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INSIGHTS FOR A NEW LINEAGE OF THE MONOTYPIC GENUS Hemiodontichthys BLEEKER 1862 (SILURIFORMES: LORICARIIDAE) IN THE EASTERN AMAZON

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Abstract

The armored catfish *Hemiodontichthys acipenserinus* is a monotypic species of Neotropical freshwater fish belonging to the family Loricariidae. In the last decade, several studies have questioned the monotypic status of this species, proposing the occurrence of cryptic species and the existence of different lineages under the 'umbrella' of a single species. Recent studies have described the occurrence of this species in the hydrographic basins of northeastern Brazil. Based on this, this study aimed to verify, through molecular analyses, whether specimens from a population in the Turiaçu River (State of Maranhão, Eastern Amazon) belong to this species or to one of the known molecular lineages. To this end, sequences of the *Cox*1 gene were produced and compared with sequences from the five lineages of this species available in the BOLD Systems and NCBI (GenBank). The genetic distance between the populations was calculated, in addition to performing five species delimitation analyses: BIN, ASAP, ABGD, bPTP, and GMYC. The relationships between the obtained lineages were analyzed using a phylogenetic tree through Bayesian Inference (BI), and a molecular clock was constructed to identify the divergence time between the identified lineages. The results of all analyses revealed that the Turiaçu River (State of Maranhão, Eastern Amazon) population constitutes a different lineage from the previously identified lineages, with genetic distances between 3.89% and 6.21% from the other lineages, the greatest distance being to *H. acipenserinus* and the smallest to the Guamá River lineage, the closest geographically. The phylogenetic tree also indicates greater proximity to the Guamá River lineage, while the molecular clock indicates that these lineages separated from the others approximately 1.4 Ma ago. The results obtained here confirm the monophyly of *Hemiodontichthys*, as well as the existence of different evolutionary lineages, including the Turiaçu River population. Although the species has a wide distribution throughout the Brazilian Amazonian rivers, this distribution is fragmented. This discontinuity in habitats may be a factor in the isolation of these populations, consequently promoting vicariance and allopatric speciation. However, more integrative studies with morphological and molecular data are needed to identify characters that can differentiate these populations into species.

Keywords: DNA Barcoding. Cryptic species. Neotropical fish. Northeastern drainages. Pinocchio Whiptail Catfish.

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1 Introduction

The family Loricariidae Rafinesque, 1815 is one of the most diverse families of Neotropical freshwater fishes, comprising more than 1,000 species widely distributed across the region (REIS et al., 2003; FRICKE et al., 2025). Loricariidae is composed of six subfamilies: Delturinae Armbruster, Reis & Pereira 2006, Hypoptopomatinae Eigenmann & Eigenmann 1890, Hypostominae Kner 1853, Lithogeninae Gosline 1947, Rhinelepinae Armbruster 2004, and Loricariinae Rafinesque 1815 (FRICKE et al., 2025). The subfamily Loricariinae is the second most diverse, with 277 species in 30 genera distributed throughout Neotropical drainages (FRICKE et al., 2025). Members of this subfamily are characterised by the presence of a depressed caudal peduncle and the absence of an adipose fin, which, with other synapomorphies, leads to its being considered monophyletic (SCHAEFER, 1987; COVAIN et al., 2016).

Hemiodontichthys acipenserinus (Kner 1853) was initially proposed as *Hemiodon acipenserinus* and later allocated within the genus *Hemiodontichthys* by Bleeker (1862). The genus is considered monotypic, with small specimens (up to 13 cm). In addition, they have a very depressed body, their body is covered by bony plates, and they have a well-developed extension on the rostrum, which led to it being commonly called the “Pinocchio Whiptail Catfish”. They also exhibit cryptic colouration, favouring camouflage on sandy or muddy bottoms (COVAIN; FISCH-MULLER, 2007; MENDONÇA, 2012).

