

A new species of cloud fish of the genus *Hypsolebias* from Northeast Brazil (Cyprinodontiformes: Rivulidae)

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A new species of cloud fish of the genus *Hypsolebias* is described from a temporary pool in the rio Trairi basin, Rio Grande do Norte State, Brazil. It is the first record of the genus *Hypsolebias* for the basin. The new species belongs to the *H. flammeus* species-group, which is composed of the species *H. alternatus*, *H. brunoi*, *H. delucai*, *H. fasciatus*, *H. longignatus*, *H. marginatus*, *H. multiradiatus*, and *H. flammeus*. The new species differs from all other species of the group, except *H. flammeus*, *H. multiradiatus*, and *H. brunoi*, by male color pattern and the presence of a metallic blue sheen surrounding the black spots of females. It differs from *H. flammeus*, *H. multiradiatus* and *H. brunoi* by dorsal and anal fin shape (both rounded *vs.* pointed) and by the orientation of the reddish-brown bars on the body and anal fin of males (diagonal *vs.* vertical). The new species differs from its congeners of Northeast Brazil mainly by the higher number of dorsal fin rays in males and the higher number of scales in the longitudinal series.

Keywords: Annual fishes, Caatinga, Cynolebiinae, Semiarid, Temporary pools.



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Uma nova espécie de peixe das nuvens, gênero *Hypsolebias*, é descrita de uma poça temporária localizada na bacia do rio Trairi, Estado do Rio Grande do Norte, Brasil. É a primeira ocorrência do gênero *Hypsolebias* na bacia do rio Trairi. A nova *Hypsolebias* pertence ao grupo de espécies *H. flammeus* que é composto pelas espécies *H. alternatus*, *H. brunoi*, *H. delucai*, *H. fasciatus*, *H. flammeus*, *H. longignatus*, *H. marginatus* e *H. multiradiatus*. A nova espécie difere de todas as espécies desse grupo, exceto *H. flammeus*, *H. multiradiatus* e *H. brunoi*, pelo padrão de coloração do macho e pela presença de um brilho azul metálico envolvendo as manchas pretas na fêmea. Difere de *H. flammeus*, *H. multiradiatus* e *H. brunoi* pela forma das nadadeiras dorsal e anal (arredondada *vs.* pontiaguda) e pela orientação das barras castanhas avermelhadas no corpo e na nadadeira anal nos machos (diagonal *vs.* vertical). A nova espécie difere de outras congêneres do Nordeste do Brasil principalmente pelo elevado número de raios na nadadeira dorsal nos machos e pelo maior número de escamas na série longitudinal.

Palavras-chave: Caatinga, Cynolebiinae, Peixes anuais, Poças temporárias, Semiárido.

INTRODUCTION

The Caatinga encompasses an area of 850,000 km² and is among the most biodiverse semi-arid regions in the world with high plant and animal richness (Silva *et al.*, 2018). Included among this richness are cloud fish of the genus *Hypsolebias* Costa, 2006 (Cyprinodontiformes, Rivulidae), which complete their life cycle in temporary pools that form in river floodplains during the rainy season (Myers, 1952). These pools dry up completely during periods of drought and the adult fish die, but the eggs persist in the substrate. During such dry periods the eggs enter diapause, which is very slow embryonic development, as a strategy to overcome drought. This type of development allows embryos to survive long periods of drought until hatching during the following rainy season (Wourms, 1972; Berois *et al.*, 2016).

Hypsolebias is currently the cloud fish genus with the greatest number of described species. It has a wide geographical distribution among watersheds that make up the four continental freshwater ecoregions of the Caatinga, with 32 described species: one species in the state of Parnaíba (PAR), three in Northeastern Caatinga and Coastal Drainages (NCCD), 27 in São Francisco (SFRE) and one in Northeastern Mata Atlantica (NMA) (Abell *et al.*, 2008; Lima *et al.*, 2017). Another seven representatives are found in the rio Tocantins basin and ecoregion in the Brazilian Cerrado (Costa, 2007; Nielsen *et al.*, 2012). The genus *Hypsolebias* is one of the most endangered continental fish groups in the Caatinga, with around 20 endangered species, according to recent lists and official ordinances (MMA, 2022). *Hypsolebias* was originally described as a subgenus of *Simpsonichthys* Carvalho, 1959 by Costa (2006), along with *Hypsolebias* the taxa *Xenurolebias* Costa, 2006, *Ophthalmolebias* Costa, 2006, and *Spectrolebias* Costa & Nielsen, 1997, which were also considered subgenera of *Simpsonichthys*. All these subgenera have since been elevated to the level of genus (Costa, 2007). The systematics

