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A Matryoshka of scales: a single specimen reveals multiple new aspects of diet and distribution of snakes

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Snakes comprise approximately 3,800 species (Uetz and Hošek, 2020), all of which are carnivorous, consuming an enormous variety of prey types captured by active foraging or ambush methods (Greene, 1997; Grundler 2020). Despite recent advances, detailed information on feeding ecology is still scarce, particularly for many species of the rich snake fauna of the Neotropics (e.g., Marques and Sazima, 1997; Hartmann and Marques, 2005; Gaiarsa et al., 2013; Roberto and Souza, 2020). The frequency of prey items found in the stomachs of specimens collected or housed in scientific collections is low (e.g., Vitt and Vangilder, 1983; Marques and Sazima, 1997) and the observation of a predation event in the field is rare and unpredictable (e.g., Guedes, 2017; Guedes et al., 2018; Pelegrini et al., 2019; Almeida et al., 2020; Costa and Andrade, 2020). Thus, even isolated new records of diet and predation represent valuable contributions to our understanding of the trophic ecology of snakes.

The Neotropical snakes *Clelia plumbea* (Wied, 1820) are the largest members of the genus *Clelia*, reaching 2,790 mm snout-vent length (Pizzatto, 2005). They are widely distributed through cis-Andean South America from the Brazilian Amazon in the north (6.0666°S, 49.9000°W) to the Atlantic Forest of Brazil and Paraguay in the south (29.3683°S, 49.8494°W) (Nogueira et al., 2019), mainly in moist forested areas (Gaiarsa et al., 2013). This terrestrial and nocturnal species mainly preys upon other snakes, including eight species of four families (Teixeira and Vrcibradic, 2003; Drummond et al., 2010; Gaiarsa et al., 2013). Lizards and mammals are also eaten (Cunha and Nascimento, 1978; Gaiarsa et al., 2013). Much of what is known about the diet of *C. plumbea* is based on the analysis of gut contents of preserved specimens (Cunha and Nascimento, 1978; Gaiarsa et al., 2013), with two reports about prey ingestion position being head-first (Teixeira and Vrcibradic, 2003; Drummond et al., 2010).

Here we report four interesting findings that came from the examination of a single specimen of *Clelia plumbea* housed in a scientific collection: (1) two new records of prey items for *C. plumbea*; (2) an unusual food item found in the stomach of the Yellow-bellied Puffing-snake (*Spilotes sulphureus*) eaten by the *C. plumbea*; (3) the second record of *C. plumbea* in the state of Maranhão; and (4) the second record of *S. sulphureus* in the state of Maranhão.

While examining snake specimens housed in the herpetological collection of Museu Paraense Emílio Goeldi (MPEG), I noticed a specimen of *Clelia plumbea* (MPEG 15597; Fig. 1A, B) that had been partially dissected (aperture of 50 mm) ventrally. This specimen was collected by F. P. Nascimento and R. J. R. Moraes on 14 August 1979, at Gancho do Arari, BR-222, between Miranda and Arari, in state of Maranhão, Brazil (approximate coordinates 3.5155°S, 44.7561°W; Datum SIRGAS2000). The specimen is a female (based on an incision made at the base of the tail) and measured 1,262 mm in snout-vent length (SVL) plus 256 mm tail length (TL) (using a measuring tape).

During the examination of the *C. plumbea* specimen, I carefully expanded the dissection in the venter to expose the whole stomach and its contents (Fig. 1B–D). At first, I found two stomach contents: (1) in the posterior portion of the stomach I found part of the body of a *Helicops* sp. Wagler, 1830, total length 150 mm, containing part of the venter and keeled dorsal scales, as well as paired cloacal and subcaudal scales (Fig. 1C); (2) and almost the whole body, except for the head and a small portion of the neck, of a female *Spilotes sulphureus* Wagler, 1824, SVL 586 mm, TL 300 mm, 21 rows of keeled, lanceolate dorsal scales, paired subcaudal scales (Fig. 1D). Both prey items were ingested head-first and

