

# Caryophyllidean tapeworms (Cestoda), Nearctic parasites of fish in Mexico, including description of a new species of *Isoglaridacris* and the first report of *Khawia japonensis*, an invasive parasite of common carp (*Cyprinus carpio*)

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## ABSTRACT

The first survey of caryophyllidean tapeworms parasitising catostomid and cyprinid fish in Mexico is provided, including new host and geographical records. *Isoglaridacris brevicollis* n. sp. is described from the Nazas sucker, *Catostomus nebuliferus* Garman (type host), in Durango, *C. bernardini* Girard in Sonora, and *Moxostoma austrinum* Bean (Cypriniformes: Catostomidae) in Jalisco. The new species differs from congeners mainly in the shape of the scolex, which is rounded, and by the absence of a defined neck (distinct, often long in other congeners). *Pseudoglaridacris confusa* found in *Ictiobus meridionalis* (also a member of the family Catostomidae) from Oaxaca and Veracruz represents the southern-most report of species of this Nearctic genus. Three morphotypes of the holarctic *Archigetes* Leuckart, 1878 were found in two leuciscid fishes (*Notropis caliensis* and *N. nazas*) and in silverside *Chirostoma* sp. (Atherinidae). It is the first record of any caryophyllidean in atheriniform fish. The first record of *Khawia japonensis* (Yamaguti, 1934) (syn. *K. iowensis* Calentine et Ulmer, 1961), a parasite of common carp (*Cyprinus carpio* L.), in Mexico represents another evidence of its invasive potential. The caryophyllidean fauna of Mexican freshwater fish is depauperate compared to that in the United States and Canada, which seems to be related to a much lower number of species of suckers (Catostomidae) occurring in Mexico, possibly also to the lower number of fish in the population.

## 1. Introduction

Mexico is a hotspot of biodiversity, being situated in two principal zoogeographical regions, Nearctic and Neotropical. This transient position makes Mexico a very attractive country from the biogeographical point of view, including the zoogeography of fish parasites (Aguilar-Aguilar et al., 2003; Pérez-Ponce de León and Choudhury, 2005, 2010; Choudhury et al., 2017). These authors analysed the composition and zoogeographical origin of several groups of fish parasites including proteocephalid tapeworms (Essexiellinae) (Pérez-Ponce de León and Choudhury, 2002, 2005; Scholz et al., 2003; Rosas-Valdez et al., 2004; Rosas-Valdez and Pérez-Ponce de León, 2008).

The Nearctic and Neotropical regions considerably differ from each other in the composition of their cestode faunas of freshwater fishes (Scholz and Kuchta, 2017). Proteocephalid tapeworms (freshwater representatives of the order Onchoproteocephalida) are dominant

component of fish parasite fauna in the Neotropical region, representing as many as 95% of more than 100 species of fish tapeworms. In contrast, caryophyllidean tapeworms are the principal component of the Nearctic fauna of freshwater fish cestodes, representing more than a half of tapeworm species occurring as adults in freshwater fishes of North America (Scholz and Kuchta, 2017; Kuchta et al., 2020).

Current knowledge of caryophyllideans in Mexico is limited to very few records, mostly of juvenile tapeworms from atypical hosts for caryophyllideans. Identification of most of these immature worms was not possible. Salgado-Maldonado (2006) listed a single caryophyllidean identified to the species level, *Glaridacris confusa* Hunter, 1927 (= *Pseudoglaridacris confusa*) from a “bagre” (= a catfish; apparently accidental or postcyclic host) in Oaxaca. In addition, unidentified tapeworms allegedly belonging to the Caryophyllidea, either larvae (metacestodes) or adults were reported from the catostomid *Ictiobus meridionalis* (Günther) in Tabasco by Pineda-López et al. (1985) and in

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Veracruz by Pérez-Ponce de León and Choudhury (2005), the cyprinid *Algansea lacustris* Steindachner in Michoacán by Mendoza-Garfias et al. (1996), in the goodeid *Characodon audax* Smith & Miller in Durango by Martínez-Aquino et al. (2007), and in the catostomid *Moxostoma austrinum* Bean by Pérez-Ponce de León et al. (2013). Oros et al. (2018) reported *P. confusa* from *I. meridionalis* found by one of the authors in Veracruz.

In the present paper, we provide a synopsis of data on the occurrence of caryophyllidean tapeworms in freshwater fishes in Mexico, which represents the southern-most zone of the natural distribution of these fish cestodes in the Americas. This synopsis is mainly based on the evaluation of tapeworms recently collected by Mexican researchers and their collaborators, and supplemented with previously published data.

## 2. Materials and methods

The present paper is largely based on the evaluation of caryophyllidean tapeworms collected by the second author (G.P.P.L.) and his collaborators. Newly collected specimens were fixed with hot (steaming) 4% formalin, stained with Delafield's haematoxylin, or Mayer's paracarmine, dehydrated in a graded ethanol series, cleared in methyl salicylate and mounted as permanent slides using Canada balsam. Illustrations were made using a drawing attachment of an Olympus BX microscope; measurements were taken using Quick Photo programme and are expressed in micrometres ( $\mu\text{m}$ ) unless otherwise stated. Specimens studied are deposited in the National Helminthological Collection of Mexico, Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City, Mexico (CNHE), and the Helminthological Collection of the Institute of Parasitology, Biology Centre of

the Czech Academy of Sciences, České Budějovice, Czech Republic (IPCAS).

