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Parasitology aiding fish taxonomy: *Hyphessobrycon nicolasi* as a jr. synonym of *H. meridionalis* (Characiformes: Acestrorhamphidae)

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Abstract: This study provides strong evidence in favor of considering *Hyphessobrycon nicolasi* as a junior synonym of *Hyphessobrycon meridionalis*. The analysis of the type material of *H. nicolasi* shows that the main diagnostic character between those species, which was based on supposed differences in coloration patterns due to the presence of an oblique black stripe along the margin of the caudal fin lobes in *H. nicolasi*, was in fact caused by metacercarial infection in the type specimens of *H. nicolasi*. Additionally, further examination of the types and other comparative materials did not reveal any other consistent phenotypic differentiation between these two taxa. Therefore, we consider *Hyphessobrycon nicolasi* as a junior synonym of *Hyphessobrycon meridionalis*. This finding highlights the importance of carefully considering the presence of parasites while describing new species of fishes as they can cause color changes or morphological alterations in their hosts.

Keywords: Digenea, Host-parasite interaction, Melanin deposits, Parasitic infection, Morphology

Resumen: La parasitología como apoyo a la taxonomía de peces: *Hyphessobrycon nicolasi* como sinónimo junior de *H. meridionalis* (Characiformes: Acestrorhamphidae). Este estudio proporciona evidencia sólida a favor de considerar *Hyphessobrycon nicolasi* como un sinónimo junior de *Hyphessobrycon meridionalis*. El análisis del material tipo de *H. nicolasi* muestra que el principal carácter diagnóstico entre estas especies, basado en las supuestas diferencias en los patrones de coloración debido a la presencia de una franja negra oblicua a lo largo del margen de los lóbulos de la aleta caudal en *H. nicolasi*, se debe en realidad a la presencia de una infección por metacercarias en los especímenes tipo de *H. nicolasi*. Además, un examen más detallado de los tipos y de otros materiales comparativos no permitió establecer ninguna diferenciación fenotípica consistente entre estos dos taxones. Por lo tanto, consideramos a *Hyphessobrycon nicolasi* como un sinónimo junior de *Hyphessobrycon meridionalis*. Este hallazgo resalta la importancia de considerar cuidadosamente la presencia de parásitos al describir nuevas especies de peces, ya que estos pueden generar cambios en la coloración o alteraciones morfológicas en sus hospedadores.

Palabras clave: Depósitos de melanina, Digenea, Infección parasitaria, Interacción hospedador-parásito, Morfología

INTRODUCTION

The genus *Hyphessobrycon* Durbin, 1908, originally described as a subgenus of *Hemigrammus* Gill, 1858, is one of the most diverse and geographically widespread genera of Neotropical fishes and the second most diverse genus within Characiformes (Dagosta & de Pinna, 2019; Marinho & Dagosta 2024). Nevertheless, numerous phylogenetic analyses have revealed that *Hyphessobrycon* is polyphyletic, necessitating the re-evaluation and generic reassignment of many species (Mirande, 2010; Oliveira *et al.*, 2011; Mirande, 2019; Terán *et al.*, 2020; Melo *et al.*, 2024). In the Lower La Plata basin, about nine species are currently assigned to *Hyphessobrycon*, but many of these are not probably to be closely related to the genus's type species, *Hemigrammus compressus* (Meek, 1904), native to Central America. For example, some species, such as *Deuterodon luetkenii* (Boulenger, 1887) and *Psalidodon anisitsi* (Eigenmann, 1907), have been recently reassigned to other genera (Terán *et al.*, 2020). Similarly, *Hyphessobrycon meridionalis* has been recovered as more closely related to *Moenkhausia xinguensis* clade (see Terán *et al.*, 2020 Appendix S4).