of *Hypsolebias* is currently organized into four species groups: the *H. antenori* group, the *H. flammeus* group, the *H. magnificus* group, and the *H. notatus* group (Costa, 2007).

The *Hypsolebias flammeus* group is distinguished from the other groups of *Hypsolebias* by having a long posterior process of the supraoccipital (*vs.* short) and an elongated anal fin of females (*vs.* short) (Costa, 2007). The *H. flammeus* group comprises nine species, all threatened with extinction, that are distributed in the São Francisco, Tocantins, and Pacoti basins: *H. alternatus* (Costa & Brasil, 1994) (EN - Endangered), *H. brunoi* (Costa, 2003) (VU - Vulnerable), *H. delucai* (Costa, 2003) (VU), *H. fasciatus* (Costa & Brasil, 2006) (VU), *H. flammeus* (Costa, 1989) (EN), *H. longignatus* (Costa, 2008) (VU), *H. marginatus* (Costa & Brasil, 1996) (CR - Critically Endangered), *H. multiradiatus* (Costa & Brasil, 1994) (CR), and *H. tocantinensis* Nielsen, Cruz & Babbista, 2012 (CR) (Nielsen *et al.*, 2012; MMA, 2022). The present work describes a new species of the *H. flammeus* group found in the rio Trairi microbasin in the State of Rio Grande do Norte, Northeast Brazil. The rio Trairi is a coastal river that originates in the Serra do Doutor (in the municipalities of Campo Redondo and Coronel Ezequiel, in Rio Grande do Norte), on the Borborema Plateau, and flows into the Atlantic Ocean at Guaraíras lagoon between the municipalities of Tibau do Sul and Senator Georgino Avelino, also of Rio Grande do Norte (Medeiros *et al.*, 2019).

MATERIAL AND METHODS

Collected specimens were anesthetized in a Eugenol solution (Eugenol was dissolved in alcohol in a clove oil to alcohol ratio of 1:9, and this solution was diluted with water to obtain a concentration of 0.40 mL of clove oil per 1000 mL of water) (Lucena *et al.*, 2013). The specimens were then fixed in 10% formalin and preserved in 70% alcohol.

Specimen measurements were taken point by point with a digital caliper to the nearest 0.1 mm, always on the left side of specimens and under a stereomicroscope, following Costa (1995, 2007). Measurements are shown in table and are expressed as a percentage of standard length (SL), except for head measurements, which are expressed as a percentage of head length (HL). Vertebra and pleural ribs counts were performed on two paratypes (male and female) that were cleared and stained (c&s) according to Taylor, Van Dyke (1985). The composite caudal centrum was counted as a single element in the vertebra count.

The morphological, morphometric, and meristic data of species not included in the Comparative Material Examined section used for comparisons were extracted from original description and redescription studies of the species (Costa, 1989, 2007, 2008; Costa, Brasil, 1994; Nielsen *et al.*, 2012). All specimens were deposited in the ichthyological collection of the Universidade Federal da Paraíba, João Pessoa (UFPB) and Universidade Federal do Rio Grande do Norte, Natal (UFRN).

RESULTS

Hypsolebias lulai, new species

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(Figs. 1–2, 6; Tab. 1)

Holotype. UFPB 14713, 44.9 mm SL, male, Brazil, Rio Grande do Norte State, Lagoa Salgada Municipality, Capim Grosso Lagoon, Recanto II settlement, Trairi River basin, 06°10'S 35°31'W, 4 Aug 2022, T. P. A. Ramos, S. Y. Lustosa-Costa & Y. G. Abrantes.