The species is endemic to South America, being found in several rivers such as Essequibo, Marañon, Madre de Dios, Ucayali, Paraguay, Amazon, Guaporé, Solimões, Negro, Amazon, Madeira, Javari, Juruá, Trombetas, Tocantins and Guamá-Capim, distributed in Bolivia, Brazil, Colombia, Ecuador, French Guiana, Guyana and Peru (FRICKE et al., 2025). Recent studies have expanded the occurrence of this species to river basins in northeastern Brazil (BARROS et al., 2011; ABREU et al., 2019; GUIMARÃES et al., 2020, 2021; LONDOÑO-BURBANO; REIS, 2021; LIMEIRA-FILHO et al., 2023; VIEIRA et al., 2023). Records have been made in at least four northeastern basins: Turiaçu, Mearim, Itapecuru, and Munim.

Due to this wide distribution, some recent studies have questioned the monotypic status of this species and proposed the existence of cryptic species or a species complex (COVAIN; FISCH-MULLER 2007; COVAIN et al., 2016; CARVALHO et al., 2018). Furthermore, a large morphological variation through morphometric and meristic characters has already been reported for this species (ISBRÜCKER; NIJSSEN, 1974). In addition, different genetic and cytogenetic lineages have also been reported for different populations throughout the area of occurrence of this species (CARVALHO et al., 2018). Based on this and with the recent records of this species in river basins in northeastern Brazil, this study aimed to evaluate, through molecular methods, whether a population of *Hemiodontichthys* from the Turiaçu River basin belongs to one of the already known lineages of *Hemiodontichthys* or whether it constitutes a new Operational Taxonomic Unit (OTU).

2 Material and Methods

Specimens of *Hemiodontichthys* (Figure 1) were collected in the Turiaçu River Basin located in the State of Maranhão, in the Eastern Amazon, with authorization from the Brazilian Institute of Environment and Renewable Natural Resources (IBAMA; SISBIO license: 85746).

Tissue samples were collected from the fins of the specimens, preserved in absolute ethanol (100%), and deposited in the *Coleção de Tecidos e DNA da Fauna Maranhense* (COFAUMA) of the *Universidade Estadual do Maranhão* (UEMA, Brazil). DNA was extracted using the Wizard Genomic DNA Purification Kit (Promega), following the manufacturer's protocol.

The mitochondrial cytochrome c oxidase subunit I gene (*coxI*) was amplified by polymerase chain reaction (PCR) using the primers FishF1 and FishR1 (WARD et al., 2005). PCR reactions were performed in a final volume of 25 µL, containing 14.3 µL of ultrapure water, 4 µL of dNTPs (1.25 mM), 2.5 µL of 10× buffer, 1 µL of $MgCl_2$ (25 mM), 1 µL of each primer (10 µM), 0.2 µL of Taq DNA polymerase (5 U/µL), and 1 µL of genomic DNA.

The PCR cycling conditions consisted of an initial denaturation at 95 °C for 3 minutes, followed by 30 cycles of 94 °C for 30 seconds, 58 °C for 30 seconds, and 72 °C for 30 seconds, with a final extension at 72 °C for 3 minutes. Amplification products were visualized on 1% agarose gels and purified using the Illustra GFX PCR DNA and Gel Band Purification Kit (GE Healthcare).

Purified samples were sequenced in both directions using the forward and reverse primers and the BigDye Terminator v3.1 Cycle Sequencing Kit (Thermo Fisher Scientific) in the ABI 3730 DNA Analyzer (Thermo Fisher Scientific).

Sequence quality was assessed in BioEdit v7.0.5.3 (HALL, 1999), and alignments were performed using ClustalW v2.0.3 (LARKIN et al., 2007). All sequences produced here are deposited in BOLD Systems with the following corresponding accession numbers: HBMA018-25 and HBMA019-25.

To conduct the analyses, public sequences available in the BOLD Systems and NCBI databases were used.

Figure 1. Specimen of *Hemiodontichthys acipenserinus* (107.52 mm SL – Standard length) from Turiaçu river basin, Amazon.

