SUPPLEMENT

REVISTA DE Biología Tropical

https://doi.org/10.15517/3bqqkx82

First record and range extension of *Metachromadora* (*Metachromadora*) *chandleri* (Chitwood, 1952) Timm, 1961 (Nematoda: Desmodoridae) from the Pacific coast of Costa Rica, with comments on its taxonomical status

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Received 12-VIII-2025. Corrected 21-IX-2026. Accepted 22-IX-2026.

ABSTRACT

Introduction: Costa Rican marine nematofauna has been poorly studied despite it is one of the most abundant and numerous group in sediment samples.
Objective: To report the first finding of *Metachromadora chandleri* from Costa Rica, on the Pacific coast.
Methods: Fresh samples of several marine substrates from the North Pacific Costa Rican coasts were analyzed to extract the nematodes; they were identified to genus level. Key features were photographed, phylogenetic analyses were done with the obtained sequences.
Results: Four individuals from two locations matched the description of *M. chandleri*; we obtained the first three COI sequences of this species.
Discussion: This is the first report of this species in Costa Rica and the second for the Pacific, but it is more widespread in the Atlantic. Some comments on the taxonomical status, molecular knowledge on the genus and distribution of the species are given.
Conclusion: *Metachromadora chandleri* is present on both coasts of the American continent with most reports from the Atlantic; the species are scarcely represented in molecular databases. This first record of *M. chandleri* in Costa Rica reinforces the need of further local studies to reveal the diversity of marine taxa and enrich our understanding of the global distribution of species.

Key words: Área de Conservación Guanacaste; *Ichtyodesmodora*; marine species; *Metachromadora parasitifera*; sequences.

RESUMEN

Primer registro y ampliación de rango de *Metachromadora chandleri* (Chitwood, 1952) Timm, 1961 (Nematoda: Desmodoridae) de la costa pacífica de Costa Rica con comentarios sobre su estado taxonómico

Introducción: La nematofauna marina costarricense ha sido poco estudiada a pesar de ser uno de los grupos más abundantes y numerosos en muestras de sedimentos.
Objetivo: Reportar el primer hallazgo de *Metachromadora chandleri* en Costa Rica, de la costa Pacífica.
Métodos: Se analizaron muestras de varios sustratos marinos de las costas costarricenses del Pacífico Norte para extraer los nematodos, se identificaron a nivel de género y las características clave se fotografiaron. Se realizaron análisis moleculares con las secuencias obtenidas.
Resultados: Cuatro individuos de dos localidades coincidieron con la descripción de *M. chandleri* y se obtuvieron las tres primeras secuencias genéticas COI de la especie.
Discusión: Este es el primer reporte de dicha especie en el país y el segundo del Pacífico, está más ampliamente distribuida en el Atlántico. Se comparten algunos comentarios sobre el estado taxonómico, la representación del género en bases moleculares y la distribución de esta especie.
Conclusión: *Metachromadora chandleri* está presente en ambas costas del continente americano, con la mayoría de los informes en el Atlántico. La representación del género en bases moleculares es escasa. Este primer registro de *M. chandleri* en Costa Rica evidencia la necesidad de realizar más estudios locales para revelar la diversidad marina y enriquecer el conocimiento de la distribución global de especies.

Palabras claves: Área de Conservación Guanacaste; especies marinas; *Ichtyodesmodora*; *Metachromadora parasitifera*; secuencias.

INTRODUCTION

Costa Rican biodiversity has been largely studied for several decades (Avalos, 2019; Wehrtmann & Cortés, 2009), however, marine nematofauna is vastly unknown. Records of Nematoda are common in Costa Rican marine surveys but few dealt with species identification, hence, only five free-living species and five parasitic species have been reported (Sánchez-Monge & Cortés, 2024; Solano-Barquero et al., 2023).