Paratypes: All from Brazil. Trairi River basin, Rio Grande do Norte State: UFPB 13354, 3 females (35.9–40.9 mm SL), collected with holotype, Lagoa Salgada, Capim Grosso Lagoon, Recanto II settlement, 06°10'S 35°31'W, 4 Aug 2022, T. P. A. Ramos, S. Y. Lustosa-Costa & Y. G. Abrantes. UFPB 13352, 4 males (37.5–50.4 mm SL), 20 females (32.8–40.6 mm SL), Lagoa Salgada, Malhadas Dam, Recanto II settlement, 06°10'57"S 35°31'35"W, 4 Aug 2022, T. P. A. Ramos, S. Y. Lustosa-Costa & Y. G. Abrantes. UFPB 13353, 4 males (44.9–51.1 mm SL), 8 females (34.9–40.3 mm SL), Lagoa Salgada, Quixabeira Dam, Recanto II settlement, 06°10'33"S 35°31'47"W, 4 Aug 2022, T. P. A. Ramos, S. Y. Lustosa-Costa & Y. G. Abrantes. UFRN 5905, 5 males (40.4–45.8 mm SL), 4 females (38.1–41.2 mm SL), Lagoa Salgada, Malhadas Dam, Recanto II settlement, 06°10'57"S 35°31'35"W, 4 Aug 2022, T. P. A. Ramos, S. Y. Lustosa-Costa & Y. G. Abrantes.

Diagnosis. *Hypsolebias lulai* differs from the remaining species of the *H. flammeus* species-group, by the male body color pattern sides of body metallic blue, with 14–18 slim reddish brown bars, this bars are prominent on the caudal peduncle and lose definition near of the pelvic fin (*vs.* reddish brown wide bar alternating in a bright blue background), by the anal fin color pattern light blue, with 11 reddish brown bars (*vs.* being bright blue in *H. tocantinensis*, *H. brunoi*, *H. flammeus*, *H. multiradiatus*, bright brownish yellow with 9–10 dark brown to black bars slightly posteriorly inclined in *H. delucai*, bright brownish yellow, with 8–11 reddish gray bars slightly posteriorly inclined in *H. alternatus*, light pinkish gray, with 9–10 reddish brown bars in *H. fasciatus*, metallic greenish blue, with 11–13 pale reddish brown bars in *H. longignatus*); absent bars in caudal fin and dorsal fin in males (*vs.* presence). Additionally, *H. lulai* differs from the remaining species of the *H. flammeus* species-group except from *H. multiradiatus* and *H. longignatus* by the high number of dorsal fin rays in males 26 (*vs.* 18–23 of the other species in the group); differs from *H. multiradiatus* and *H. longignatus* by the high number of scales in longitudinal series 30 (*vs.* 26–27 in *H. multiradiatus* and 24–26 in *H. longignatus*).

Description. Morphometric data presented in Tab. 1. Largest specimen examined 51.1 mm SL. Body relatively deep, laterally compressed, greatest body depth at level of pelvic fin origin in male. Snout blunt. Dorsal profile concave on head, moderately

convex from nape to end of dorsal-fin base posterior, nearly straight or moderately concave on caudal peduncle. Ventral profile convex from lower jaw to the end of anal fin base, nearly straight on caudal peduncle. Eyes positioned on upper portion of side of head. Urogenital papilla cylindrical and short in males, pocket-shaped in females.

Tip of dorsal and anal fins pointed in males, with one or two short filamentous rays on tip reaching vertical through caudal-fin base; extremity of dorsal and anal fin rounded in females, filaments absent in females. Caudal fin rounded. Pectoral fins elliptical.



FIGURE 1 | *Hypsolebias lulai*, holotype, UFPB 14713, 44.9 mm SL, male; Brazil, Rio Grande do Norte, Lagoa Salgada, Coelho stream, rio Trairi basin.



FIGURE 2 | *Hypsolebias lulai*, paratype, UFPB 13354, 40.9 mm SL, female; Brazil, Rio Grande do Norte, Lagoa Salgada, Coelho stream, rio Trairi basin.

