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New and previously known ectoparasitic monogenoids (Platyhelminthes) on native and non-native fishes from tributaries of the Usumacinta River basin (southern Mexico), a Neotropical transition zone

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ABSTRACT

During a research on morphological diversity of gill ectoparasites on native and non-native fishes from tributaries (Palizada, El Recreo and Lacantún rivers) of the Usumacinta River Basin in the states of Campeche, Tabasco, and Chiapas (southern Mexico), the following monogenoids were found: *Icelanonchohaptor tropicalis* n. sp. on Usumacinta buffalo *Ictiobus meridionalis* (Günther, 1868) (Catostomidae); *Heteropriapulus simplexiodes* n. sp. and *Heteropriapulus heterotylioides* n. sp. on catfishes *Pterygoplichthys pardalis* (Castelnau, 1855) (Loricariidae) (type host) and *Pterygoplichthys disyunctivus* (Weber, 1991); *Ligictaluridus mirabilis* (Mueller 1937; Klassen and Beverley-Burton1985 from the southern blue catfish *Ictalurus meridionalis* (Günther, 1864) (Ictaluridae); *Aristocleidus mexicanus* Mendoza-Franco and Vidal-Martínez, 2001 on *Eugerres mexicanus* (Steindachner, 1863) (Gerreidae) (all monogenoidean species in the Dactylogyridae); and *Diplectanocotyla megalopis* Rakotofiringa and Oliver1987 (Diplectanidae) on tarpon *Megalops atlanticus* Valenciennes, 1847 (Megalopidae). The new species of *Icelanonchohaptor* and *Heteropriapulus* are herein described for the first time from a native catostomid and non-native *Pterygoplichthys* spp., respectively. While *I. tropicalis* n. sp. and *L. mirabilis* are morphologically comparable with their congeners from the Nearctic (i.e., United States and Canada), all other monogenoids exhibited Neotropical affinities. Present study shown that the gill monogenoids on native and non-native fishes in the Neotropical Mexican transition zone of the Usumacinta River basin are equally represented by species with Nearctic and Neotropical affinities including those adapted to freshwater environment in this area from marine ancestry.

1. Introduction

The upper Usumacinta ecoregion, centrally located in Mesoamerica within eastern Chiapas and southern Tabasco in Mexico, and northwestern of Guatemala (this area belongs to the Neotropical Mexican Transition Zone according to Morrone et al., 2022) is characterized by its large size (73, 945 km^2), ecological heterogeneity and high biological diversity mixing that have resulted from southward and northward migrations of multiple taxa from the Nearctic and Neotropical biotas (see Soria-Barreto et al., 2018; Jiménez-López et al., 2023). In this scenario, the fish species richness from the Usumacinta is influenced by its hydrological dynamics, geological history and its connectivity with the Gulf of Mexico and it is composed of 50 families and 172 species, of which 75 species are freshwater (i.e., cichlids, characids and catostomids among others) 8 estuarine (i.e., megalopids and gobiids) and 89 marine (i.e., centropomids, haemulids, belonids and gerreids) (see Granados-Dieseldorff et al., 2012; Soria-Barreto et al., 2018). The non-native fish species are also inhabiting the area, some of them (i.e., the African tilapias [Cichlidae] and Asian carps [Cyprinidae]) part of the artisanal fishery except of the South American suckermouth armored catfishes *Pterygoplichthys* spp. (Loricariidae) (Barrientos et al., 2018). During 2015 and 2021, native and non-native fish species from the

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Palizada, Recreo and Lacantún rivers (tributaries of the Usumacinta River basin) located in the Mexican southern states of Campeche, Tabasco, and Chiapas, respectively, were collected for investigating their gill monogenoidean parasites. Here, we provided some supplemental observations, data on morphometry variability of individual species from different hosts, and new descriptions of the following species found: *Icelanonchohaptor tropicalis* n. sp. on native *Ictiobus meridionalis* (Catostomidae); *Heteropriapulus simplexioides* n. sp. and *Heteropriapulus heterotylioides* n. sp. on the introduced catfishes *Pterygoplichthys pardalis* (type host) (Castelnau) (Loricariidae) and *Pterygoplichthys disyunctivus* (Weber, 1991); *Ligictaluridus mirabilis* (Mueller 1937; Klassen and Beverley-Burton (1985) is reported on native southern blue catfish *Ictalurus meridionalis* (Günther, 1864) (Ictaluridae) from the Recreo (new host record) and Lacantún (new host and locality records) rivers; *Aristocleidus mexicanus* Mendoza-Franco and Vidal-Martínez, 2001 is reported on native *Eugerres mexicanus* (Steindachner, 1863) (Gerreidae) from the Recreo river (new locality record); and *Diplectanocotyla megalopis* Rakotofiringa and Oliver (1987) is reported on tarpon *Megalops atlanticus* Valenciennes, 1847 (Megalopidae) from the Recreo river (new geographical and locality records), this latter host species with circumtropical distribution. Additionally, the biogeography of all these monogenoidean species from the called Neotropical Mexican transition zone is briefly discussed in relation with their affinities to North and South America.

2. Materials and methods

In most cases, fishes were collected by fishermen from the Palizada, Recreo, and Lacantún rivers (tributaries of the Usumacinta River Basin) in the states of Campeche, Tabasco, and Chiapas, respectively (southern Mexico), from June 2015 to 2021. Permit for ictalurid fish collections from Lacantún river were issue by the Secretaría del Medio Ambiente y Recursos Naturales (SEMARNAT), Mexico (permit number: SGPA/DGVS/03492). The host's gill basket was removed soon after capture at the site of collection and placed in vials containing 4% formalin for relaxation and fixation of attached helminths. The vials containing the gills and respective fluids were labelled, shaken vigorously, and subsequently shipped to the Laboratory of Aquatic Parasitology of the Institute of EPOMEX (Autonomous University of Campeche, Mexico) for study. In the laboratory, parasites were subsequently detached from the gills or sediment using a small probe under dissecting microscope Leica EZ4, mounted unstained on microscope slides in Gray and Wess medium or in a mixture of lactic-acid (LA) and glycerin-ammonium picrate (GAP), and then remounted in Canada balsam (Mendoza-Franco et al., 2013) to obtain measurements and line drawings of haptoral structures and the copulatory complex; other specimens were stained with Gomori's trichrome and mounted in Canada balsam for observing and measuring internal soft organs. Illustrations were made with the aid of a drawing tube, using a Leica microscope DM 2500 with Nomarski interference contrast. Measurements, all in micrometers (μm), represent straight-line distances between extreme points of the structures measured which are presented as the mean followed by the range and number (n) in parentheses. Definitions of ecological terms (prevalence and mean intensity) are those suggested by Bush et al. (1997). Type and voucher specimens were deposited in the National Helminthological Collection of Mexico (CNHE), Institute of Biology, National Autonomous University of Mexico, Mexico. Fish hosts were identified by the collectors using various resources available at the respective collection sites and facilities; scientific and common names of fishes were also verified in Miller (2009), and Froese and Pauly (2023).