With 28 valid (Pinto & Neres, 2020) and ten invalid species (Maria et al., 2014), *Metachromadora* is a challenging genus subdivided into five subgenera: *Bradylaimus*, *Metachromadora*, *Metachromadoroides*, *Metonyx* and *Neonyx*. However, this subdivision remains controversial and has not been universally accepted. Tchesunov (2014) elevated each subgenus to genus rank, arguing that subgenera are rarely recognized in marine nematodes and that the morphological differences among these taxa are sufficient to justify their recognition as distinct genera.

Following these criteria, Tchesunov's (2014) diagnosis of the genus, i.e., "Head cuticle longitudinally striated. Cephalic setae short and may be reduced to papillae. Amphideal fovea strongly cuticularized. Distinct dorsal tooth in buccal cavity. Posterior pharyngeal bulb well-developed with a thick internal cuticular lining often partitioned into two or three sections", would encompass nine species (Tchesunov, 2014). In contrast, under the subgeneric classification, *Metachromadora* (*Metachromadora*) Filipjev, 1918 is defined primarily by the presence of longitudinal striations on the head and comprises only three species: *M. chandleri* (Chitwood, 1952) Timm, 1961, *M. itoi* Kito, 1978, and *M. macrouteura* Filipjev, 1918 (Maria et al., 2014). Moreover, when the five subgenera are considered collectively, Maria et al. (2014) recognized a total of 25 species, whereas Tchesunov (2014) recognized 31 species when the corresponding taxa, treated as separate genera, are combined. This discrepancy alone illustrates the taxonomic complexity of the group.

As part of the ongoing survey on marine nematofauna within the BioMar-ACG project (Cortés & Joyce, 2020), we report the first finding of *M. chandleri* in Costa Rica, which is also the second report in the Pacific coast of the

continent. This is the sixth free-living marine nematode species identified for Costa Rica.

MATERIALS AND METHODS

Several locations and substrates have been sampled since 2023 to study the marine nematofauna of the Área de Conservación Guanacaste; Tomás Bay (10°55'27.8"N & 85°43'03.5"W) and Playa Pochote (11°01'59.9"N & 85°43'03.9"W) among them. Sediment core samples (i.d. 27 mm, pushed down 5–7 cm) were obtained at each location and stored in 50 ml Falcon-tubes at -80 °C for further analyses. After defrosting at room temperature, 2 ml subsamples were analyzed with a stereomicroscope Luxeo 6Z; nematodes were hand-picked and mounted on temporary slides for videovouchering in an ICOE BE520T microscope equipped with an Omax digital camera model A35140U. Pictures and videos were obtained with the program ToupLite version 2.1.19728.20211022. All analyses were performed in the Center for Research in Marine Science and Limnology (CIMAR), University of Costa Rica but the extraction and sequencing of the COI region was done at The Biodiversity Institute for Conservation Synthesis, University of Guelph, Ontario, Canada. COI sequences were analyzed using Geneious Prime® 2026.0.2. Sequences were MAFFT aligned (Katoh & Standley 2013), and trimmed to the same length for the generation of the phylogenetic tree. A Maximum Likelihood tree was generated using the GTR + gama substitution model (selected with the online tool IQ-TREE), 200 bootstraps.

Image edition was done with the GNU Image Manipulation Program (GIMP 2.10.30) and the measurements were done from photographs with the program UTHSCSA Image Tool for Windows Version 3.00. The rounding off of measurements and De Man's ratios (a, b and c) was made sensu De Ley as detailed in Mokievsky et al. (2024).

RESULTS

Four specimens identified as *Metachromadora chandleri* were isolated from two locations in the North Pacific coasts of Costa Rica, Tomás Bay and Playa Pochote, two specimens from each site. Females were not found and one of the specimens was a juvenile, hence, measurements were based on the three males (Fig. 1): body length and De Man's ratios were as follows: n = 3, L: 1061–1394 µm, a: 19–21, b: 4.5–6.0, and c: 11–13.