Hyphessobrycon nicolasi Miquelarena & López, 2010 was originally distinguished from *Hyphessobrycon meridionalis* Ringuelet, Miquelarena & Menni, 1978 by "the presence of an oblique black stripe along the caudal fin lobes" and "shorter pectoral fins that did not reach the base of the pelvic fins" (Miquelarena & López, 2010). *Hyphessobrycon meridionalis* was described from Canal Delgado, Río de la Plata, and has since been recorded throughout the La Plata River basin, including tributaries of the Paraná and Uruguay rivers, as well as several coastal rivers in Argentina, Brazil, and Uruguay. In contrast, *H. nicolasi* was described from El Pelado Stream in the lower Uruguay River, a location within the known range of *H. meridionalis*, and has not been recorded elsewhere.

Carvalho (2011), in his comprehensive thesis on the genus *Hyphessobrycon*, questioned the validity of *H. nicolasi*, proposing that the distinctive black markings along the caudal fin—previously considered diagnostic—might instead result from metacercarial infections (Digenea) between the fin rays. A subsequent targeted re-examination of the type material by two of the present authors (GET and SB) independently supported this interpretation. However, due to the lack of direct evidence, the issue remained unresolved. In this study, we test Carvalho's hypothesis through direct examination and histological analysis of specimens from the type series, aiming to clarify the taxonomic status of *H. nicolasi*.

MATERIAL AND METHODS

Here, we revised the entire type series of *Hyphessobrycon nicolasi* Miquelarena & López, 2010, for morphological and meristic analyses. Measurements were taken from the holotype and 29 paratypes (Bogan *et al.*, 2019). For *Hyphessobrycon meridionalis* Ringuelet, Miquelarena & Menni, 1978, only the holotype is available from the type series at the MLP collection, the lot containing nine paratypes appear to be missing (Miquelarena & Nadalin, 2014). Standard length (SL) is expressed in millimeters (mm), while all other measurements are given as percentages of SL, except for subunits of the head, which are expressed as percentages of head length. Measurements followed the morphometric table of Marinho & Dagosta (2024). Institutional abbreviations: CI-FML, Colección Ictiológica, Fundación Miguel Lillo. CFA-IC, Fundación de Historia Natural Félix de Azara Ichthyological Collection, Buenos Aires, Argentina; MLP-Ict, fish collection of the Museo de La Plata, MACN-Ict, fish collection of the Museo Argentino de Ciencias Naturales.

To corroborate the hypothesis of metacercariae infection as the cause of the pigmentation (Carvalho, 2011) in the caudal fin of *H. nicolasi*, material from the type series was analyzed for parasitological studies. Tissue samples were taken from paratypes in lots CFA-IC 11809 and CFA-IC 11811, yielding eight samples: three from cysts on the body, four from caudal fin segments, and one from the dorsal fin.

Segments were examined under a stereomicroscope, and portions of the fins were mounted on slides with glycerinated alcohol (50:50) to clear the structures for detailed observation under an Olympus BX51 microscope equipped with an AmScope MU1000 10 MP digital camera (United Scope LLC, Irvine, USA). Samples were dehydrated, embedded in paraffin, sectioned at 5 μm, and stained with hematoxylin and eosin (H&E) for histological examination.

ZooBank registration number: urn:lsid:zoobank.org:pub:60BF674D-B4F8-44DA-AD24-B8073C8A2DAF

RESULTS

Hyphessobrycon meridionalis Ringuelet, Miquelarena & Menni, 1978
(Fig. 1)

Hyphessobrycon nicolasi Miquelarena & López, 2010 — syn. nov.
(Fig. 2, 3)

Morphometric data of type specimens analyzed is

Fig. 1. Holotype of *Hyphessobrycon meridionalis* MLP 8339, 45.0 mm SL, from Los Talas, Buenos Aires Province, Argentina.

Fig. 2. Holotype of *Hyphessobrycon nicolasi* ILPLA 1808, 49.1 mm SL, from El Pelado stream, Entre Ríos Province, Argentina.