These sequences belong to four different lineages identified by Carvalho et al. (2018). According to the authors, *Hemiodontichthys* presents at least four distinct lineages from Amazon populations, been identified by then as (Figure 2): *Hemiodontichthys acipenserinus* from Madeira River Basin; *Hemiodontichthys* sp.1 from São Francisco River and *Hemiodontichthys* sp.2 from Iquiri River, both from Purus River Basin; and two lineages identified as *Hemiodontichthys* sp.3 occurring in the Tocantins River Basin and Tapajos River Basin (CARVALHO et al., 2018).

For species delimitation and genetic distance analyses, we are considering groupings defined by Barcode Index Numbers (BINs). Pairwise genetic distances (Kimura 2-Parameter model) were calculated using MEGA X (KUMAR et al., 2018), with BINs as grouping criteria for the sequences. Species delimitation was performed using five approaches: BIN (BOLD Systems), Automatic Barcode Gap Discovery (ABGD — PUILLANDRE et al., 2012), Assemble Species by Automatic Partitioning (ASAP — PUILLANDRE et al., 2021), Generalized Mixed Yule Coalescent (GMYC; PONS et al., 2006) and Bayesian implementation of the Poisson Tree Process (bPTP; ZHANG et al., 2013).

The ABGD analysis was performed on the web interface (http://wwwabi.snv.jussieu.fr/public/abgd/abgdweb.html) following the Kimura 2 parameter (K2P) nucleotide substitution model.

The ASAP analysis was performed on the web interface (https://bioinfo.mnhn.fr/abi/public/asap/asapweb.html), also following the Kimura 2 parameter (K2P) nucleotide substitution model. To bPTP analysis, we used a Bayesian Inference (BI) tree as input.

GMYC analysis (PONS et al., 2016) was implemented in the SPLITS package in R (R Core Team, 2019).

This analysis requires an ultrametric genealogical tree, estimated in BEAST 2.4.7 (BOUCKARET et al., 2014), available in CIPRES Science Gateway (MILLER et al., 2010).

The analysis was run with 200 million generations in 4 runs, sampled every 1,000 states with a burn-in of the first 10% of the generations excluded. The maximum credibility tree was visualized with TreeAnnotator 1.8.1 (Drummond & Rambaut, 2007) after an additional burn-in period of 20,000.

