipality, unnamed creek tributary to Cuminapanema River, Curuá River basin, approx. 0°57’S 55°30’W. *Ctenuloricaria platystoma*: AUM 37942, 1, 67.2 mm SL, Guyana, Essequibo River basin, Region 10 Upper Demerara-Berbice, Essequibo River at Kurukupari, east bank. AUM 38822, 4, 47.8–157.3 mm SL, Guyana, Essequibo River basin, Region 9 Upper Takutu and Essequibo, Kuyuwini River at Kuyuwini Landing. AUM 39038, 4, 47.8–102.4 mm SL, Guyana, Essequibo River basin, Region 9 Upper Takutu and Essequibo, Essequibo River at Yukanopito Falls, 44.5 km southwest mouth of Kuyuwini River. AUM 39055, 11, Guyana, Essequibo River basin, Region 9 Upper Takutu and Essequibo, Essequibo

River at Kassi-Attae rapids, 5.5 km SE mouth of Kuyuwini River. AUM 44325, 1, 56.2 mm SL, Guyana, Essequibo River basin, Region 8 Essequibo River at Kurukapari Falls, upstream from Iwokrama. AUM 45341, 12, 53.9–74.4 mm SL, Guyana, Essequibo River basin, Region 8 Potaro-Siparuni, Essequibo River, in rapids. AUM 45352, 11, 51.0–85.3 mm SL, Guyana, Essequibo River basin, Region 8 Potaro-Siparuni, Essequibo River, side channel in rapids. AUM 48174, 8, 1 c&s, 86.7–140.3 mm SL, Guyana, Rupununi-Essequibo River drainage, Region 8 Potaro-Siparuni, Burro Burro River at Suraima.

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AUTHOR'S CONTRIBUTION

Alejandro Londoño-Burbano: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Software, Supervision, Visualization, Writing-original draft, Writing-review and editing.

Marina Barreira Mendonça: Data curation, Formal analysis, Investigation, Methodology, Project administration, Supervision, Visualization, Writing-original draft, Writing-review and editing.

Roberto E. Reis: Conceptualization, Data curation, Formal analysis, Funding acquisition, Methodology, Project administration, Visualization, Writing-original draft, Writing-review and editing.

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The research was authorized by the Brazilian System of Biodiversity Information and Authorization (SISBIO), license number 4681–1. It was also approved by the Ethics Committee on the Use of Animals in Research of the Federal University of Pará, process CEUA 8293020418.

COMPETING INTERESTS

The authors declare no competing interests.

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