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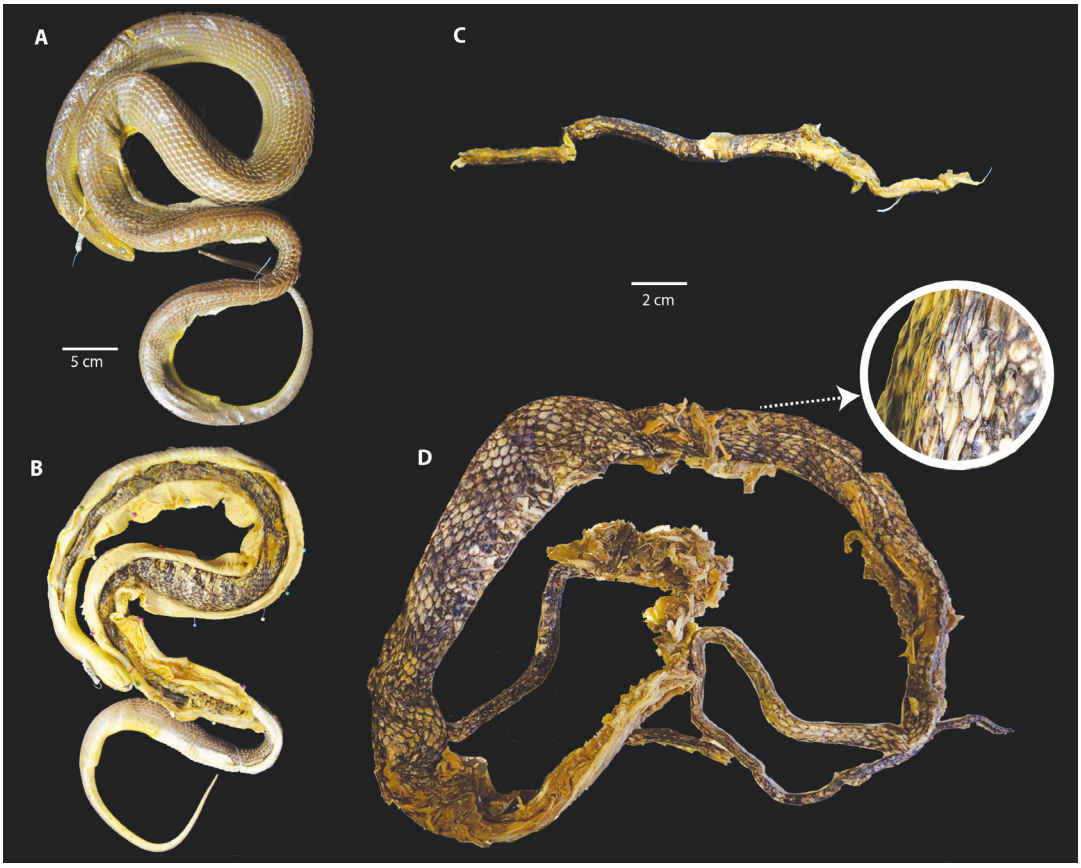

Figure 1. Specimen of *Clelia plumbea* (MPEG 15597) from Arari, Maranhão, Brazil examined in this study: (A) Dorsal view; (B) Ventral view of the dissected venter exposing the prey items; (C) Body parts of *Helicops* sp. found in the posterior portion of the stomach, ingested head-first; (D) *Spilotes sulphureus* ingested head-first and found in the anterior portion of the stomach; inset: the lanceolate and keeled dorsal scales of *S. sulphureus*. Photographs by Thaís B. Guedes (A–C) and Ana L.C. Prudente (D).

identified through inspection of diagnostic characters on external morphology (pholidosis and pattern of colour) based on current literature (Peters and Orejas-Miranda, 1970).

While examining the *Spilotes sulphureus*, I observed a bolus in its stomach and decided to investigate. I performed a dissection exposing the whole stomach of the *S. sulphureus* (Fig. 2A) and found a partially digested catfish (total length 200 mm; Fig. 2B–D) of the family Callichthiydae (order Siluriformes). The fish was identified based on the observation of diagnostic characters (measurement and counting of the scales and spines) and comparison with material housed in the MPEG ichthyological collection (Fig. 2C, D).