Fig. 3. Some of the paratypes of *H. nicolasi* CAF-ICT 11811 showing the variability of the black-striped line on the caudal fin.

presented in Table 1.

The shorter pectoral fin of *H. nicolasi*, previously considered diagnostic by Miquelarena & López (2010), was observed to exhibit intraspecific variation, including within the type series (Fig. 3). Additionally, similar counts of anal-fin rays for both species, (31–40 for *H. meridionalis* and 30–36 for *H. nicolasi*), tas well as tooth counts and overall morphological similarities, were observed.

The presence of a well-defined, oblique black stripe along the caudal fin lobes in *H. nicolasi* is conspicuous in the holotype but this marking varies among the paratypes, appearing faint or absent in some specimens (Fig. 2 and 3). A closer examination revealed that these markings are irregular in pattern, shape, and position and were likely due to metacercaria infection.

Under microscopic examination, the black-stained fin rays of *H. nicolasi* revealed rounded structures surrounded by melanin granules (Fig. 4A). When clarified with glycerinated alcohol and subjected to slight pressure, these structures were identified as metacercariae (Fig. 4B). The spinous tegument and visible suckers further confirmed the presence of parasites, rather than a species-specific coloration pattern. Histological sections (Fig. 4C-F) support this finding. Transverse and longitudinal sections of fin rays show metacercariae encased within cysts (Fig. 4C, D). Melanin deposits surround the cysts, contributing to the dark appearance of the fin rays. Sections also illustrate the double-layered cyst walls formed by both parasite and host (Fig. 2E)

Comparative material examined. *Hyphessobrycon meridionalis*. All from Argentina. CI-FML 3931, 2 C&S; San José del Rincón, Santa Fé, Paraná, Colastiné; 03/XII/91; Fernández, Scrocchi & Lavilla. CI- FML 6165; 14 (2 C&S); Puente Victoria Santa Fe, Santa Fé; 01/IX/14; Terán, Alonso & Calviño. CI-FML 6166; 12 (1 C&S); Colonia Huegues, Colón, Entre Ríos; Köerber, Fernandez Santos. MACN-Ict 7710; 5; Desborde del Arroyo Feliciano, Entre Ríos; 15/VIII/1974; Castello; MACN-Ict 7872; 5; Charcos en Isla frente a Helvecia, Santa Fé; 27/IX/1974; Castello. MACN-Ict 8126; 73; Río Paraná, Ramallo, Buenos Aires; 01/VIII/1961; Tonina. MACN-Ict 8226; 140; Parque Unzué, Gualeguaychú, Entre Ríos; Taberner. MACN-Ict

Table 1. Morphometric data of available specimens of *Hyphessobrycon meridionalis* and *H. nicolasi*