3. Results

3.1. Qualitative descriptors of dactylogyrid parasites on freshwater fishes from the Usumacinta River basin

All catostomid, ictalurid, loricariid, gerreid and megalopid host species examined were parasitized with monogenoids. A total of six monogenoid species (three new) were identified, two of which were found simultaneously on the introduced loricariids *P. pardalis* (type host) and *P. disyunctivus* (see Table 1).

3.2. Morphology of monogenoids

3.2.1. Taxonomic summary

Class Monogenoidea Bychowsky, 1937.
Subclass Polyonchoinea Bychowsky, 1937.
Order Dactylogyridea Bychowsky, 1937.
Dactylogyridae Bychowsky, 1933.
Icelanonchohaptor Leiby et al., 1972
Species: *Icelanonchohaptor tropicalis* n. sp. (Fig. 1A–F)
See comparative measures in Table 2.

Type host: Usumacinta buffalo *Ictiobus meridionalis* (Günther, 1868) (Catostomidae: Cypriniformes).

Site of infection: Gill lamellae.

Prevalence and intensity of infection: 2 fish infected of 8 examined (25%); mean intensity of infection 1.5 parasites per infected fish.

Type locality: Recreo river (tributary of the Usumacinta River basin) located in the municipality of Tenosique, in the state of Tabasco (17°28′40.05″N; 91°25′47.8″W) southern Mexico.

Specimens deposited: Holotype, CNHE (12041); 2 paratypes, CNHE (12042).

Etymology: The specific name of this species relates to the tropical region from which this parasite was collected.

Description (based on 1 specimen mounted unstained in Gray and Wess medium and 2 stained with Gomori's trichrome and mounted in Canada balsam). Body fusiform, with broad cephalic region including well developed head organs in lateral cephalic lobes, conical trunk and elongate tapered peduncle; greatest width at level of gonads. Approximately 7–9 cephalic glands in anterolateral trunk, extending from level of the posterior margin of pharynx to anterior region of the copulatory complex. Eyes four; anterior pair closer together than members of posterior pair; accessory chromatic granules absent. Mouth subterminal surrounded by muscles (observed only in paratypes). Pharynx pyriform wide, covered with delicate frills in rows; esophagus moderately long. Haptor cup-shaped. Hooks similar in shape and size; each with uniform shank, perpendicular thumb with tip slightly directed posteriorly and recurved shaft and point; filamentous hook (FH) loop about 60% shank length. Common genital pore ventral at level of intestinal bifurcation. Male copulatory organ (MCO) Y-inverted shaped, hooked at distal end, sharply pointed. Accessory piece robust, slightly arched on its midportion with Y-shaped distal end. Testis subspherical; ovate seminal vesicle lying on body midline; vas deferens not observed; prostatic reservoir short. Germarium looping right intestinal cecum; oviduct, uterus, oötype and Mehlis' gland not observed. Vaginal opening dextromarginal, ventral, comprising of distal sclerotized corrugated vestibule, large, followed by proximal conical chamber in continuity to slightly sclerotized vaginal tube, delicate and coiled, before discharging into seminal receptacle situated anterior to germarium. Vitelline follicles densely scattered throughout trunk except in regions of reproductive organs. Egg ovate with short filament.

3.2.1.1. Remarks. Present specimens found on *I. meridionalis* are morphologically consistent with generic characteristics (i.e., cephalic glands in 2 bilateral groups in anterolateral trunk, germarium looping right intestinal cecum, vagina dextroventral, MCO and accessory piece

Table 1
Monogenoids (Platyhelminthes) parasitizing gills of native and non-native freshwater fish species from the Usumacinta River basin (Southeastern Mexico).

Hosts						
Parasite	*Ictiobus meridionalis* (Catostomidae)	*Eugerres mexicanus* (Gerreidae)	*Megalops atlanticus* (Megalopidae)	*Ictalurus meridionalis* (Ictaluridae)	*Pterygoplichthys pardalis*[a] (Loricariidae)	*Pterygoplichthys disyunctivus* (Loricariidae)
Icelanonchohaptor tropicalis n. sp.	+	–	–	–	–	–
Heteropriapulus simplexioides n. sp.	–	–	–	–	+	+
Heteropriapulus heterotylioides n. sp.	–	–	–	–	+	+
Ligictaluridus mirabilis (Mueller 1937; Klassen and Beverley-Burton (1985)	–	–	–	+	–	–
Aristocleidus mexicanus Mendoza-Franco and Vidal-Martínez, 2001	–	+	–	–	–	–
Diplectanocotyla megalopis Rakotofiringa and Oliver (1987)	–	–	+	–	–	–

[a] Type host.

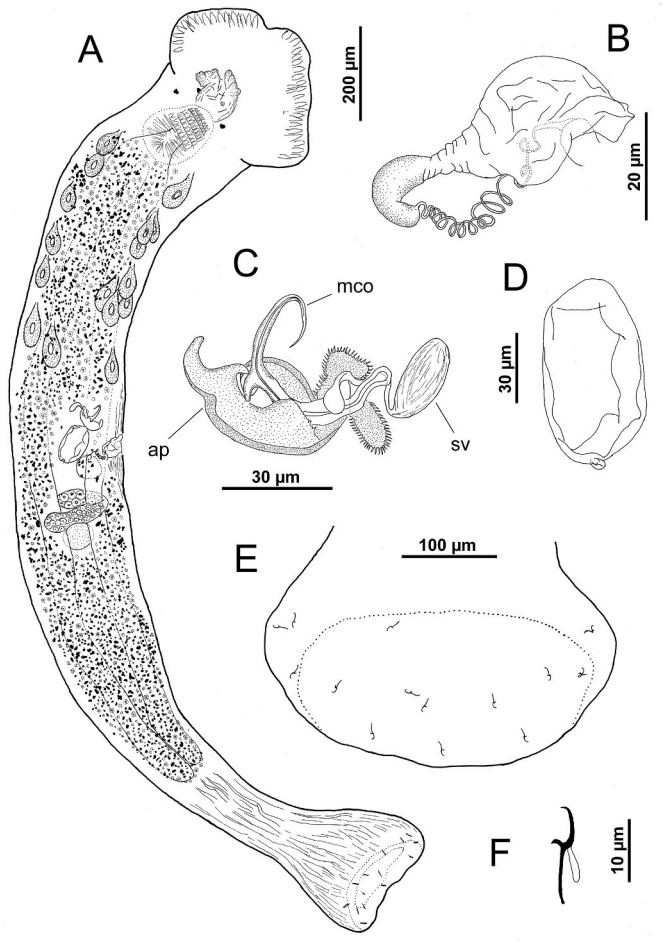

Fig. 1. *Icelanonchohaptor tropicalis* n. sp. on the Usumacinta buffalo *Ictiobus meridionalis* (Catostomidae) from the Usumacinta river basin (southern Mexico). A – whole mount (composite, dorsal view); B – vagina; C – copulatory complex (ventral view); D – egg; E – Haptor; F – Hook. Abbreviations: mco – male copulatory organ; ap – accessory piece; sv – seminal vesicle.

articulated, haptor cup-shaped, 7 pairs of hooks, and anchors and bars absent) of *Icelanonchohaptor* that are exhibited by its type and only known species of the genus, *I. icelanonchohaptor* on *Ictiobus cyprinellus* from the Missouri River in North Dakota and South Dakota, USA (see Leiby et al., 1972). Thus, former specimens are accommodate within this latter genus as *I. tropicalis* n. sp. This new species differs most notably

Table 2
Measurements of *Icelanonchohaptor* spp. (Monogenoidea: Dactylogyridae) parasitizing the gill lamellae of *Ictiobus* spp. (Catostomidae) from USA and the Usumacinta River (southern Mexico).