Both snakes, *Helicops* sp. and *Spilotes sulphureus*, are new records for the diet of *Clelia plumbea* and the former represents the first record of *C. plumbea* preying upon an aquatic snake species (Table 1). Our results reinforce the diet of *Clelia plumbea* as a snake specialist (Gaiarsa et al., 2013). Cunha and Nascimento (1993) mentioned that *C. plumbea* has a preference for humid places and the margins of streams in the Amazon. The area where the specimen of *C. plumbea* was collected is located between the Itapecuru River and Mearim River Basins (Fig. 3A). An interesting finding is that it is the second record of *C. plumbea* in the state of Maranhão, extending its distribution 233 km in a straight line from the the Gurupi Biological Reserve, state of Maranhão (Freitas et al., 2017; Unvouchered specimen); and the second record of the species *Spilotes sulphureus* for the state of Maranhão (Fig. 3B) extending its distribution 190 km in a straight line from the municipality of Maranhãozinho, state of Maranhão (Nogueira et al., 2019). The new records are located in the boundary

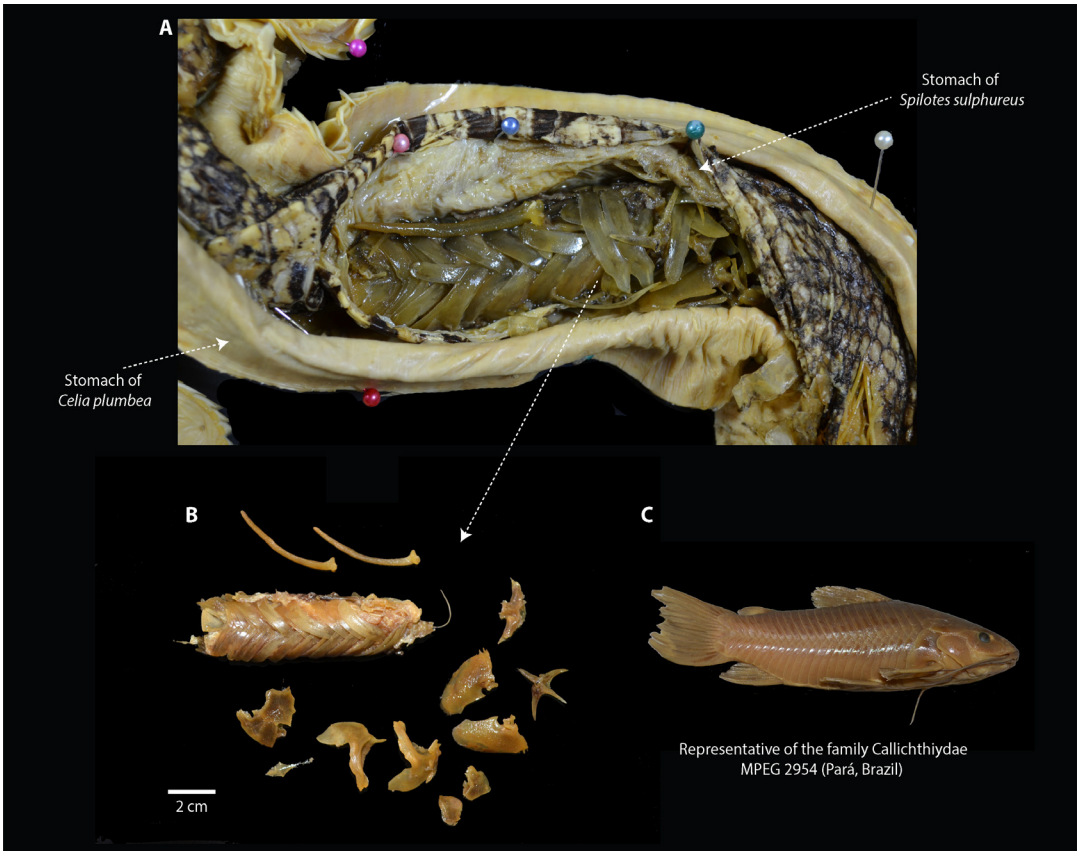

Figure 2. (A) Stomach contents of *Spilotes sulphureus* (eaten by *Clelia plumbea*) exposing the catfish; (B) The catfish (partially digested) removed from the stomach for examination and identification; (C) Representative of an undigested catfish used for comparison of characters and identification. Photographs by Thaís Guedes.

between the Amazon and Cerrado biomes (Fig. 3A, B).