The GenBank accession numbers of our COI sequences (658bp in length) are PX551897 and PZ357246 (one male, one juvenile from Playa Pochote) and PX551898 (male from Tomás Bay). Both sequences from Playa Pochote are 99.39 % similar to each other (6 bp different) and 98.94 % similar to Tomás Bay's sequence, showing only 7 bp differences. The P-distances between our sequences of *M. chandleri* and close identified species are shown in Table 1, the phylogenetic tree is shown in Fig. 2.

DISCUSSION

Taxonomy: Key features match with all descriptions of what it is considered *M. chandleri* (see taxonomic information below), nonetheless, specimens were generally smaller than previously recorded; L: 1061–1394 µm, a: 19–21, b: 4.5–6.0, and c: 11–13 (this paper) vs L: 1270–1350 µm, a: 22–23, b: 6.4–7.6, and c: 14–17 (*Metachromadora parasitifera* Timm, 1952) and L: 1300–1335 µm, a: 21–22, b: 5.8–6.1, and c: 14–15 (Gerlach, 1955). The smaller size of our specimens may be due to storage conditions, i.e. -80 °C, as low temperatures tend to shrink biological material. However, phenotypic plasticity and the specific environmental conditions at each collection site cannot be excluded as potential contributors to the observed differences, as demonstrated in other

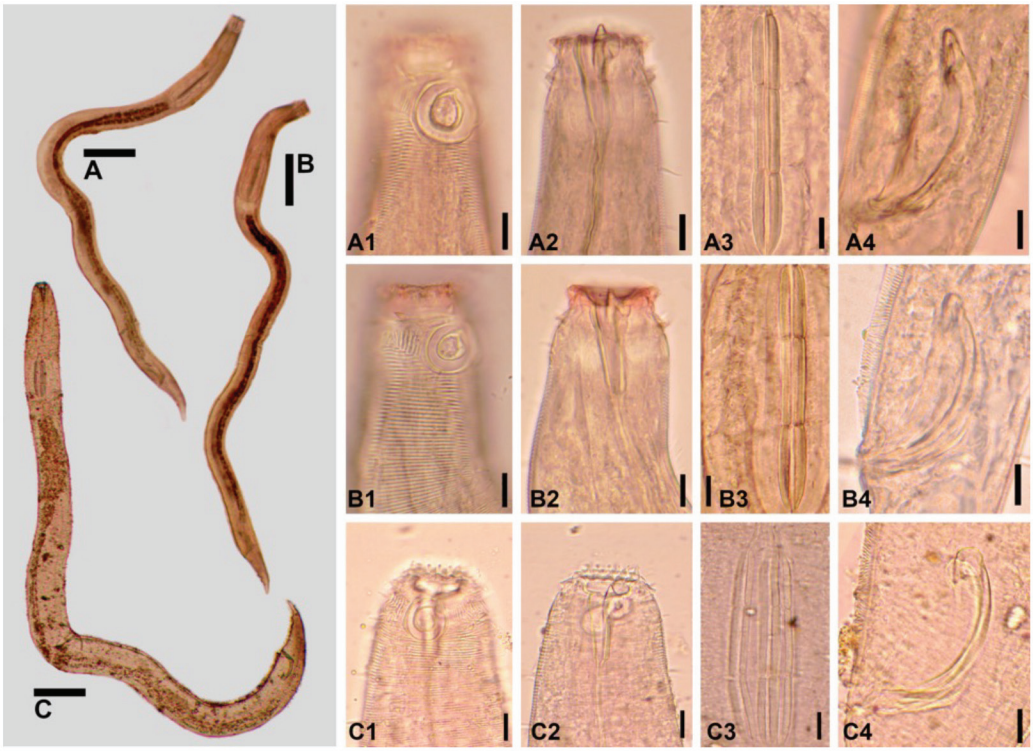


Fig. 1. Males of *Metachromadora* (*Metachromadora*) *chandleri* found in Tomás Bay (A and B) and Playa Pochote (C). A1, B1, C1: amphids and longitudinal anterior striations. A2, B2, C2: mouth morphology. A3, B3, C3: the tripartite division of the esophageal bulb sclerotization. A4, B4, C4: details of spicules. Scale bars of A, B and C: 100 µm; A1-A4, B1-B4 and C1-C4: 10 µm.