Parasite/host	*Icelanonchohaptor tropicalis* n. sp. on *Ictiobus meridionalis*	*Icelanonchohaptor icelanonchohaptor* on *Ictiobus cyprinellus*
Localities	Usumacinta	Missouri River in North and South Dakota, USA[a]
Body length	2,952 (2,080–3,900; n = 3)	4,970 (3,930–5,780)[b]
Greatest width	225–262	952 (792–1,060)
Pharynx length	140–150	–
Pharynx width	112–115	473 (341–561)
Haptor width	250–262	922 (704–1,160)
Hook length	15 (n = 10)	18–19
MCO length	39 (37–42; n = 3)	78 (56–87)
Accessory piece length	48 (46–49; n = 3)	86 (64–98)
Germarial length	68	–
Germarial width	70–75	246 (220–264)[c]
Testis length	22	–
Testis width	28–55	222 (187–242)[c]
Egg length	85	112–135
Egg wide	48	–

[a] Measurements from the original description.
[b] Converted from mm to µm from the original description.
[c] Greatest diameter.

from *I. icelanonchohaptor* in having smaller size of the body (2,080–3,900 vs 3,930–5,780 long in *I. icelanonchohaptor*), haptor (250–262 vs 704–1,160 width in *I. icelanonchohaptor*), pharynx (112–115 vs 341–561 width in *I. icelanonchohaptor*), accessory piece (46–49 vs 64–98 length in *I. icelanonchohaptor*) and hooks (15 vs 18–19 long in *I. icelanonchohaptor*) (see Table 2), 7–9 cephalic glands on each side on the trunk (75 cephalic glands in *I. icelanonchohaptor*), and by the general morphology of the vagina, i.e., distal corrugated vestibule vs distal opening less differentiated in *I. icelanonchohaptor* (see Fig. 6 in Leiby et al., 1972, Fig. 1B in the present study), and by lacking hooks with shank flanged proximally (present *I. icelanonchohaptor*) (see Leiby et al., 1972; present study). The presence of "2 central hooks" on haptor is a generic characteristic clearly described and illustrated for *I. icelanonchohaptor* by Leiby et al. (1972). Although that position of hooks resulted in a significant distortion based on our specimen mounted in Gray and Wess'medium (as illustrated in Fig. 1E), we considered that it is in general agreement with that defined by Leiby et al. (1972).

Heteropriapulus simplexioides n. sp. (Fig. 2A–I)

Type host: *Pterygoplichthys pardalis* (Castelnau, 1855) (Loricariidae: Siluriformes).

Type locality: Palizada river (18°5′12.95″N, 92°5′27.25″W) (tributary of the Usumacinta River basin) in the state of Campeche (southern Mexico).

Site of infection: Gill lamellae.

Another host: *Pterygoplichthys disyunctivus* (Weber, 1991) from the Recreo river (17°28′40.05″N; 91°25′47.8″W) located in the municipality of Tenosique, in the state of Tabasco (southern Mexico). Prevalence and intensity of infection: 19 fish infected of 19 examined (100%); mean intensity of infection 11 parasites per infected fish from Palizada river; 11 of 11 fish examined from Recreo river (100%; 9).

Specimens deposited: Holotype, CNHE (12045); 33 paratypes, CNHE (12046); 10 voucher specimens on *P. disyunctivus* from the Recreo river in CNHE (12047).

Etymology: The specific name indicates the similarity of the copulatory complex of this species to that of *Heteropriapulus simplex* Li and Huang (2012).

Description (based on 10 specimens mounted unstained in Gray and Wess medium and 24 unstained with LA-GAP mixture; measurements of specimens on *P. disyunctivus* from the Recreo river are in brackets and those from the type locality are in parentheses): Body 164 (130–200; n = 25) [240 (120–305; n = 9)] long, fusiform; greatest width 60 (52–70; n = 5) [101 (55–120; n = 4)] usually in posterior trunk at level of gonads. Terminal cephalic lobes well developed, containing large head organ; 3 bilateral pairs of head organs lying posterior to cephalic lobes; cephalic glands indistinct. Accessory (melanistic) granules infrequent in cephalic region. Pharynx subspherical, 18–19 [26 (25–28; n = 3)] in diameter. Testis 8–10 x 10–13, ovate to pyriform; seminal vesicle tapered at each end, in left side of body near mid-length; prostatic reservoirs pyriform. Copulatory organ 42 (31–53; n = 26) [35 (28–48; n = 10)] long, with rounded base, elongated and slender sigmoid tube (distal region tapered), intertwined with accessory piece. Accessory piece 37 (31–43; n = 15) [28 (24–30; n = 4)] long, a single straight or arched unit. Germarium subspherical, 29 (24–35; n = 3) long, 24–25 wide. Vaginal pore mid-ventral; vaginal canal short, poorly sclerotized; seminal receptacle inconspicuous, immediately internal to vaginal pore. Vitelline follicles moderately dense. Peduncle broad to non-existent, slightly tapered posteriorly. Haptor 53 (45–60; n = 14) [64 (50–85; n = 5)] wide, heptagonal. Hooks 11 (10–12; n = 6) long, with upright acute thumb and slender shank. Ventral anchor 33 (31–37; n = 43) [35 (32–37; n = 15)] long, with flattened base, elongate shaft and point with recurved tip; base 10 (9–11; n = 13) [9 (8–11; n = 12)] wide; shaft and point of ventral anchors extending posteroventrally from haptor; anchor filament double, well developed (not illustrated). Dorsal anchor 20 (19–23; n = 25) [20 (19–21; n = 10)] long, with short to non-existent deep root, tapered superficial root, evenly curved shaft and elongate point extending past level of superficial root; base 7 (6–8; n = 10) [7 (6–9; n = 7)] wide. Ventral bar 45 (41–51; n = 12) [47 (41–51; n = 7)] long, slightly arched anteriorly, with tapered ends directed posteriorly. Dorsal bar 17 (16–19; n = 5) long, narrow, rod-shaped.