Posterior margin of pectoral fins reaching vertical through base of 3th anal-fin ray in males; in females the posterior margin of pectoral fins it does not reach the base of the anal-fin, reaches half the length of the pelvic fin. Tip of each pelvic fin reaching base of 3rd anal-fin ray separated by interspace equal to pelvic-fin base in width, in males; in females the tip of each pelvic fin reaching base of 1rd anal-fin ray. Dorsal-fin origin on vertical anterior to pelvic-fin origin in males; in females, between origins of pelvic- and anal-fins. Anal-fin origin on vertical through base of fourth dorsal-fin ray, in males and in females anterior to dorsal-fin origin. Anal-fin origin on vertical through base of fourth dorsal-fin ray, in males and in females anterior to dorsal-fin origin. Dorsal-fin origin between neural spines of vertebrae 6 and 7 in males, and neural spines of vertebrae 11 and 12 in females. Anal-fin origin between pleural ribs of vertebrae 7 and 8 in males, and pleural ribs of vertebrae 8 and 9 in females. Dorsal-fin rays 26 in males, 18–21 in females; anal-fin rays 23–24 in males, 20–23 in females; caudal-fin rays 21; pectoral-fin rays 12–13; pelvic-fin rays 6. Longitudinal series of scales 30–32; transverse series of scales 11–12; scale rows around caudal peduncle 12–13. Small papillae contact organ only on inner surface of three dorsal-most rays of pectoral fins in males, absent in scale of flank and ventral portion of opercular area. Total vertebrae 26.

Cephalic neuromasts: supraorbital 15, preorbital 2–3, infraorbital 3 + 23–24, parietal 2, anterior rostral 1, posterior rostral 1, otic 2, post-otic 2, supratemporal 1, median opercular 1–2, ventral opercular 3–4, preopercular plus mandibular 28–30, lateral mandibular 8, paramandibular 1. One or two neuromasts on center of each scale of lateral line, anal and caudal fins base.

Coloration in life. Males (Fig. 1). Sides of body metallic blue, with 14–18 slim reddish brown bars, this bars are prominent on the peduncle caudal and lose definition near of the pelvic fin. Dorsum reddish brown with the scales edge in metallic blue. Venter pale orange. Opercular region light metallic yellow. Iris light yellow, with dark black bar. Dorsal fin reddish brown with blue spots and dots, with small filaments. Anal fin light blue, with 11 reddish brown bars, presence of small filaments at the tip of each ray. Caudal-fin light reddish brown with blue spots and dots and distal area hyaline. Pectoral fins hyaline. Pelvic blue. Females (Fig. 2). Body sides light gray, with gray bars from peduncle to opercular area, black spot in central of body. Dorsum gray. Ventral area pale yellow. Opercular region light gray. Iris light yellow, with dark gray stripe through center of eye. Dorsal fins, anal fin, pectoral, pelvic and caudal fins hyaline.

Geographical distribution. *Hypsolebias lulai* was recorded in three bodies of water in the rural area of the municipality of Lagoa Salgada, state of Rio Grande do Norte, within the Caatinga biome (Fig. 3). Two of the three bodies of water where the species was recorded are artificial, being reservoirs of the small Malhadas and Quixabeira dams. The third body of water is a temporary natural pool known as Capim Grosso. Due to the heavy rains in the period (2022), the temporary pool overflowed, resulting in the release of water into the two artificial reservoirs below, in a cascading effect. However, the natural location of the new species is probably just the Capim lagoon, and its record in the artificial reservoirs was caused by the heavy rains that caused this lagoon to overflow and the fish to reach the reservoirs.

TABLE 1 | Morphometric and meristic data for the holotype (H) and paratypes of *Hypsoblebias lulai*.

	Holotype	Paratypes	
	Male	Male	Female
Standard length (mm)	44.9	42.7–48.4	34.9–40.4
Percentage of standard length			
Body depth	43.2	38.2–42.6	37.5–39.3
Caudal peduncle depth	17.3	15.8–18.2	14.9–16.0
Pre-dorsal length	44.5	40.4–43.8	52.4–57.3
Pre-pelvic length	41.1	43.1–45.0	50.5–63.6
Length of dorsal-fin base	45.9	44.4–48.4	25.5–29.1
Length of anal-fin base	40.4	38.5–43.7	24.9–31.4
Caudal-fin length	30.2	26.3–31.9	24.4–28.7
Pectoral-fin length	23.3	20.8–21.6	20.1–21.7
Pelvic-fin length	7.3	8.3–9.7	9.0–10.6
Head length	29.4	27.2–29.5	23.3–30.1
Percentage of head length			
Head depth	111.2	85.1–107.4	98.8–130.7
Head width	59.7	60.0–66.7	60.7–76.9
Snout length	20.1	21.7–22.3	23.7–29.6
Lower jaw length	20.4	40.0–40.6	34.2–45.9
Eye diameter	28.0	25.1–28.1	24.3–33.1