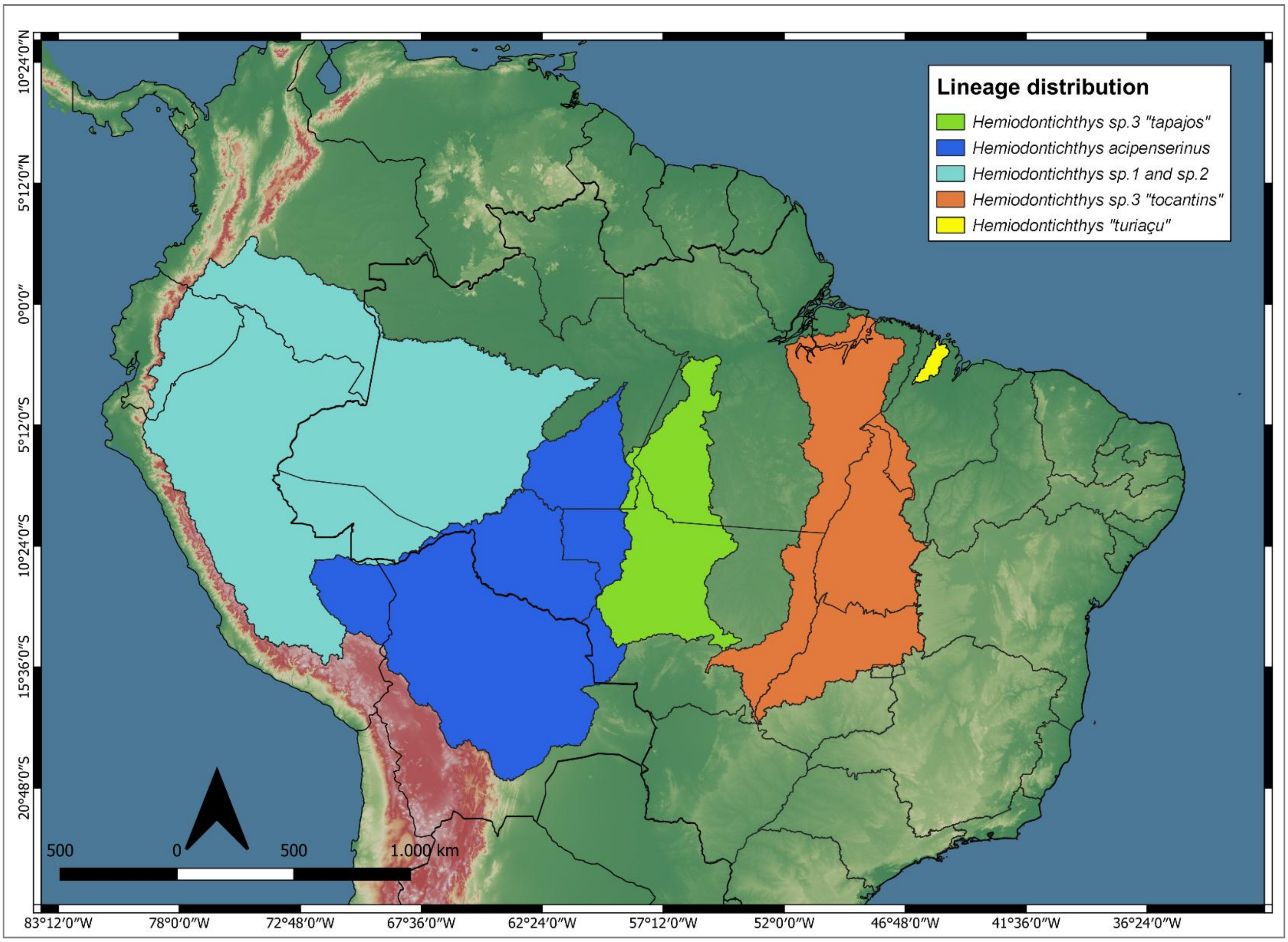

Figure 2. Distribution of knowledge lineage of *Hemiodontichthys acipenserinus*.

3 Results

The results of all our analyses revealed that the population found in the Turiaçu River constitutes a different lineage from the lineages previously identified by Carvalho et al. (2018), with genetic distances between 3.89% and 6.21% from the other lineages (Table 1), highlighting the greatest distance to *H. acipenserinus* and the smallest to the lineage from the Guamá River, in the Tocantins basin, the closest geographically.

The Bayesian inference tree also indicates greater proximity to the *Hemiodontichthys* sp.3 lineage, while the molecular clock indicates that these lineages separated from the others about 1.4 Ma ago, with the Turiaçu lineage separating from *Hemiodontichthys* sp.3 about 1.2 Ma ago (Figure 3). The five species delimitation analyses found the same result, where the Turiaçu population represents a different OTU from the previously identified lineages, indicating the occurrence of cryptic *Hemiodontichthys* species in the Amazon.

4 Discussion

Here, using molecular methods for species delimitation, we identified a new lineage of *Hemiodontichthys* from the Eastern Amazon. The armored catfish *Hemiodontichthys acipenserinus* is a freshwater fish species, belonging to the family Loricariidae, the largest and most diverse of the order Siluriformes (FRICKE et al., 2025).

In the last decade, several studies have questioned the monotypic status of this genus, proposing the occurrence of cryptic species and the existence of different lineages, although they are currently identified as a single specific taxon (COVAIN; FISCH-MULLER, 2007; CARVALHO et al., 2018).

Furthermore, recent studies have expanded the distribution of this species with records of occurrence in the hydrographic basins of Maranhão, in northeastern Brazil (KOERBER et al., 2022).

Table 1. Genetic distance (Kimura 2 parameters) among different lineages of *Hemiodontichthys acipenserinus*. The shortest and longest distances to the population of Turiaçu are highlighted in bold.