3.2.1.2. Remarks. Heteropriapulus (Jogunoori et al., 2004; Kritsky, 2007 (as amended by Acosta et al., 2017) accommodates dactylogyrid species having eyespots dissociated, gonads overlapping, unarticulated copulatory organ and accessory piece, MCO tubular (sigmoid or straight), accessory piece composed of a single or variable number of subunits, vaginal pore mid-ventral, and ventral anchors lacking roots with elongate shaft imperceptible joining point. Currently, eight species of *Heteropriapulus* have been recognized from South American loricariid catfishes of *Pterygoplichthys*, *Hypostomus* and *Rhinelepis* (see Acosta et al., 2017). Some of these species of *Heteropriapulus*, described and/or reported from India, China, Japan and Mexico are from their introduced or invasive hosts of South America origin (Jogunoori et al., 2004; Mendoza-Franco et al., 2012; Nitta and Nagasawa, 2013; Rodríguez-Santiago et al., 2016). Based on comparative copulatory complex morphology, *H. simplexioides* n. sp. on *P. pardalis* from Palizada River (southern Mexico) most resembles *H. simplex* which was originally described by Li and Huang (2012) on *Hypostomus plecostomus* (Linnaeus) introduced to China and later reported by Acosta et al. (2017) on *Pterygoplichthys ambrosettii* (Holmberg) from Brazil. Both species, *H. simplexioides* n. sp. and *H. simplex* possess an accessory piece as a single straight unit. *Heteropriapulus simplexioides* n. sp. differs from *H. simplex* by the shape of its MCO, i.e., an elongate, slender sigmoid tube and intertwined with accessory piece (a robust sigmoid tube in *H. simplex*). Furthermore, *H. simplexioides* n. sp. can be distinguished by having a slender dorsal bar (robust in *H. simplex*), dorsal anchor with elongate point extending past level of superficial root (moderately short point in *H. simplex*), and by the size of its ventral anchor (length 31–37 vs 15–20, 24–31 in *H. simplex* from Li and Huang [2012)] and Acosta et al., [2017], respectively) and slightly by the size of its ventral bar (41–51 length vs 48–58, 50–74 in *H. simplex* from Li and Huang, [2012] and Acosta et al., [2017], respectively) (see Fig. 2 in the present study and Fig. 3 in Acosta et al., 2017). The introduced *P. pardalis* to southeastern Mexico was initially reported to be parasitized with *Heteropriapulus* sp. from Lacantún river in the state of Chiapas (Mendoza-Franco et al., 2012) and infected with *Heteropriapulus heterotylus* Jogunoori et al., 2004 (also on *P. disyunctivus*) from two localities (Santa Gertrudis and La Rivera) of the Palizada River (Rodríguez-Santiago et al., 2016). However, what is noteworthy is that these latter authors also reported *Urocleidoides vaginoclaustrum* Jogunoori et al., 2004 (Dactylogyridae) on *P. pardalis*. *Urocleidoides vaginoclaustrum* was originally described on the green swordtail *Xiphophorus helleri* Heckel, 1848(Poeciliidae) and its

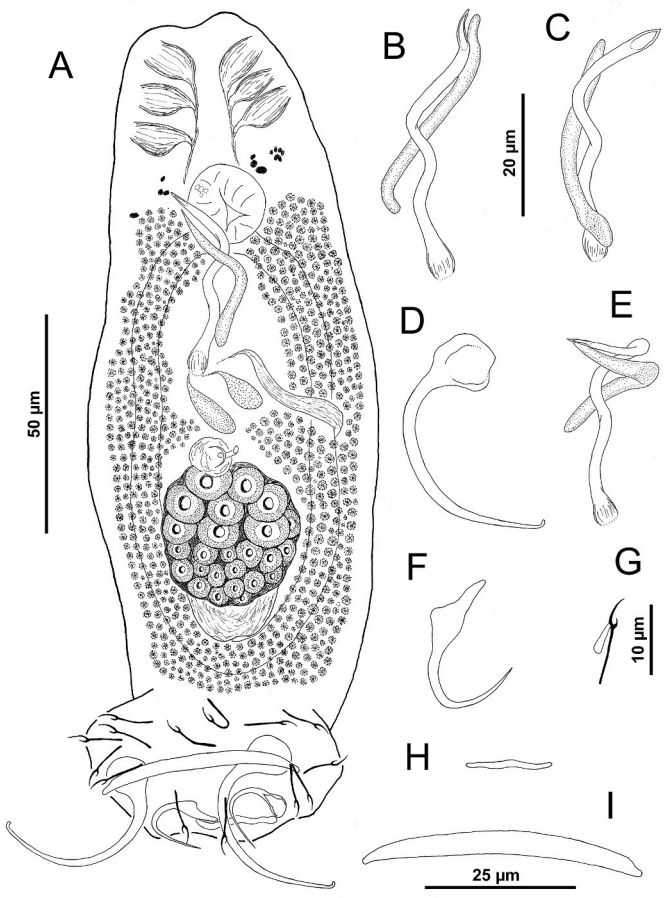

Fig. 2. *Heteropriapulus simplexioides* n. sp. on *Pterygoplichthys pardalis* (Loricariidae) from the Usumacinta river basin (southern Mexico). A – whole mount (composite, ventral view); B, C, and E – copulatory complexes; D – ventral anchor; F – dorsal anchor; G – hook; H – dorsal bar; I – ventral bar.

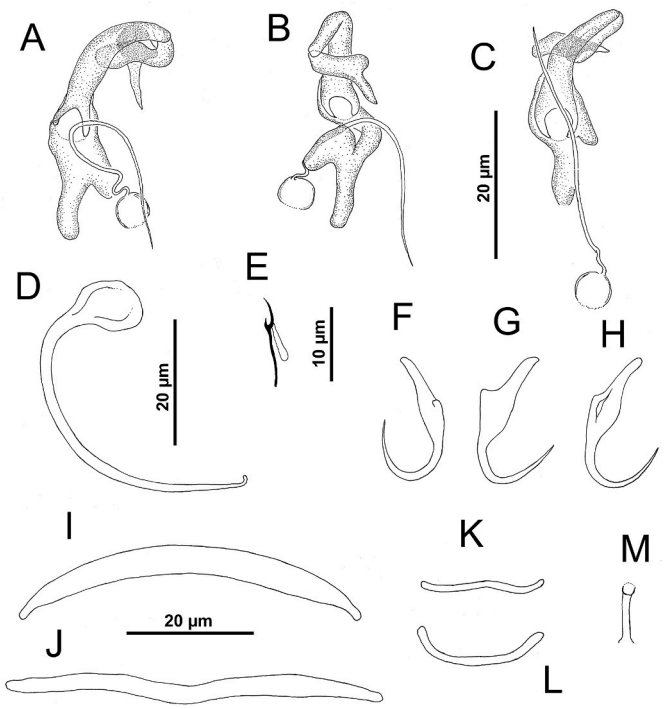

Fig. 3. Haptoral and copulatory complex sclerites of *Heteropriapulus heterotylioides* n. sp. on *Pterygoplichthys pardalis* (Loricariidae) from the Usumacinta river basin (southern Mexico). A, B, and C – copulatory complexes (A and C in dorsal view; B in ventral view); D – ventral anchor; E – hook; F, G and H – dorsal anchors; I and J – ventral bars; K and L – dorsal bars; M – vaginal tube.

occurrence on *P. pardalis* seems unlikely to happen because species of *Urocleidoides* sensu stricto (see Kritsky et al., 1986), are only known from hosts of the Characiformes, Cyprinodontiformes and Gymnotiformes (see MendozaFranco and Reina, 2008; Mendoza-Franco et al., 2015; Santos and Domingues, 2023) and the potential transfer of *U. vaginoclaustrum* from native hosts to siluriforms, i.e., *P. pardalis* appears low. Furthermore, Rodríguez-Santiago et al. (2016) did not provide any supplemental observation and/or morphometric data for reporting *U. vaginoclaustrum* (which was misspelled as *vaginoclastrum*) which is morphologically well differentiated (see Mendoza-Franco et al., 2015) from *Heteropriapulus* spp. (i.e., the elongate shaft and point with recurved tip is lacking in *U. vaginoclaustrum*) to support the occurrence of *U. vaginoclaustrum* on *P. pardalis*. *Heteropriapulus simplexioides* n. sp. represents the first description of a dactylogyrid on a non-native host species of *Pterygoplichthys* in Mexico.