Table 1
P-distances between *Metachromadora chandleri* and the close related species *Onyx litorale*.

	KC014985.1 *O. litorale*	KC014986.1 *O. litorale*	PX551897 *M. chandleri*	PZ357246 *M. chandleri*
KC014985.1 *O. litorale*	1			
KC014986.1 *O. litorale*	0.005	1		
PX551897 *M. chandleri*	**0.202**	**0.205**	1	
PZ357246 *M. chandleri*	**0.207**	**0.210**	0.006	1
PX551898 *M. chandleri*	**0.204**	**0.207**	0.010	0.010

Values in bold show the interspecific P-distances much higher (p-distance > 0.02) than expected for intraspecific variation.

marine nematodes (Apolônio Silva De Oliveira et al., 2017; Armenteros et al., 2009).

One of the examined males (Fig. 1C) is remarkably large, surpassing the maximum body length documented in previous descriptions of *M. chandleri*. More strikingly, it exhibits conspicuous asymmetry in the amphideal foveae, differing in both size and shape (Fig 1 C1 vs. Fig. 1 C2). Although sexual differences in amphid morphology have been documented in marine nematodes (Leduc & Wharton, 2010; Tu et al., 2011), we are not aware of any previous reports of this type of asymmetry in a single individual. This condition

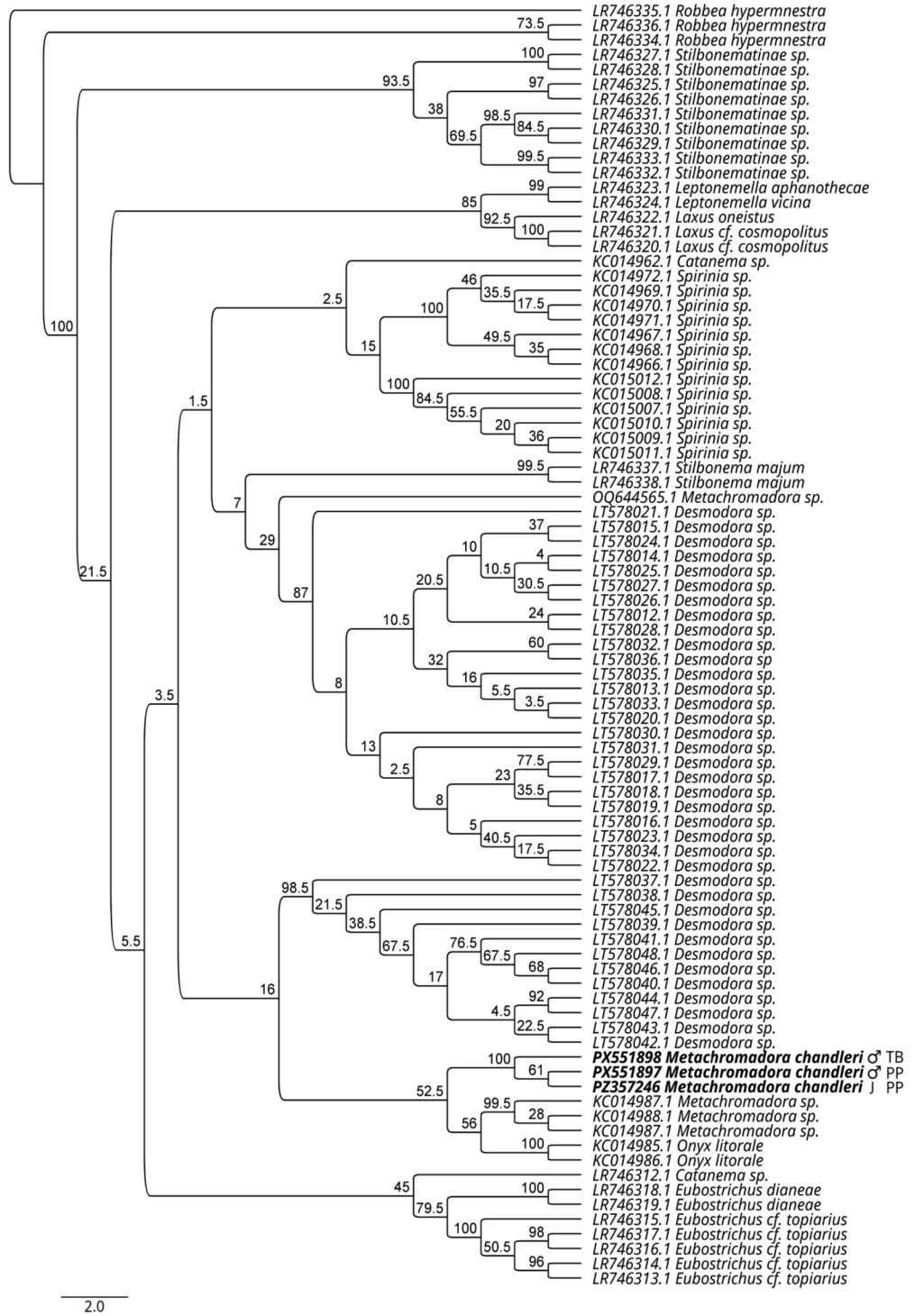


Fig. 2. COI Maximum Likelihood tree based on 624 bp showing the three new *Metachromadora* (*Metachromadora*) *chandleri* sequences from specimens found in Tomás Bay (TB; B male from Fig. 1) and Playa Pochote (PP), Costa Rica.