	Hyphessobrycon meridionalis					***Hyphessobrycon nicolasi***				
	Holotype	Non types CI-FML 6165 and MACN-Ict 8126 n=24				Holotype	Paratypes			
		Mean	Min	Max	SD		Mean	Min	Max	SD
Standard length (mm)	45.0	38.8	34.6	49.1	3.1	48.5	43.2	36.2	49.6	3.7
Percentages of standard length										
Depth at dorsal-fin origin	38.4	40.1	37.4	43.8	1.7	42.8	43.3	39.9	46.4	1.8
Snout to dorsal-fin origin	53.5	53.1	50.8	55.3	1.6	55.9	55.3	52.2	59.7	2.0
Snout to pectoral-fin origin	27.3	28.3	26.3	30.2	1.3	26.9	26.6	24.7	29.8	1.4
Snout to pelvic-fin origin distance	44.3	46.6	43.4	47.9	1.5	46.5	45.8	42.0	51.2	2.0
Snout to anal-fin origin distance	56.4	59.6	56.9	63.2	1.8	59.3	58.8	54.5	62.5	2.1
Caudal-peduncle depth	10.9	11.1	8.2	13.0	0.8	10.6	10.3	8.3	12.6	1.1
Caudal-peduncle length	11.3	10.7	9.5	12.1	0.8	9.4	11.8	9.4	13.8	1.3
Pectoral-fin length	15.0	18.6	17.1	20.3	0.8	15.9	18.2	15.9	20.2	1.1
Pelvic-fin length	14.9	15.3	14.1	17.3	0.9	14.0	14.9	12.9	18.8	1.4
Pelvic-fin origin to anal-fin origin distance	11.3	14.8	13.0	16.5	1.0	15.1	15.4	11.8	19.0	1.7
Dorsal-fin length	26.1	28.3	26.6	30.8	1.3	26.0	26.1	23.7	30.6	1.6
Dorsal-fin base length	14.3	13.7	11.5	15.7	1.1	11.9	13.7	11.2	17.0	1.5
Anal-fin base length	39.8	40.6	35.8	45.0	2.4	38.3	38.8	34.7	42.6	1.9
Eye to dorsal-fin origin distance	40.0	41.5	39.6	44.8	1.4	42.6	42.2	39.3	46.1	1.9
Dorsal-fin origin to caudal-fin base distance	54.7	52.9	49.7	56.6	1.9	51.0	52.4	48.6	57	2.1
Head length	24.2	27.0	25.5	28.6	1.1	25.3	24.3	22.3	25.9	1.1
Percentages of head length										
Horizontal eye diameter	38.2	35.4	32.6	38.2	1.6	38.6	39.7	36.0	45.8	2.6
Snout length	27.7	24.5	21.3	30.1	2.7	20.4	26.6	20.4	33.4	2.9
Interorbital width	40.5	35.8	32.0	39.1	2.5	34.7	37.3	30.5	44.1	2.9
Upper jaw length	45.0	34.2	29.9	38.0	2.4	37.1	40.6	31.4	53.0	5.6

8227; 27; Arroyo Los Loros, Parque Nacional El Palmar, Colón, Entre Ríos; Fernández Santos. MACN-Ict 9482; 5; Arroyo La Arena, Pilar, Buenos Aires; VIII/2008; López & Bentos. MACN-ict 10518; 1; Boca Laguna Irupé, Parque Nacional Pre Delta, Entre Ríos; 21/VIII/2009; Ciotek & Giorgis. MACN-Ict 12882; 5; Gral. Mansilla, Buenos Aires (35° 8'15.57"S; 57°42'42.77"W); 22/I/2019; Paracampo & Paredes del Puerto. MACN-Ict 13178; 23; Estancia Curupicay, en el embalse, Mercedes, Corrientes (29° 16'14.7"S, 58°41'49.5"W); 5/12/2009; Brancolini, Minotti & Parimbelli.

DISCUSSION

Parasitology remarks

The genera *Uvulifer* Yamaguti, 1934, *Crassiphiala* Van Haitsma, 1925, and *Posthodiplostomum* Dubois, 1936, as well as heterophyids belonging to the genera *Cryptocotyle* Lühe, 1899, and *Apophallus* Lühe, 1909, have been identified as causative agents of black spot disease (Kristoffersen, 1991; Kurochkin & Biserova, 1996; Krause *et al.*, 1999; Quist *et al.*, 2007; Rodnick *et al.*, 2008). However, the morphological characteristics of these metacercariae often make identification to the species or even genus level very difficult (Graczyk, 1991; Niewiadomska & Szymanski, 1991; Pérez-Ponce de León, 1995; Locke *et al.*, 2010). Since the material examined in this study corresponds to that used in the description of *H. nicolasi*, it was not possible to identify the metacercariae due to the need for a different fixation methodology. Molecular and morphological analyses of appropriately fixed material are necessary to accurately determine the species- or genus-level identity of the metacercariae responsible for black spot disease.