***Heteropriapulus heterotylioides* n. sp.** (Fig. 3A–M)

Type host: *Pterygoplichthys pardalis* (Castelnau) (Weber, 1991) (Loricariidae: Siluriformes).

Site of infection: Gill lamellae.

Prevalence and intensity of infection: see *H. simplexioides* n. sp.

Type locality: Palizada river (18°5′12.95″N, 92°5′27.25″W) (tributary of the Usumacinta River basin) in the state of Campeche (southern Mexico).

Another host: *Pterygoplichthys disyunctivus* (Weber, 1991) from the Recreo river (17°28′40.05″N; 91°25′47.8″W) located in the municipality of Tenosique, in the state of Tabasco (southern Mexico).

Specimens deposited: Holotype, CNHE (12048); 31 paratypes, CNHE (12049); 7 voucher specimens on *P. disyunctivus* from the Recreo river in CNHE (12050).

Etymology: The specific name reflects the close morphological resemblance of the new species to *H. heterotylus* (type species of the genus) parasitizing *Hypostomus* sp. (type host) introduced to India.

Description (based on 29 specimens mounted unstained in Gray and Wess medium and 3 unstained with LA-GAP mixture; measurements of specimens on *P. disyunctivus* from the Recreo river are in brackets and those from the type locality are in parentheses): Body 167 (128–190; n = 13) [237 (190–270; n = 6)] long, fusiform; greatest width 62 (50–80; n = 6) [90–120] usually in posterior trunk at level of gonads. Terminal cephalic lobes well developed, containing large head organ; 3 bilateral pairs of head organs lying posterior to cephalic lobes; cephalic glands indistinct, lying posterolateral to pharynx. Accessory (melanistic) granules extending from level of gonads to cephalic lobes. Pharynx subspherical, 18 (14–18; n = 5) in diameter. Testis 15 long, 10 wide, subspherical; seminal vesicle in left side of body near mid-length; prostatic reservoirs pyriform. Copulatory organ 36 (33–40; n = 16) [35 (33–40; n = 7)] long, a delicate tube (usually bent on its midportion) with sigmoid proximal portion and rounded base. Accessory piece 29 (25–33; n = 7) [33 (30–34; n = 3)] long, a complex of 3 subunits: 1 rod-shaped subunit, distally bent and proximally bifurcated; 1 subunit, variable, with submedial spine-like branch; 1 Y-inverted shaped subunit. Germarium ovate, 34 (31–36; n = 5) long, 21 (14–25; n = 5) wide. Vaginal pore mid-ventral; vaginal canal short, poorly sclerotized; seminal receptacle inconspicuous, immediately internal to vaginal pore. Vitelline follicles moderately dense. Peduncle broad to non-existent, slightly tapered posteriorly. Haptor 62 (55–68; n = 13) [70 (55–82; n = 6)] wide, subtrapezoidal. Hooks 12 (11–12; n = 18) long, with upright acute thumb and slender shank. Ventral anchor 38 (35–43; n = 39) [38 (33–42; n = 16)] long, with flattened base, elongate shaft and point with recurved tip; base 9 (8–12; n = 28) [8 (7–9; n = 11)] wide; shaft and point of ventral anchors extending posteroventrally from haptor; anchor filament double, well developed (not illustrated). Dorsal anchor 20 (19–23; n = 31) [22 (20–24; n = 15)] long, variable, with short to non-existent deep root, rounded superficial root, evenly curved shaft and elongate point extending past level of superficial root; base 6 (5–9; n = 13) [6 (5–7; n = 3)] wide. Ventral bar 51 (43–55; n = 22) [53 (47–61; n = 7)] long, variable in shape, straight to bowed, with tapered ends directed posteriorly. Dorsal bar 21 (18–25; n = 18) [22 (20–25; n = 5)] long, narrow, rod-shaped, straight to slightly arched posteriorly.

3.2.1.3. Remarks. In *P. pardalis* and *P. disyunctivus*, a simultaneous infection with *H. simplexioides* n. sp. and *H. heterotylioides* n. sp. was found. Since all worms could not be properly identified, the data on infection rate relate to both monogenoidean species on each of these hosts. *Heteropriapulus heterotylioides* n. sp. on *P. pardalis* most resembles *H. heterotylus*, this latter originally described on the introduced *Hypostomus* sp. to India by Jogunoori et al. (2004) and subsequently reported on *P. pardalis*, *P. disyunctivus*, *H. plecostomus* and *P. ambrosettii* from Mexico, China, Japan and Brazil (see Remarks section for *H. simplexioides* n. sp. and Acosta et al., 2017). Both monogenoidean species possess anchors/bars of similar size, i.e., ventral (length 35–43 vs 34–41) and dorsal anchors (length 19–23 vs 18–21); and ventral (length 43–55 vs 40–47) and dorsal (length 18–25 vs 18–23) bars. The new species differs from *H. heterotylus* in having an accessory piece composed of 3 subunits (compare Fig. 3A–C [present study]) (4 subunits in *H. heterotylus*), in lacking a patch on ventral anchor base, an asymmetrical thickened wall of the MCO base, a vaginal pore as a transverse slit with thickened anterior and posterior margins (as a short vaginal tube in *H. heterotylioides* n. sp.) and by size of its hooks (length 11–12 vs 13–15 in *H. heterotylus*). The noted shape differences of the subunits of the accessory piece, anchors and bars in *H. heterotylioides* n. sp. might be considered intraspecific variation. Rodríguez-Santiago et al. (2015, 2016) reported *H. heterotylus* on *P. pardalis* and *P. disyunctivus* from southern Mexico. While no morphometric evidence is available that would suggest that the report was based on specimens representing two distinct species (i.e, *H. heterotylioides* n. sp. and *H. simplexioides* n. sp.) (see Remarks section for this latter species), confirmation of the identity of *H. heterotylus* may depend on examination of newly collected specimens.

Ligictaluridus mirabilis (Mueller 1937; Klassen and Beverley-Burton

(1985) (Fig. 4A and B).

See comparative measures in Table 3.