	Hemiodontichthys "turiaçu"	*Hemiodontichthys acipenserinus*	*Hemiodontichthys sp1*	*Hemiodontichthys sp2*	*Hemiodontichthys sp3 "tapajós"*
Hemiodontichthys "turiaçu"					
Hemiodontichthys acipenserinus	**6,21%**				
Hemiodontichthys sp1	5,31%	5,19%			
Hemiodontichthys sp2	4,70%	4,98%	4,10%		
Hemiodontichthys sp3 "tapajós"	4,69%	6,84%	5,31%	3,48%	
Hemiodontichthys sp3 "tocantins"	**3,89%**	6,22%	4,50%	2,70%	2,30%

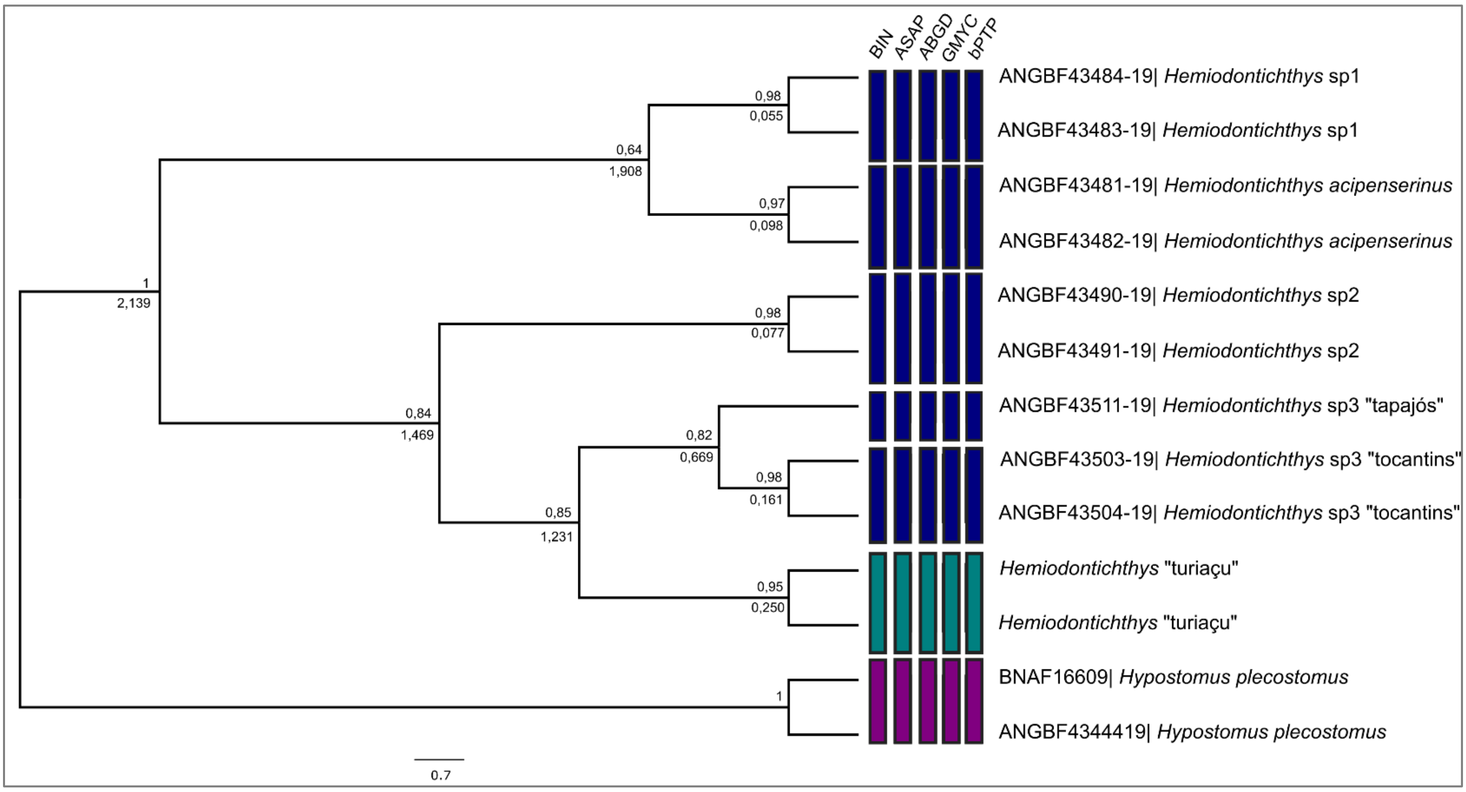

Figure 3. Bayesian Inference Tree for de gene *Cox*1 to populations of *Hemiodontichthys acipenserinus*. Color bars represent the results of species delimitation analyses. Number above the branches indicate the posterior probability values and number below indicate the divergence time.