In *Hyphessobrycon nicolasi*, we recorded two types of metacercariae: isolated black spots on the epidermis (Fig. 5), and black spots arranged along the fin rays, forming a distinct line on the

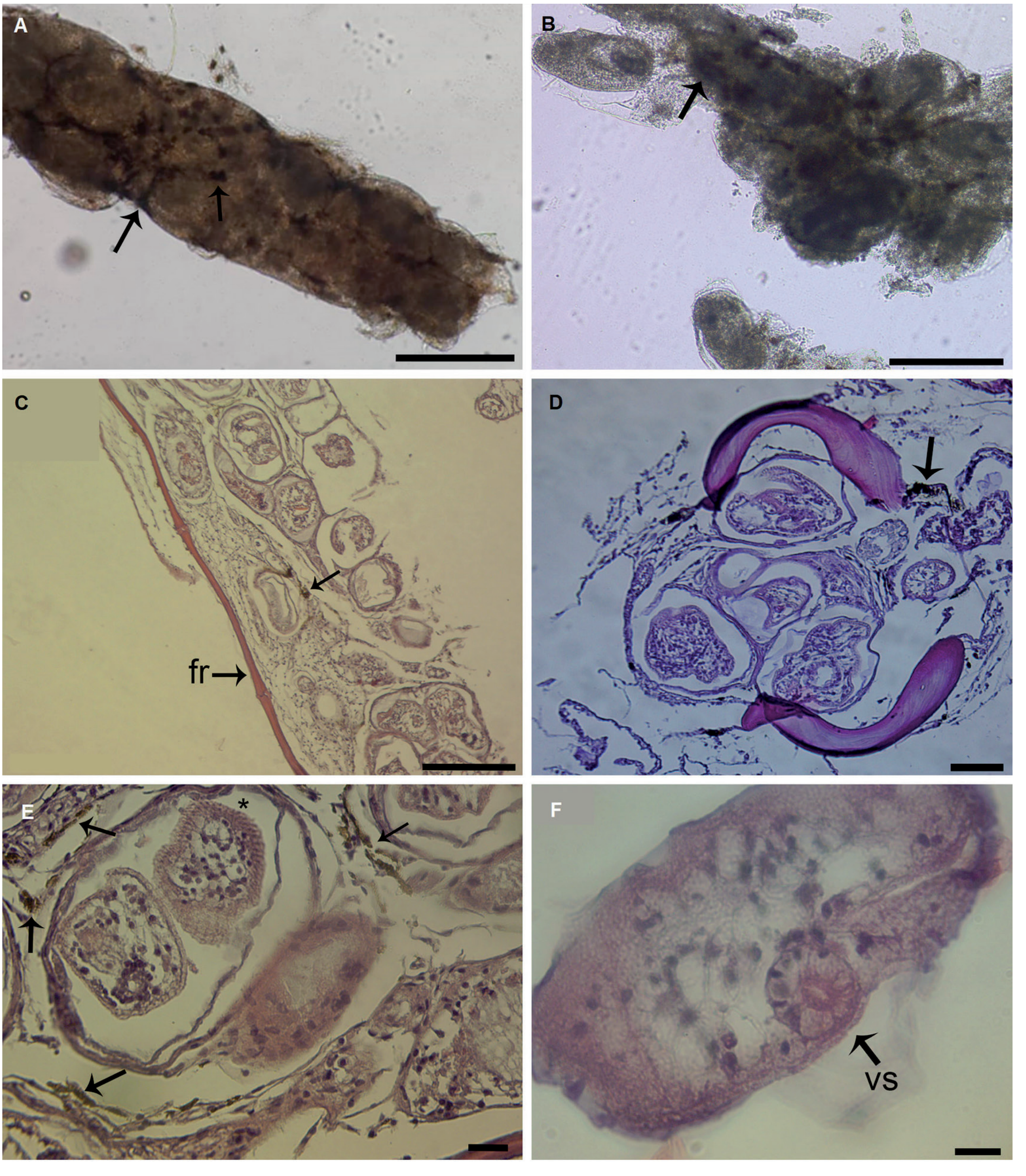

Fig. 4. Metacercariae infection photographs: (A) Microphotograph showing a section of the black-striped line on the caudal fin. (B) Section of infected tissue after applying slight pressure to release the metacercariae. (C) Longitudinal histological section of the caudal fin ray showing severe infection by digenean metacercariae. (D) Transverse histological section of the caudal fin ray (fr) showing severe infection by digenean metacercariae inside the fin ray. (E) Encysted metacercariae displaying tegument spines (asterisk) and a double cyst wall with melanin deposits (arrows). (F) Longitudinal section of a metacercaria inside the cyst, illustrating the ventral sucker (vs). Scale bars: A–C = 200 μm; D, E = 50 μm; F = 20 μm.