Host: Southern blue catfish *Ictalurus meridionalis* (Günther, 1864) (Ictaluridae: Siluriformes).

Localities: Recreo river (17°28′40.05″N; 91°25′47.8″W) river, located in the municipality of Tenosique, in the state of Tabasco; and Lacantún river in the Biosphere Reserve Montes Azules (BRMA), Chiapas, Mexico (19°09″96.6″N, 90°95″56.8″W) (both tributaries of the Usumacinta River basin, southern Mexico).

Site of infection: Gill lamellae.

Prevalence and intensity of infection: 15 fish infected of 15 examined (100%); mean intensity of infection 4 parasites per infected fish from the Recreo river; 7 of 7 fish examined from Lacantún river (100%; 8).

Specimens deposited: 12 and 31 voucher specimens in CNHE (12043 and 12044 from Recreo and Lacantún rivers, respectively).

3.2.1.4. Remarks. Ligictaluridus was proposed by Beverley-Burton (1984) for gill and olfactory chamber monogenoids of North American catfishes (Ictaluridae). This ictalurid-specific genus was primarily characterized by dactylogyrids having a MCO characterized as a sclerotized curved tube proximally articulated with accessory piece which possess distal limb with one or more terminal projections; a sinistral vaginal opening; dorsal and ventral anchor/bar complexes; and hooks of disimilar shape and size. Klassen and Beverley-Burton (1985) revised diagnosis of *Ligictaluridus* above mentioned, redescribed and/or transferred to it dactylogyrids previously assigned in *Cleidodiscus* (sensu Beverley-Burton and Suriano, 1980) as *Ligictaluridus pricei* (Mueller, 1936) (type species), *L. monticellii* (Cognetti de Martis, 1924), *L. floridanus* (Mueller, 1936), *L. mirabilis* and *L. bychowskyi* (Price and Mura, 1969) (see Klassen and Beverley-Burton, 1985). *Ligictaluridus mirabilis* was originally described on flathead catfish *Pylodictis olivaris* (Rafinesque, 1818) from Mississippi River, USA from which other two *Ligictaluridus* spp. have also been described and/or reported, *Ligictaluridus michaelalicea* Leis et al. (2018), *L. floridanus* and *L. pricei*. Additionally, *Ligictaluridus posthon* Klassen and Beverley-Burton, 1985 has been described on *Noturus flavus* Rafinesque, 1818 from Ontario, being a

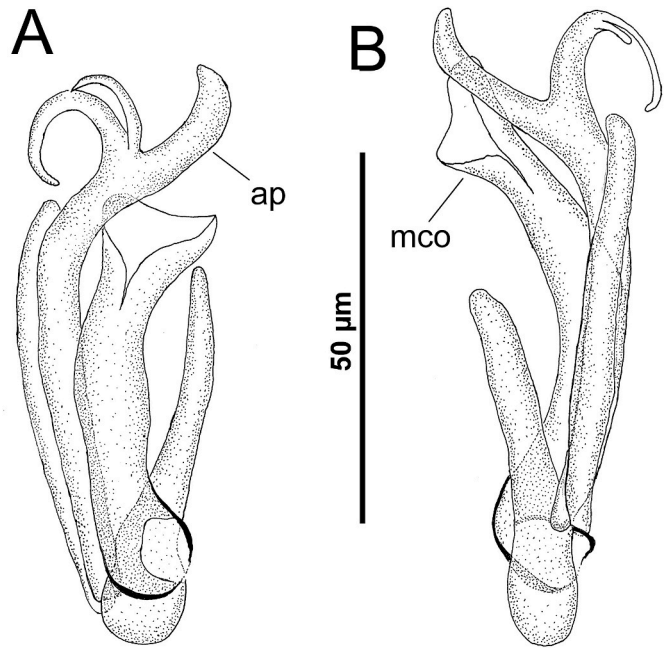

Fig. 4. Copulatory complexes of *Ligictaluridus mirabilis* (Mueller 1937; Klassen and Beverley-Burton (1985) on Southern blue catfish *Ictalurus meridionalis* (Ictaluridae) from the Usumacinta river basin (southern Mexico). A – copulatory complex in ventral view; B – copulatory complex in dorsal view. Abbreviations: mco – male copulatory organ; ap – accessory piece.

Table 3
Measurements of *Ligictaluridus mirabilis* (Mueller 1937; Klassen and Beverley-Burton (1985) (Dactylogyridae) parasitizing the gill lamellae of siluriform fishes from North America and tributaries of the Usumacinta river Basin (southern Mexico).

Hosts	*Ictalurus meridionalis*[a]	*Ictalurus meridionalis*[a]	*Pylodictis olivaris*[b]	*Ictalurus punctatus*[c]
Localities	Recreo river	Lacantún river	Mississippi USA	Ontario Canada
Body length	725 (387–1140; n = 12)	581 (412–975; n = 31)	1300	884 (725–1128)
Greatest width	161 (122–200; n = 9)	135 (87–187; n = 25)	185	272 (167–379)
Pharynx width	39 (32–50; n = 10)	33 (22–50; n = 24)		25 (18–30)
Haptor width	131 (105–155; n = 11)	116 (87–150; n = 22)		77 (55–114)
Ventral anchor length	65 (56–70; n = 14)	58 (43–71; n = 32)		68 (54–80)
Ventral anchor width	38 (30–40; n = 9)	30 (22–42; n = 23)	73	
Dorsal anchor length	62 (57–66; n = 7)	58 (46–71; n = 31)	73	65 (47–72)
Dorsal anchor width	33 (32–35; n = 6)	30 (20–40; n = 25)		
Ventral bar length	76 (70–82; n = 9)	87 (70–103; n = 19)	89	116 (88–143)
Dorsal bar length	84 (73–94; n = 13)	86 (68–104; n = 12)	89	114 (94–131)
Hook length	17 (17–18; n = 6)	16 (16–17; n = 7)		16–25
MCO length	86 (78–95; n = 9)	85 (77–98; n = 17)		
Accessory piece length	80 (70–90; n = 10)	75 (70–80; n = 19)	89	107 (87–121)
Germarial length	67 (50–80; n = 10)	53 (37–93; n = 10)		
Germarial width	50 (42–65; n = 11)	39 (30–55; n = 13)		
Testis length	91 (70–120; n = 6)	66 (53–80; n = 11)		
Testis width	51 (45–60; n = 5)	37 (28–45; n = 8)		

[a] Present study.
[b] Measurements from the original description.
[c] From Klassen and Beverley-Burton (1985).