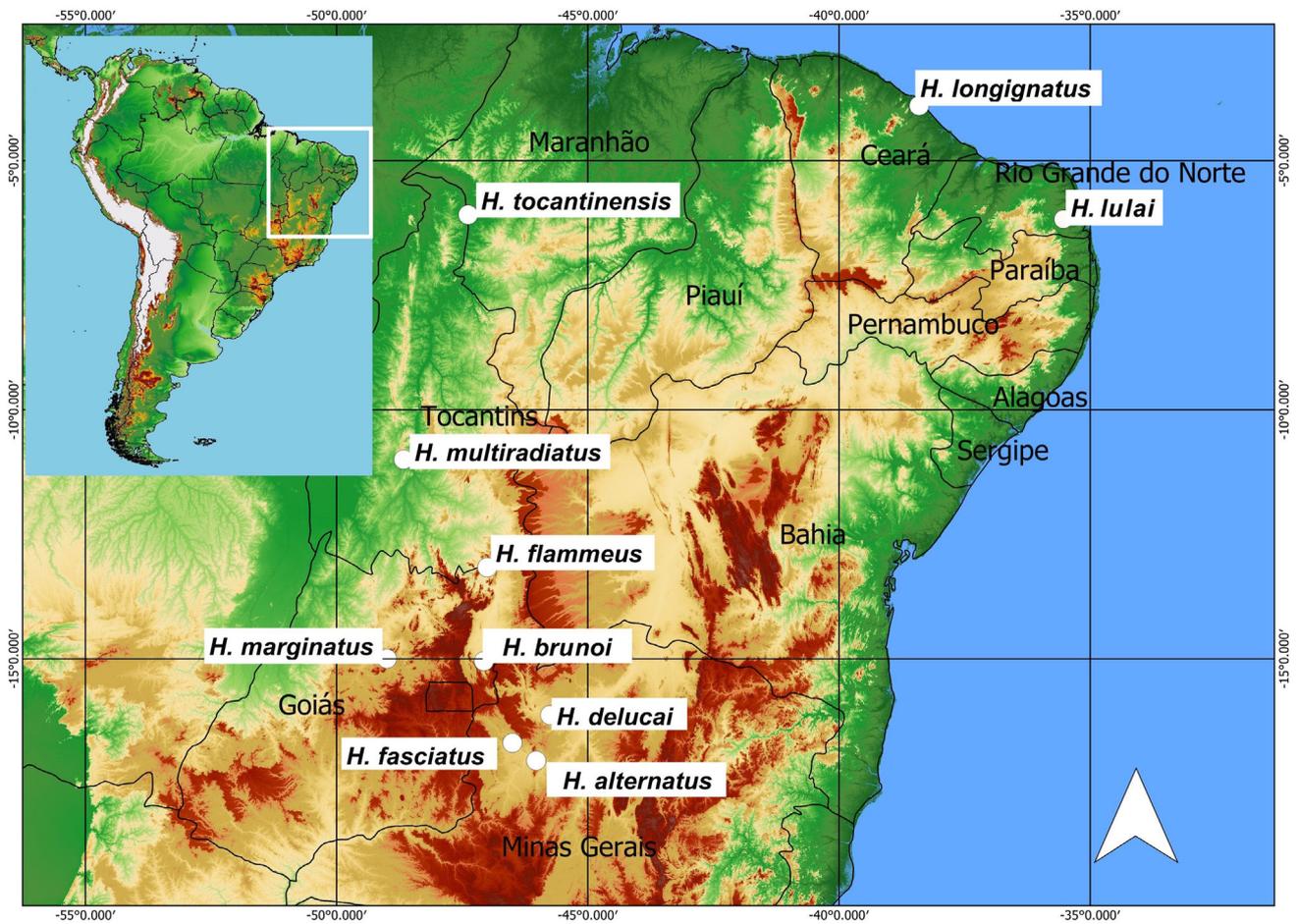


FIGURE 3 | Type-locality of species of *Hypsoblebias flammeus* species-group.