could represent an uncommon developmental anomaly or an overlooked form of intraspecific variation; alternatively, it may reflect a separate lineage, nonetheless, see the phylogenetic discussion below. Despite this unusual feature, all other morphological traits agree with the published diagnosis and existing identification keys, supporting its assignment to *M. chandleri*. Additional collections will be required to clarify the taxonomic significance of this observation.

It should be noted that the limited number of specimens collected, the absence of females, and the quality of the supporting images acquired at intermediate magnifications precluded the observation and documentation of additional morphological characters. Consequently, only those features that could be reliably examined and documented are reported herein.

Metachromadora (*Metachromadora*) *chandleri*
(Chitwood, 1951) Timm, 1961
Syn. *Ichthyodesmodora chandleri*
Chitwood, 1951
Syn. *Metachromadora parasitifera*
Timm, 1952

Metachromadora chandleri was originally described by Chitwood in 1951 as *Ichthyodesmodora chandleri* based on one juvenile whose description includes a single drawing of the head region (Fig. 3A). Timm (1952) described *M. parasitifera* with illustrations of the anterior region of both sexes and the male tail. In 1955 Gerlach redescribed *I. chandleri* adding measurements of both, males and females, together with a plate of seven illustrations including four of the anterior region and one of the pharynx region. Subsequently, and considering that the longitudinal striations on the head differentiate the subgenus *Metachromadora*, Timm (1961)