caudal fins. The cysts in the skin appeared mostly empty, while those associated with the differentiation of *H. nicolasi* were found within the fin rays, presenting as characteristic melanized spots.

The use of fin rays by this type of metacercaria is similar to that of *Pseudexorchis major* (Hasegawa, 1935) Yamaguti, 1938. The behavior of cercariae of this species—penetrating fish fins

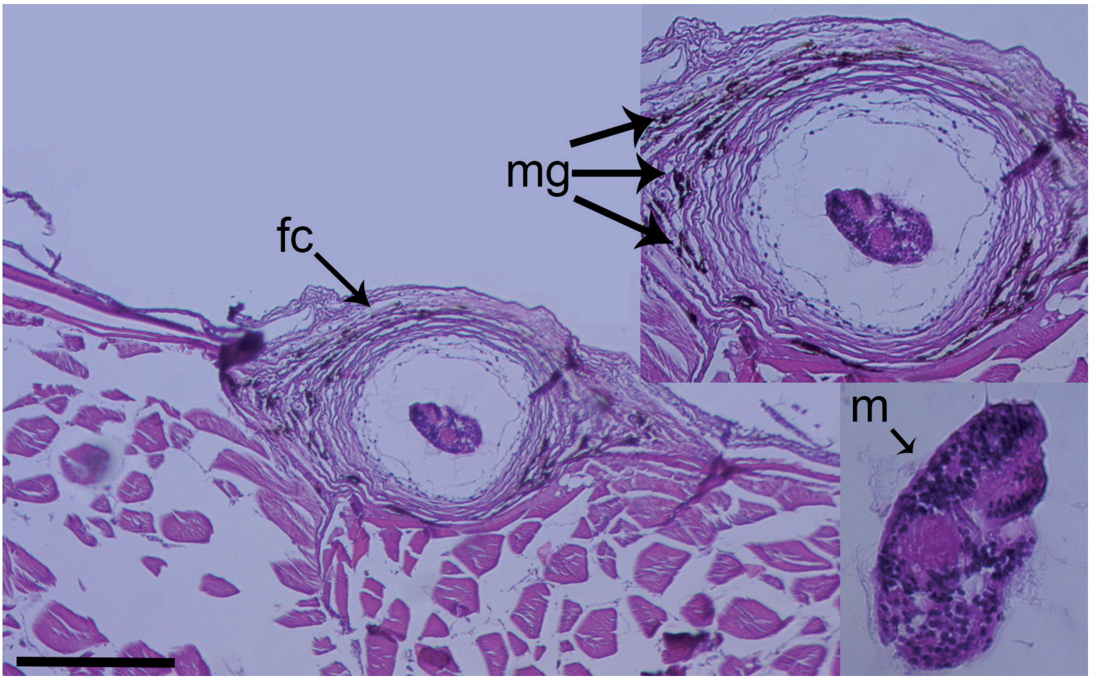

Fig. 5. Metacercariae “Neascus”-type (m) in a fibrous cyst (fc) with inclusions of melaningrains (mg). Scales: 7.1 = 200 μm.

and encysting within the fin rays—was described by Ito (1956), who outlined the stages of infection, though without describing the melanization process. It is possible that melanization requires days, weeks, or even months to occur. We observed metacercariae in fin rays that had not yet formed black spots, possibly due to early-stage infections.