Ecological notes. The habitat is a temporary lagoon in the drainage of the rio Trairi basin, a river that has its upper and middle courses in the Caatinga biome and its mouth in the Atlantic Forest biome (Fig. 4). The substrate of the lagoon is composed of clay and sand and the water is a slightly dark tea-color. The lagoon reached a depth of 2 m during the sampling period, but its average depth is about 1.3 m. The aquatic vegetation is dense with abundant *Echinodorus* sp. and *Nymphaea* sp. The average annual temperature in the region is 28° C, with a maximum of 34° C and a minimum of 20° C. The rainy season occurs from January to June. *Hypsolebias lulai* was found with *Astyanax bimaculatus* (Linnaeus, 1758) at the type-locality and *A. bimaculatus* and *Oreochromis niloticus* (Linnaeus, 1758) in the artificial reservoirs. Individuals of the new species were also collected in areas of currents in the drainages that formed between the water bodies of Lagoa Capim Grosso and Malhadas and Quixabeira dams.

Etymology. The species is named in honor of Luiz Inácio Lula da Silva, the current Brazilian president, responsible for restoring conservation actions and socio-environmental enhancement and resuming incentives for Brazilian science. A patronym.

Conservation status. *Hypsolebias lulai* is an endemic species in the semi-arid region, occurring only a small pond in the Trairi River basin, State of Rio Grande do Norte, Brazil. The species is limited to just three sampling points, all interconnected, in a heavily occupied and modified area. Due to the significant impact of agriculture in the region where this species was recorded, as well as the presence of an exotic species,



FIGURE 4 | Type-locality of *Hypsolebias lulai*, Brazil, Rio Grande do Norte, Lagoa Salgada, Coelho stream, rio Trairi basin.

Oreochromis niloticus, in two of the three registration points for *H. lulai*, the species faces several threats. First, its restricted area of occupation, which covers less than 1 km². Second, the conversion of Caatinga areas into pastures and also the construction of dams in natural wetlands, which drives to decline in habitat quality. For these reasons, we categorize the new species described as Vulnerable (VU), according to the D2 criterion of the International Union for Conservation of Nature (IUCN Standards and Petitions Subcommittee, 2022).

DISCUSSION

Hypsolebias lulai is easily distinguished from other members of the *H. flammeus* group by the color pattern of males, with the sides of the body exhibiting a metallic blue with 14–18 slender reddish-brown bars. These bars are prominent on the caudal peduncle and become less defined near the pelvic fin. The striped color pattern of males is characteristic of the *H. flammeus* group, along with the long posterior process of the supraoccipital bone and the elongated anal fin of females, however, the vertical stripes of *H. lulai* are thinner and more numerous.

Hypsolebias lulai appears to be more closely related to *H. longignatus* (Fig. 5) due to the shared presence of the following characteristics: a high number (exceeding 10) of vertical stripes on the body; small blue spots on the caudal fin; absence of long filaments in the dorsal fin; and males possessing 26 dorsal fin rays. Furthermore, they both occur in a small coastal hydrographic basin in Northeast Brazil, where the paleodrainage was defined in the Miocene by the former course of rio São Francisco (Costa *et al.*, 2017,



FIGURE 5 | *Hypsolebias longignatus* from a temporary pool close to type-locality of species, 03°53'52.3"S 38°24'15.26"W, Aquiraz, Ceará, Brazil, rio Pacoti basin.

2018). However, *H. lulai* differs from *H. longignatus* by the color pattern of the dorsal fin, with no black spots on the anterior portion (*vs.* presence in *H. longignatus*). Additionally, the color pattern of the caudal fin of *H. lulai* consists of 11 reddish-brown parallel stripes and there are small filaments at the tip of each ray (*vs.* 7–8 reddish-brown stripes not arranged in parallel and no small filaments). Furthermore, the opercular region of *H. lulai* is light metallic yellow (*vs.* light metallic blue), and it has fewer caudal fin rays 21 (*vs.* 23–25), and vertebrae 26 (*vs.* 27–29) in males and a rounded anal fin (*vs.* elongated, spatula-shaped).