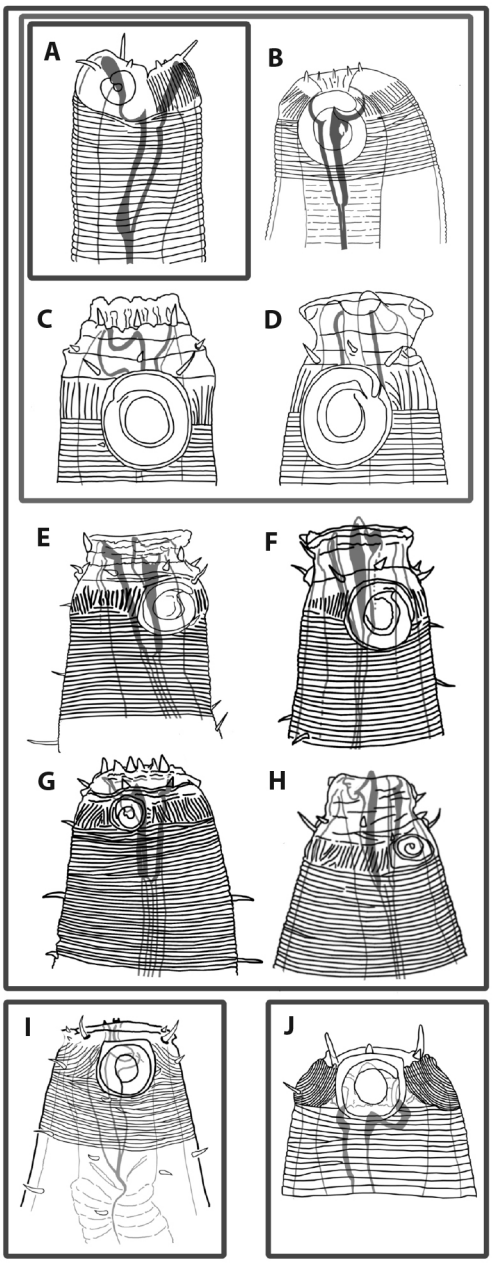


Fig. 3. Drawings of males and juveniles' anterior regions of *Metachromadora* (*Metachromadora*) species based on the original illustrations and new material. (A) Juvenile described as *Ichtyodesmodora chandleri* (Chitwood 1951) now *M. chandleri* (Timm 1961). (B) Male of *M. parasitifera* (Timm 1952), synonymized with *M. chandleri* by Timm (1961). (C) and (D) Males, redescription of *I. chandleri* (Gerlach 1955). (E) and (F), *M. chandleri*, males, fresh samples from Tomás Bay. (G) and (H) *M. chandleri* fresh samples from Playa Pochote, male and juvenile, respectively. (I) *M. itoi* Kito, 1978, male. (J) *M. macroteura* Filipjev, 1918, female (the male anterior region was not illustrated in the species description).

transferred *I. chandleri* to *Metachromadora* and synonymized *M. parasitifera* with *M. chandleri.*

From the three species that belong to the subgenus *Metachromadora*: *chandleri*, *itoi* and *macrouteura* (*sensu* Maria et al. 2014) only *M. chandleri* has longitudinal lines that are almost perpendicular to the annuli, which are evident in *M. parasitifera* (see Timm 1952 and Fig. 3), hence, we support the synonimyzation proposed by Timm in 1961. Nonetheless, *M. parasitifera* is still an accepted species in the World Database of Nematodes (Nemys, 2026) and the World Register of Marine Species (WoRMS Editorial Board [WoRMS], 2026) and it is, apparently, listed as a valid species by Maria et al. (2014) and Pinto & Neres (2020). Interestingly, Maria et al. (2014) did not include *M. parasitifera* in their key to valid species; remarkably and following such key, the resulting identification of *M. parasifera sensu* Timm 1952 would be *M. chandleri* based on the pronounced longitudinal striations in the head (subgenus *Metachromadora*, not annotated in the species list), sexual dimorphism in amphids (those are equal in *M. macroteura*) and at least 12 but less than 15 preanal supplements (21–25 in *M. itoi*).

Phylogenetic data: Nominal *Metachromadora* species are scarcely represented in sequences databases, to current day and excluding ours, there were 62 nucleotides' and 14 proteins' entries under "*Metachromadora*" (Taxonomy ID: 70431) in the National Library of Medicine (NIH). However, only 13 sequences [in brackets] are linked to an identified taxon, namely *M. gerlachi* [1], *M. orientalis* [2], *M. remanei* [8], *M. suecica* [1], *M. xiamenensis* [1] and *M. cf vulgaris/minor* [1], while 47 sequences are labelled as "*Metachromadora* sp.". Out of the 62 entries, 51 are rDNA sequences (12 LSU and 39 SSU) and 11 are COI sequences, among the latter, all but two (*M. gerlachi* and *M. orientalis*) belong to unidentified species. There are also three *Metachromadora* mitochondrial sequences available in the BOLDSystems database that show a similarity of 82 %, 84 % and 94 % with our sequences; other desmodorids show a maximum similarity of 84 %. Unfortunately, such sequences are not public.