The results obtained here confirm the monophyly of *Hemiodontichthys*, as well as the existence of different evolutionary lineages, including the Turiaçu River population, corroborating the hypothesis of cryptic species (COVAIN; FISCH-MULLER, 2007; CARVALHO et al., 2018). Although the species has a wide distribution throughout the Amazonian rivers in Brazil, the Guianas, and Peru, this distribution is fragmented (MENDONÇA, 2012; CARVALHO et al., 2018). This habitat discontinuity may be a factor in isolating these populations, consequently promoting vicariance and allopatric speciation (ALBERT; REIS, 2011).

The divergence time observed here corroborates other findings for the region with other fish species, such as *Schizodon dissimilis* and *Prochilodus lacustris* (ABREU et al., 2020b), where it was identified that the last 1 Ma was of great importance for the distribution and consequent speciation of freshwater fish species in the state of Maranhão (ABREU et al., 2019, 2020a). Events such as marine transgressions and regressions, associated with geomorphological events and headwater capture, were identified as having a great influence on the study area (ABREU et al., 2019, 2020a). Therefore, they may have influenced the emergence of this new OTU identified here.

Furthermore, the proximity to the population of the Tocantins basin, more specifically, the Guamá River, corroborates the hypothesis of dispersal through paleobasins between Amazonian and northeastern populations, via the rivers of Maranhão. This is because it is a lowland region (ABREU et al., 2019, 2020a, 2020b).

However, more morphological studies are needed to identify characters that can actually differentiate these populations into species. Although Isbrücker and Nijssen (1974) described several diagnostic characters for the genus and found great variation in morphometric characters, they were unable to differentiate populations into species. This has been the case in other studies involving morphological and morphometric data from populations of this species (MENDONÇA, 2012).

The difficulty in sampling this species can also be a limiting factor in delineating its cryptic species and, consequently, in describing new species. As the analysis of new populations progresses, doubts about monotypicity, as well as about the relationship between populations, may arise. For example, do the populations distributed in northeastern Brazil comprise a single lineage? Are this or these lineages close to the Amazonian lineages?

However, the results found here, combined with the results already existing in the literature, indicate that analyses with greater geographic coverage with different populations of this species can help in elucidating these questions. However, the need for integration of different data is evident. Carvalho et al. (2018), combining morphological, molecular, and cytogenetic data, managed to identify the occurrence of five lineages represented by distinct populations. These data suggest that only the integration of different data sources may be able to elucidate this species complex.

With the emergence of new methodologies, especially in the field of molecular biology, this species may become an excellent model for the use of genomic data in the species identification process.

5 Conclusions

The results presented here represent another piece in the puzzle that is the history of *Hemiodontichthys*. Despite recognizing the monophyly of the genus, our results indicate the presence of a possible new species and corroborate previous findings that suggest different lineages occurring within the genus. However, a complete taxonomic revision of the genus is necessary, with the widest possible distribution coverage and integrative analyses (morphology, morphometry, osteology, and molecular) to elucidate the monotypic status of *Hemiodontichthys acipenserinus*.

CREDIT AUTHORSHIP CONTRIBUTION STATEMENT

JMSA contributed to Conceptualization, Field sample, Data curation, Formal analysis, Methodology, Project administration, and Writing. WSP contributed to the Field sample, Data curation, Formal analysis, Methodology, Project administration, and Writing. LT contributed to Conceptualization, Data curation, Formal analysis, Methodology, Project administration, and Writing.

DECLARATION OF INTEREST

The authors disclose that they have no known competing financial interests or personal relationships that could have appeared to influence the study reported in this manuscript.

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