Larger specimens of *Hypsolebias lulai* possess a concavity in the frontal region of the head (Fig. 6). According to Costa (2007, 2008), members of the *H. flammeus* group have a conspicuously concave dorsal profile of the head, instead of the approximately straight dorsal profile of the other groups. This concavity of *H. lulai* is supposedly associated with age, as this characteristic has been noted in larger specimens (45.3 mm SL and greater for males and 40.1 mm SL and greater for females). Large individuals maintained in aquariums for up to three months after collection retained this concavity, whereas collected smaller individuals (less than 35.1 mm) developed the concavity when grown in aquariums. Nonetheless, additional research is necessary, both in the laboratory and in the natural environment, to better understand this phenomenon.

The long posterior process of the supraoccipital and the elongated anal fin of females are synapomorphies of the *Hypsolebias flammeus* group (Costa, 2007). *Hypsolebias lulai* possesses a long posterior process of the supraoccipital but its anal fin is rounded, making the latter an autapomorphy of the species within the group.

Hypsolebias lulai is yet another species of the family Rivulidae described for the hydrographic basins that drain the Caatinga in Northeast Brazil. There are currently 63 known species of the family Rivulidae in the Caatinga, making it the third richest fish



FIGURE 6 | *Hypsolebias lulai*, male, 50.6 mm SL, Brazil, Rio Grande do Norte, Lagoa Salgada, Coelho stream, rio Trairi basin.

family in the biome (Lima *et al.*, 2017). Of this total, 34 have been assigned some level of endangered status (MMA, 2022). The last thirty years have seen a large-scale advance of changes to ecosystems of the Caatinga. Desertification, has made the Northeast semi-arid region drier and is responsible for the loss of about 10% of its native vegetation cover and 8.4% of its water surface (MapBiomas; <https://brasil.mapbiomas.org/>). These impacts have been identified as the main causes of the high loss of rivulid habitat (ICMBio, 2012; Abrantes *et al.*, 2020).

The hydrographic basins of Northeast Brazil have a complex biogeographical history, which reflects both ancient and recent biogeographical events that underwent strong changes throughout the Plio/Pleistocene. In the meantime, watersheds tell different stories about dispersal and vicariance processes, with species of the family Rivulidae being excellent biogeographical indicators in these discussions as they generally have distribution patterns closely related to current hydrographic basins and those of a recent past (Costa, 1995, 2010; Nielsen, 2008).

The diversity and geographic distributions of small terrestrial vertebrates endemic to the region of Northeast Brazil, were shaped by geological events and vicariance. These changes were closely related to gradual changes in the course of Rio São Francisco (Rodrigues, 2003; Werneck *et al.*, 2015). One of the most important of such episodes that shaped the drainages of Northeast Brazil was the uplift of the Borborema-Araripe massif during the Miocene, which isolated the rio São Francisco basin from the rio Jaguaribe and Piranhas basins, altering the lower paleocourse of the rio São Francisco to a course close to or even coinciding with rio Parnaíba, today on the border of the states of Piauí and Maranhão. The formation of Chapada do Araripe with the elevation of the São Francisco arch must have altered the distribution of fish populations (Mabesoone *et al.*, 1994; Britzke *et al.*, 2016). In addition, several tectonic faults were reactivated during the Quaternary, which probably altered the distribution of several species through the capture of the headwaters of these rivers (Ribeiro, 2006; Britzke *et al.*, 2016). It is important to note that Borborema is the second largest hydrographic disperser on the Brazilian Atlantic Plateau (Ab'Saber, 1952).