total of seven currently known *Ligictaluridus* spp. from North American catfishes (see Cloutman et al., 2018; Klassen and Beverley-Burton, 1985; Leis et al., 2018). Among these *Ligictaluridus* spp., *L. floridanus*, *L. pricei* and *L. mirabilis* have been extensively reported on native and/or introduced *Ictalurus* spp. and cyprinids to Mexico and Japan (see Mendoza-Garfias et al., 2017; Nitta and Nagasawa, 2015; Rábago-Castro et al., 2011, 2014). However, not any taxonomic account is described and/or provided in these reports from Mexico to support identification of these dactylogyrids, overall due to the confusion over the identity of *L. mirabilis* and *L. floridanus*. Both monogenoidean species are morphologically closer to each other and differ primarily in the size and shape of the copulatory complex (see Klassen and Beverley-Burton, 1985; Leis et al., 2018). In the present study, drawings and measurements of the morphological features (i.e., copulatory complex) of the specimens identified as *L. mirabilis* on *I. meridionalis* from southern Mexico are provided (see Fig. 4 and Table 3). Measurements of these specimens are consistent with those originally used to describe and redescribe this species (on *P. olivaris* and *Ictalurus punctatus*, respectively) from North America (see Table 3) and with the most updated taxonomic key

provided by Leis et al. (2018) for *Ligictaluridus* spp., thus separating *L. mirabilis* from *L. floridanus* (i.e., accessory piece 70–90 [from the Recreo river], 70–80 [from the Lacantún river] long, with distal tip possessing two recurved points in present specimens (see Fig. 4) vs 40–47 long, with single recurved point in *L. floridanus* (see Table 3, and drawings/measurements of *L. floridanus* from the key to Leis et al., 2018). While not within the scope of the present study, it is noted urgent need of a formal revision of those dactylogyrids referenced as *L. floridanus*, *L. pricei* and *L. mirabilis* on *Ictalurus* spp. and cyprinids from Mexico. *Ictalurus meridionalis* represents a new host record for *L. mirabilis* in the Recreo river and new host and locality records from Lacantún river.

Aristocleidus mexicanus Mendoza-Franco and Vidal-Martínez, 2001

Host: *Eugerres mexicanus* (Steindachner, 1863) (Gerreidae: Perciformes).

Locality: Recreo river (17°28′40.05″N; 91°25′47.8″W) (tributary of the Usumacinta River basin) located in the municipality of Tenosique, in the state of Tabasco southern Mexico.

Site of infection: Gill lamellae.

Prevalence and intensity of infection: 13 fish infected of 16 examined (81%); mean intensity of infection 3 parasites per infected fish.

Specimens deposited: 5 voucher specimens in CNHE (12061).

Supplemental observations (original measurements of this species by Mendoza-Franco et al. [2015] follow those of the present study in brackets, respectively): Body 577 (505–625; n = 5) [425–630] long; greatest width (excluding haptor) 98 (90–110; n = 4) [85–150]. Haptor 96 (85–102; n = 3) [90–120] wide. Pharynx 33 (30–34; n = 4) [25–45] wide. Copulatory complex 31 (28–38; n = 5) [27–50] long. Ventral anchor 50 (46–52; n = 9) [46–50] long, base 18 (16–22; n = 5) [13–18] wide; dorsal anchor 45 (42–48; n = 7) [43–51] long, base 17 (15–21; n = 5) wide. Ventral bar 28 (24–35; n = 4) [23–30] long; dorsal bar 44 (42–47; n = 4) [42–47] long. Hook 12 (12–13; n = 11) [12–13] long. Egg 55–62 long, 42–58 wide.

3.2.1.5. Remarks. Aristocleidus mexicanus is clearly a member of a group of five species distributed from Neotropical region surveyed on Atlantic coasts from Florida to Brazil, and Pacific coast of Mexico on species of *Gerres*, *Diapterus*, *Eucinostomus* and *Eugerres* (Gerreidae) inhabiting in marine, brackish and freshwater environments (see Kritsky and MendozaFranco, 2008; Mendoza-Franco et al., 2009; Cohen et al., 2022). *Aristocleidus mexicanus* was originally described on *E. mexicanus* inhabiting in the freshwater environment of the Lacantun River. This latter species of *Aristocleidus* and *Aristocleidus lacantuni* Mendoza-Franco and Vidal-Martínez, 2001, on the same host species are the only two known species of *Aristocleidus* occurring in freshwater waters. The Recreo river in the municipality of Tenosique, Tabasco represents a new locality record for *A. mexicanus*.

Diplectanocotyla megalopis Rakotofiringa and Oliver (1987).

Host: tarpon *Megalops atlanticus* Valenciennes, 1847 (Megalopidae: Elopiformes).

Locality: Recreo river (17°28′40.05″N; 91°25′47.8″W) (tributary of the Usumacinta River basin) located in the municipality of Tenosique, in the state of Tabasco, southern Mexico.

Site of infection site: Gill lamellae.

Prevalence and intensity of infection: 2 fish infected of 2 examined (100%); mean intensity of infection 6 parasites per infected fish.

Specimens deposited: 7 voucher specimens, CNHE (12062).

Supplemental observations (measurements of those specimens used to redescribed this species by Mendoza-Franco et al. [2004] follow those of the present study in brackets, respectively): Body 409 (337–525; n = 6) [387–454] long; greatest width (excluding haptor) 83 (75–90; n = 5) [81–101]. Haptor 116 (100–125; n = 6) [123–138] wide; haptoral sucker 50 (42–60; n = 7) [44–54] width. Pharynx 24 (22–27; n = 6) [22–27] wide. Copulatory complex 22 (19–25; n = 7) [20–33] wide. Ventral anchor 33 (32–33; n = 6) [33–38] long, base 14 (13–15; n = 3) [12–16] wide; dorsal anchor 35 (33–37; n = 5) [30–37] long, base 12 (11–13; n = 3) [9–14] wide. Ventral bar 47 (42–51; n = 7) [39–51] long; dorsal bar 44 (42–47; n = 7) [36–50] long. Hook 9 (9–10; n = 6) [9–11] long.

3.2.1.6. Remarks. Diplectanocotyla megalopis was originally described on Indo-Pacific tarpon *Megalops cyprinoides* (Broussonet, 1782) from Madagascar by Rakotofiringa and Oliver (1987). Subsequently, *D. megalopis* was reported and redescribed from the Atlantic tarpon, *Megalops atlanticus* Cuvier and Valenciennes, 1847 from the Atlantic coasts of Nicaragua and Mexico (Yalahau Lagoon in the Caribbean State of Quintana Roo) by Mendoza-Franco et al. (2004) who also recognized this monogenoidean species on *M. atlanticus* from Puerto Rico. Currently, there are four species allocated within *Diplectanocotyla* Yamaguti, 1953 (as emended by Mendoza-Franco et al., [2004], and Lim and Gibson, [2007]): *D. megalopis*, *D. gracilis* Yamaguti, 1953 (type species) on *M. cyprinoides* (Broussonet, 1782) from Makassar, East Indies and off Peninsular Malaysia; *Diplectanocotyla parva* Lim and Gibson (2007); and *Diplectanocotyla langkawiensis* Lim and Gibson (2007) on *M. cyprinoides* from off Peninsular Malaysia. Present specimens of *D. megalopis* did not differ morphometrically from those originally described and redescribed (see measurements above and Table 1 in Mendoza-Franco et al., 2004). The occurrence of *D. megalopis* on *M. atlanticus* from the marine and brackish waters of Nicaragua and off Mexico vs freshwater from the Usumacinta River basin (see Mendoza--Franco et al., 2004; present study) is noteworthy. It would suggest that salinity variation of the waters might not affect the presence and distribution of this monogenoidean species. A similar factor of salinity gradients has been suggested to restrict distribution of species of *Rhabdosynochus* (Diplectanidae) that parasitize snooks (Centropomidae) from which worms show varying tolerances to salinity during diadromous migrations of their hosts (see Kritsky et al., 2010). The Recreo river represents a new geographical and locality record for *D. megalopis*.