A total of 87 COI sequences, 624 bp long, were used to generate the phylogenetic tree. The Maximum Likelihood tree (Fig. 2) shows our three new sequences clustering together with a member from the same subfamily Spirininae, *Onix*, which agrees with the review of the family Desmodoridae published by Armenteros et al (2014). Another *Metachromadora* sp. sequence, i.e. GBOQ644565, appeared in a far distant position, probably due to missidentification. The family Desmodoridae is highly diverse, however, COI sequences are represented only to genus level, as observed in our tree.

Derycke et al. (2010) proposed K2P distance thresholds of < 2 % for conspecific marine nematodes, 2–5 % as a potential "gray zone" that may include cryptic taxa requiring additional evidence, and 5–10 % for distinct species within the same genus. Although the observed P-distances in our specimens (Table 1) should be interpreted with caution because COI data for *Metachromadora* and closely related species remain scarce, the interspecific distances largely exceeds the 2 % threshold. Conversely, the estimated divergence between our *M. chandleri* specimens (Table 1) fall within the range for intraspecific distances reported for marine taxa. However, given the morphological variations and despite the molecular evidence, further studies should be conducted to cover potential population's phenotypic variability.

Distribution and habitat: *Metachromadora chandleri* has been informed mostly in the Atlantic Ocean ranging from Chesapeake Bay and Texas, U.S.A. (Chitwood, 1951; Timm, 1952) and the Gulf of Mexico, Mexico (Hope, 2009) to the coast of Brazil (Sistema de Informação sobre a Biodiversidade Brasileira [SiBBr], 2025; Venekey et al., 2010). Gerlach (1955) redescribed the species with specimens found in La Unión, El Salvador, Pacific Ocean. Our finding extends southward the range of the species in the Pacific.

The reported habitats of *M. chandleri* are muddy bottoms (Timm, 1952), subemergent

vegetation (Chitwood, 1951) and muddy sand at the intertidal zone (this paper). Interestingly, georeferenced locations in Brazil correspond to the Curucá River at approximately 13 km upriver (SiBBr, 2025), while Costa Rican specimens were found in two bays, one of which was near a mangrove forest at a river delta.

Author contribution statement: ASM collected the samples, isolated and documented the data of the specimens, made the plates and illustrations of this document and the first drafts. DASO ran the phylogenetic analyses, calculated and constructed the P-distances table and did the taxonomical identification. JC facilitated the access to the sampling sites and provided several suggestions along the process. All authors (ASM, DASO, and JC) contributed to the analysis and discussion of the manuscript.

Ethics statement: The authors declare that they all agree with this publication and that they have made contributions that justify their authorship; that there is no conflict of interest of any kind; and that they have complied with all relevant ethical and legal requirements and procedures. All sources of funding are fully and clearly detailed in the acknowledgements section. The respective signed legal document is in the journal's archives.

ACKNOWLEDGMENTS

We thank Frank Joyce and Jeffrey Sibaja for their efforts and guidance of BioMar-ACG, project B9508, Universidad de Costa Rica (UCR). We also thank Yelba Vega and Gilberth Ampié for their work and collaboration during sampling and the corresponding data registration; Alejandro Masís and Roger Blanco for the collecting permits from the Ministry of Environment and Energy of Costa Rica (MINAE): R-SINAC-ACG-PI-043-2015/043-2016/040-2017/004-2019/026-2020/038-2021/051-2022/045-2023/026-2024/037-2024/041-2024. The access to genetic material is permitted by resolution-047/CBio-68-2022 of the Institutional Commission on Biodiversity, Universidad de Costa Rica.

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