At the end of the Tertiary, another major biogeographical event resulted in the separation of rio São Francisco and rio Parnaíba, forming a paleodrainage of lower rio São Francisco towards the east and a connection with basins further south, such as rio Vaza-Barris and rio Itapicuru basins, at the beginning of the Pleistocene. Subsequently, rio São Francisco reached its current course, with its mouth between the states of Alagoas and Sergipe, only in the Middle Pleistocene (Rodrigues, 1992; Passoni *et al.*, 2008; Siedschlag *et al.*, 2010; Nascimento *et al.*, 2013; Werneck *et al.*, 2015). These changes in the course of rio São Francisco explain the wide distribution of the two most abundant genera of Rivulidae in the region — *Cynolebias* and *Hypsolebias*, the latter represented by the *H. antenori* species group. However, many doubts remain about the distribution of the *H. flammeus* group in the region due to the rarity of species east of rio Tocantins, which can be ameliorated with further research and the discovery of other taxa.

The *Hypsolebias flammeus* group has an intriguing geographic distribution, with three species in tributaries on the left bank of middle rio São Francisco, namely rio Urucuia (*H. delucai*) and rio Paracatu (*H. alternatus* and *H. fasciatus*) sub-basins in the State of Minas Gerais; two species in upper rio Tocantins, a tributary of rio Paraná (*H. flammeus* and *H. brunoi*) in the State of Goiás; one in middle rio Tocantins (*H. multiradiatus*); and

one further north, also in rio Tocantins (*H. tocantinenses*), in the states of Tocantins and Maranhão. *Hypsolebias longignatus* occurs in the lower portion of the rio Pacoti basin, a coastal basin in the municipality of Aquiraz, close to the city of Fortaleza, the capital of the State of Ceará. The new species, *H. lulai*, was recorded in the rio Trairi basin, which is closely linked to the rio Piranhas basin, where rio São Francisco had a connection prior to the emergence of the Borborema–Araripe plateau in the Miocene.

Costa (2008) suggests that the distribution of *Hypsolebias longignatus*, a species of the *H. flammeus* group, in the coastal basin of Northeast Brazil may have occurred along rio Tocantins. This hypothesis seemed to be supported by the description of *H. tocantinenses* in 2012. However, the discovery of *H. lulai* in the rio Trairi basin opens the hypothesis that this group arrived in the Northeast also through the rio São Francisco basin.

Despite possessing distinct ichthyofaunas, the rio Tocantins basin has been considered more similar to the Amazon basin, and the rio São Francisco basin as intermediate because it possesses connections with the basins adjacent to its limits (Lima, Caires, 2011). Still, authors argue that the ichthyofaunas of rio Tocantins and rio São Francisco meet biogeographically through Serra Geral do Tocantins. Serra Geral do Tocantins is a tectonic structure dating back to the Cretaceous that separates the headwaters of these two rivers, yet through the phenomenon called “emended waters” (Serra erosion process), dispersion from the rio Tocantins basin to rio São Francisco during the Miocene was likely (Hubert *et al.*, 2007). This dispersion may explain the presence of the *Hypsolebias flammeus* group in both of these basins, as well as the genus *Cynolebias*. However, species of the *H. flammeus* group were only known from middle rio São Francisco and the rio Tocantins basin until the description of *H. longignatus*, and now *H. lulai*, both in the intermittent basins of the Northeast Caatinga and Coastal ecoregion.

Comparative material examined. All from Brazil. Ceará State. *Hypsolebias antenori*: UFPB 11302, 5, 22.3–39.3 mm SL; UFPB 14125, 2, 19.1–26.8 mm SL; UFPB 14134, 2, 27.3–36.1 mm SL; UFPB 14155, 31, 28.3–43.1 mm SL; UFPB 14511, 4, 27.1–43.4 mm SL. *Hypsolebias longignatus*: UFPB 12084, 7, 36.3–41.3 mm SL; UFPB 12676, 2, 33.1–35.0 mm SL; UFPB 11300, 2, 34.3–40.3 mm SL. **Maranhão State.** *Hypsolebias coamazonicus*: UFPB 13356, 32, 21.3–42.3 mm SL.

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Silvia Y. Lustosa–Costa: Investigation, Methodology, Writing–review and editing.

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ETHICAL STATEMENT

The specimens used in the description were collected under a collection license authorized by the Ministério do Meio Ambiente/Instituto Chico Mendes de Conservação da Biodiversidade (MMA/ICMBio, process #56416/2022).

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The author declares no competing interests.

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