4. Discussion

The *Usumacinta River* basin in Mesoamerica (southern Mexico) flows north from the midwest and northwest highlands and empties into the Gulf of Mexico with the Palizada, Recreo and Lacantún rivers from the states of Campeche, Tabasco and Chiapas, respectively, this latter river forming the border between *Mexico* and Guatemala (Soria-Barreto et al., 2018; Castillo et al., 2023). At this Neotropical portion of Mexico, the biogeographic provinces have been recognized and delimited based on ecoregions combining climatic, geological, and biotic criteria (see Morrone et al., 2022). Consistently, these provinces belong to the Mexican transition zone (i.e., mountains areas of Mexico and Guatemala) and the Brazilian subregion Mesoamerican dominion for southern lowlands ecoregions to the Pacific lowlands province (i.e., Central and southern Mexico, and Central America). As previously referenced, the biodiversity complexity in that Neotropical transition zone evidences the confluence of taxa with morphological affinities to Neartic and Neotropical biotas including the distribution of freshwater host-specific parasites (Miller 1986; Mendoza-Franco et al., 2000, 2001; Choudhury et al., 2017; Scholz and Perez-Ponce de León, 2021). The present taxonomic study provides new knowledge about that confluence by identifying and/or clarifying the occurrence of monogenoids on host species with Neartic (i.e., the suckers and catfishes of the Catostomidae [i.e, *Ictiobus meridionalis*] and Ictaluridae [i.e, *Ictalurus meridionalis*], respectively) and Neotropical (i.e., the catfishes of the Loricariidae [i.e., *Pterygoplichthys* spp.]) affinities, including other marine derivatives as those of the Gerreidae [i.e., *Eugerres mexicanus*], and Megalopidae [i.e., *Megalops atlanticus*] with circumtropical distribution. What is noteworthy is the first finding and description of a species of *Icelanonchohaptor* (*I. tropicalis* n. sp.) on the native catostomid, *I. meridionalis* from the Usumacinta. The only and previously described

species of *Icelanonchohaptor* (*I. icelanonchohaptor*) is known solely from the North American catostomid of *Ictiobus cyprinellus* (Cypriniformes) (see Leiby et al., 1972). In Mexico, it has been inferred that radiation of catostomids occurred around the late Miocene (11.6–5.3 mya) based on fossil evidence and phylogeny of these fishes in the area (see Gray, 1977; Guzmán, 2015; Ruiz-Campos et al., 2016). In this perspective, the combined extant distributions of these 2 species of *Icelanonchohaptor*, the North American (i.e., from the Missouri River in North Dakota and South Dakota, USA) *I. icelanonchohaptor* and the Tropical *I. tropicalis* n. sp., suggests a longer history of association of these monogenoids with their catostomid hosts. Biogeographically, the five known species of buffalofishes of *Ictiobus* (including other members of the family, i.e., *Catostomus* spp.) are ranging from Southern Mexico to Canada, of which four are found in the freshwater systems of mainland Mexico, i.e., inhabiting on basins draining the Sierra Madre Occidental province, part of the Mexican Neotropical transition zone (Ruiz-Campos et al., 2016; Lyons et al., 2020; Hunt et al., 2021; Morrone et al., 2022) from which only present gill parasite finding represents the first study on a species of *Ictiobus* in Mexico. In this view, it is expected to find additional species and/or interesting diversity of monogenoids, still not discovered on these catostomid fishes in the tropics. In fact, others than gill monogenoids, for example, *Pellucidhaptor planarus* Leiby et al., 1972 and *Gyrodactylus dakotensis* Leiby et al., 1972 has been described on external surface of *I. cyprinellus* from the North Dakota and South Dakota (Leiby et al., 1972).

Similarly, species of *Ligictaluridus* are known on the North American catfishes of the Ictaluridae from which there are seven recognized species of *Ictalurus* that are native to the US and/or Mexico, this latter country considered as a center of diversity for *Ictalurus* (see Varela-Romero et al., 2021). Present study allowed confirm occurrence of *L. mirabilis* on the native southern blue catfish *I. meridionalis*. While species of *Ligictaluridus* (i.e., *L. floridanus*, *L. pricei* and *L. mirabilis*) has been extensively reported on native and introduced *Ictalurus* spp. and cyprinids to Mexico (see Klassen and Beverley-Burton, 1985; Rábago-Castro et al., 2014; Cloutman et al., 2018; and Remarks section for *L. mirabilis*), other ictalurids (i.e., *Ictalurus mexicanus*) remain unexplored for monogenoids. The non-native freshwater species of the Loricariidae were also examined closely for monogenoids and two new species of *Heteropriapulus* were described on *P. pardalis* (type host) and *P. disyunctivus*. The natural distribution area of species of *Heteropriapulus* includes the Neotropics as evidenced by the present study, a biogeography probably associated with the Brazilian subregion Mesoamerican dominion (sensu Morrone et al., 2022). These new species described herein, are likely to have originated from South America (Brazil) when their hosts were introduced to Mexico from which now comprise a large relative abundance of *Pterygoplichthys* spp. (collectively known as plecos) biomass in Tabasco and Chiapas states (Sánchez et al., 2015; Barrientos et al., 2018; Soria-Barreto et al., 2018). The marine derivatives as those of the Gerreidae and Megalopidae with circumtropical distribution have also involved and adapted in the freshwater environment of the Usumacinta River. For example, species of *Aristocleidus* occur on gerreid hosts primarily from marine or brackish waters and only *A. mexicanus* and *A. lacantuni* on *E. mexicanus* had previously been described and/or reported to occur in freshwater habitat (see Remarks section for *A. mexicanus* and *Diplecnocotyla megalopis*). The present finding of *A. mexicanus* and *D. megalopis* on *E. mexicanus* and *Megalops atlanticus*, respectively, in the Usumacinta River, argues an adaptation of these monogenoidean species on their respective hosts to different environments. Present study provides new information (i.e., description of 3 new species) to clarify the diversity of Monogenoidea with Neartic and Neotropical affinities (some of them with veterinary importance as those of *Ligictaluridus* spp. introduced along with their hosts for aquaculture purposes outside of their native ranges) on native and/or non-native hosts occurring in this transitional area of the Mesoamerica, the Usumacinta River basin.

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Declaration of competing interest

On behalf of co-authors and I, we confirm that there is not conflict of interest in the submitted manuscript entitled “New and previously known ectoparasitic monogenoids (Platyhelminthes) on native and non-native fishes from tributaries of the Usumacinta river basin (southern Mexico), a Neotropical transition zone”.

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