The callichthiyid catfish also represents a novel prey item for *Spilotes sulphureus*, which is known to be diurnal and primarily arboreal inhabitant of both Atlantic and Amazon Forests (although it can also be found in disturbed areas), which is occasionally terrestrial but not known to be aquatic (Cunha and Nascimento, 1978; Martins and Oliveira, 1998; Nogueira et al., 2019). Information about the diet of *S. sulphureus* is limited to scattered data about food items in the literature, but in general the species is known to feed on small vertebrates (mainly birds and small mammals, Table 1) (Cunha and Nascimento, 1978; 1993; Martins and Oliveira, 1998; Rivas and Kane, 2003; Alves et al., 2005). The presence of a catfish in the stomach of this species is both novel and unexpected. Callichthiyid catfishes are heavily armoured, with two lateral rows of bony plates along the length of their bodies, and strong spines in the dorsal and pectoral fins (Fig. 2C). Such armour likely makes it difficult for snakes and other predators to ingest these fishes (Camp et al., 1980; Mills, 2002). Species of callichthiyid catfishes (e.g., *Callichthys callichthys*) are known from the state of Maranhão, as well as from the Itapecuru River Basin (Barros et al., 2011).

Ophiophagy is a common feeding behaviour of many Neotropical snakes (e.g., Marques and Sazima, 1997; Martins and Oliveira, 1998; Gaiarsa et al. 2013; McKelvy et al., 2013; Guedes, 2017). However, only a few species are specialised to feed on snakes, as is the case for *Clelia plumbea* (e.g., *Boiruna sertaneja*; Gaiarsa et al., 2013). In pseudoboine snakes, ophiophagy seems to be a relevant specialisation restricted to a handful of terminal taxa (Alencar et al., 2013). The presence of closely-related species showing different feeding preferences (e.g., *C. plumbea* being a snake specialist while other species of *Clelia* are generalists) makes it

Table 1. List of prey items of *Clelia plumbea* and *Spilotes sulphureus* in literature and in this study.

Species	Prey Items	Reference
	Snake species (Family)	
	Atractus pantostictus (Dipsadidae)	Gaiarsa et al., 2013
	Bothrops jararaca (Viperidae)	Gaiarsa et al., 2013
	Bothrops jararacussu (Viperidae)	Gaiarsa et al., 2013
	Bothrops moojeni (Viperidae)	Drummond et al., 2011
	Bothrops sp. (Viperidae)	Gaiarsa et al., 2013
	Drymarchon corais (Colubridae)	Cunha and Nascimento, 1978; Gaiarsa et al., 2013
	Echinanthera undulata (Dipsadidae)	Gaiarsa et al., 2013
	Echinanthera sp. (Dipsadidae)	Gaiarsa et al., 2013
	Epicrates cenchria (Boidae)	Bernarde and Abe, 2010
	Erythrolamprus miliaris (Dipsadidae)	Teixeira and Vrcibradic, 2003
Clelia plumbea	*Helicops* sp. (Dipsadidae)	This study
	Micrurus lemniscatus (Elapidae)	Gaiarsa et al., 2013
	Spilotes pullatus (Colubridae)	Gaiarsa et al., 2013
	Spilotes sulphureus (Colubridae)	This study
	Lizard species (Family)	
	Ameiva ameiva (Teiidae)	pers. obs. MPEG 15057
	Ameiva sp. (Teiidae)	Gaiarsa et al., 2013
	Ophiodes fragilis (Diploglossidae)	Gaiarsa et al., 2013
	Gonatodes sp. (Sphaerodactylidae)	Cunha and Nascimento, 1978; Gaiarsa et al., 2013
	Mammal species (Family)	
	Metachirus nudicaudatus (Didelphidae)	Gaiarsa et al., 2013
	Rodents (unspecified)	Cunha and Nascimento, 1978
	Fish species (Family)	
	(Callichthyidae)	This study
	Bird species (Family)	
	Cryptorellus soui (Tinamidae)	Rivas and Kane, 2003
	Pitangus sp. (Tyrannidae)	Beebe, 1946
Spilotes sulphureus	*Gallus gallus* (Phasianidae)	Beebe, 1946
	Formicivora littoralis (Thamnophilidae)	Meneses and Marini, 2017
	Stelgidopteryx ruficollis (Hirundinidae)	Alves et al., 2005
	Mammal species (Family)	
	Molossus molossus (Molossidae)	Rufino and Bernardi, 1999
	Phyllomys pattoni (Echimyidae)	Bocchiglieri et al., 2019

difficult to understand the body requirements (e.g., maxillary morphology) or feeding behaviours that allow species to feed on a specific kind of prey, such as snakes (Pinto and Lema, 2002; Alencar et al., 2013; Knox and Jackson, 2020).