Melanization has been recorded in many fish species from different families and continents. It is one of the host’s immune responses to parasitism and has been studied by several authors (e.g., Chapman & Hunter, 1954; Sindermann & Rosenfield, 1954a, b; McQueen *et al.*, 1973). The effects of these “black spot” infections have been shown to cause lesions on opercular bones (Quist *et al.* 2007), be fatal (Hoffman, 1956; Lemly & Esch, 1984), reduce growth and body condition in some species (e.g., Hunter & Hunter, 1938; Lemly & Esch, 1984), or even be relatively benign (e.g., Rabideau & Self, 1953; Vaughan & Coble, 1975; Vinikour, 1977; Baker & Bulow, 1985; Hockett & Mundahl, 1989; Paradis & Chapleau, 1994). Parasite resistance may also play an important role in female mate choice, especially if males that survive parasitic infections can be distinguished from those that have not been exposed (López, 1998). However, we found no records of parasites being used to resolve taxonomic ambiguities in host species identification.

Although we have found black spots in various host species throughout central, northeastern and northwestern Argentina (unpublished data), few studies have focused on these metacercariae in South America. For Characiform fishes, studies have been conducted in Brazil and Uruguay. For instance, Teixeira-de Mello & Eguren (2008) reported black spot disease for the first time in Uruguay in *Psalidodon* aff. *fasciatus* (Cuvier, 1819) and *Oligosarcus jenynsii* (Günther, 1864) with a prevalence of 63% in the former and 100% (2 individuals) in the latter. They examined 27 species in total, many belonging to the order Characiformes, but only the two aforementioned species exhibited the disease.

In Brazil, Flores-Lopes & Thomaz (2011) sampled the Guaíba Lake basin and collected 53,408 fishes from 66 species, 22 families, and eight orders. They found 13 infected species (1,108 individuals; 2.07% of the total), with the muscle fibers of *P.* aff. *fasciatus*, *Astyanax lacustris* (Luetken, 1875), *Cyphocarax voga* (Hensel, 1870), and *Deuterodon luetkenii* (Boulenger, 1887) being the most affected. Later, Flores-Lopes (2014) reported *Psalidodon* aff. *fasciatus* as the species with the highest prevalence (8.77%) in the same basin, contradicting Teixeira-de Mello & Eguren's (2008) suggestion of host specificity between *P.* aff. *fasciatus* and black spot disease. Barrilli *et al.* (2021) studied the influence of black spot disease on the relative condition factor of *Psalidodon paranae*, finding a prevalence of 84.64% in the Ponte de Tábua stream (an impacted stream in Brazil), the only one of four sampled streams where such parasites were found. These authors reached varying conclusions, ranging from metacercarial host specificity to a lack thereof. Given the high number of genera responsible for black spot disease, it is likely that both scenarios occur in nature.

Taxonomy remarks

Our study confirms Carvalho's hypothesis, providing robust evidence that the distinctive coloration pattern of *Hyphessobrycon nicolasi* is not a taxonomically significant character but rather a consequence of parasitic infection. Moreover, based on our analysis we found no phenotypic differences between the two taxa examined and therefore consider *Hyphessobrycon meridionalis* Ringuelet, Miquelarena & Menni 1978, as the senior synonym of *Hyphessobrycon nicolasi* Miquelarena & López 2010, with *H. meridionalis* being the valid name.

In conclusion, to the best of our knowledge, this is the first instance this represents the first documented case were parasitological evidence has directly contributed to the synonymization of a fish species. This finding underscores the critical importance of interdisciplinary approaches in ichthyological taxonomy and highlights how parasites can generate potentially misleading morphological characters.

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