On the other hand, the ability to subdue, ingest, digest, and assimilate items such as armoured catfish certainly require specialisations. Aquatic species of the genus *Helicops* and *Hydrodynastes* are known to eat callichthiyid catfishes: *Helicops hagmanni* (*Corydoras* sp.), *He. infrataeniatus* (*Corydoras paleatus*), *He. leopardinus* (*Hoplosternum* sp.), *He. angulatus* (*Callicthys callictys* and *Corydoras* sp.), and *Hy. gigas* (*Callicthys callictys*) (Lopéz and Giraudo, 2003; Scartozzoni, 2009). According to Jucá-Chagas and Boccardo (2006), some species of catfish are able to breathe air and live in hypoxic and shallow waters, where they use the vegetation accumulated on the

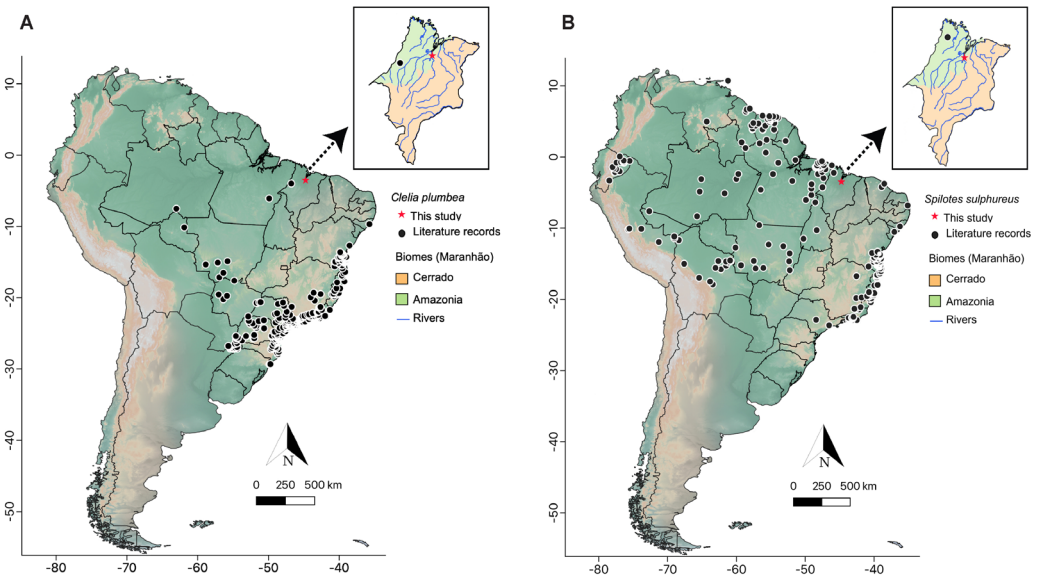

Figure 3. (A) Map showing the distribution of *Clelia plumbea* in South America and the second record of the species in the state of Maranhão; (B) Map showing the distribution of *Spilotes sulphureus* in South America and the second record of the species in the state of Maranhão. Literature records are from Freitas et al. (2017; Unvouchered specimen) and Nogueira et al. (2019) for *C. plumbea* and Nogueira et al. (2019) for *S. sulphureus*. Biome limits follow IBGE (2019) available at https://www.ibge.gov.br.

riverbanks to deposit their eggs. This behaviour could potentially explain the encounter between the catfish and the *S. sulphureus*.

Recent studies have reported new prey items for several snakes (e.g., Pelegrini et al., 2019; Roberto and Sousa, 2020) as well as new feeding behaviour (e.g., Guedes et al., 2018; Bringsoe et al., 2020; Mario-da-Rosa et al., 2020) and interactions among three trophic levels (e.g., Pelegrini et al., 2019; Smith and Scanferla, 2016). The observation reported here is intriguing, but also inspiring and highlights the relevance of detailed natural history data to understand the biotic interactions between snakes and their prey in ecological networks, as well as track the evolution of diet for conservation purposes.

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