### 2.1. A survey of species

Recently, a new classification of the order Caryophyllidea has been proposed based on a robust phylogenetic hypothesis (Scholz et al., 2021). All Nearctic caryophyllideans are now placed in the emended family Capingentidae. The former member of the Lytocestidae, *Khawia japonensis*, which originally occurred only in eastern Asia, belongs to the family Caryophyllaeidae as emended by Scholz et al. (2021).

Family Capingentidae Hunter, 1929 (as emended by Scholz et al., 2021).

#### 1. *Archigetes* sp. 1 Fig. 1A, C, F

**Material studied:** One specimen from yellow shiner, *Notropis calientis* Jordan and Snyder (Cypriniformes: Leuciscidae), Lago de Zacapu, Michoacán, collected by Berenit Mendoza-Garfias in November 2008 (CNHE 6800).

**Host:** *Notropis calientis*.

**Distribution:** Mexico (Michoacán).

#### 2.2. Remarks

The single specimen found is strongly flattened (Fig. 1A), which affected its measurements and made its anatomy difficult to observe, partly also due to extensive vitelline follicles which obscure other structures in the body. The specimen possesses characteristics typical of

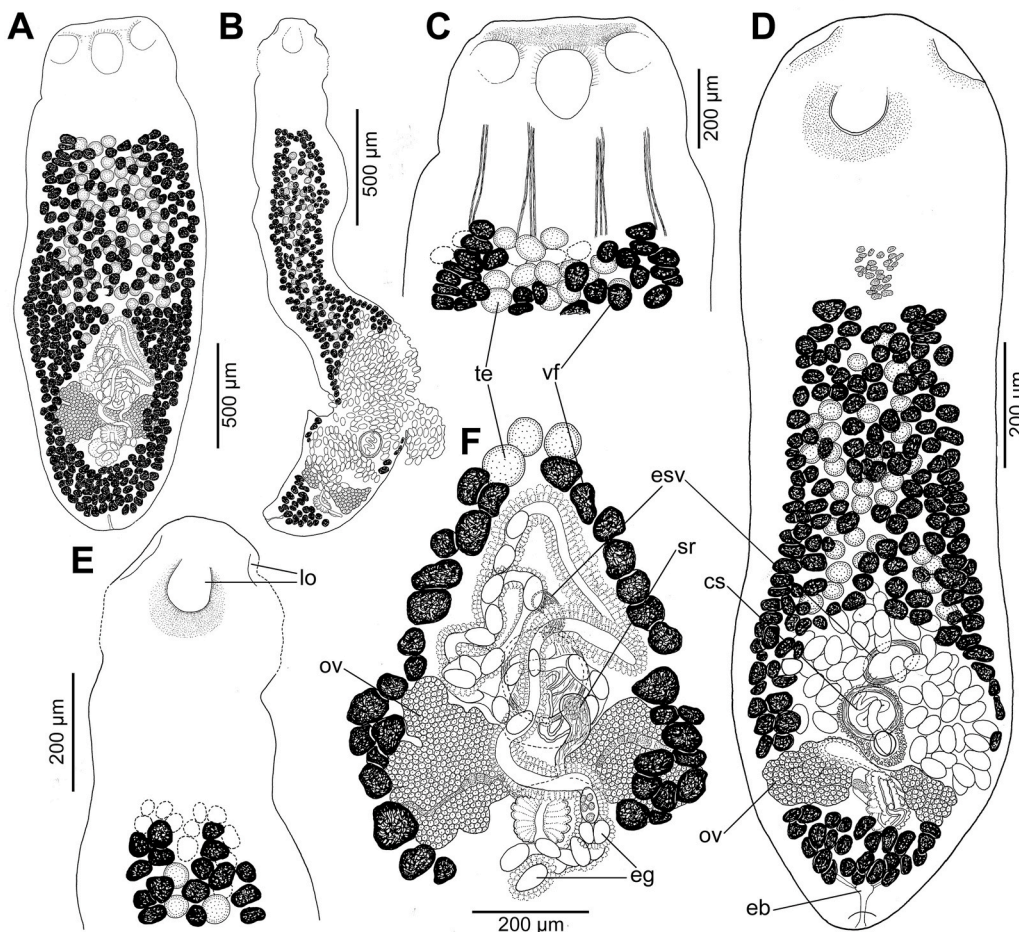


Fig. 1. *Archigetes* sp. 1 from *Notropis calientis*, Michoacán (CNHE 6800) (A, C, F); *Archigetes* (?) sp. 2 from *Notropis nazas*, Durango (CNHE 6797) (B, E); *Archigetes* sp. 3 from *Chirostoma* sp., Michoacán (CNHE 6801) (D). A, B – total view, dorsally; C, E – anterior part with scolex; note different position of anterior-most testes and vitelline follicles between C and E; D – total view, ventrally; F – ovarian and uterine region, dorsally. Abbreviations: cs – cirrus-sac; eb – excretory bladder; eg – eggs; esv – external seminal vesicle; lo – loculi; ov – ovary; sr – seminal receptacle; te – testes; vf – vitelline follicles.

*Archigetes* Leuckart (1878), namely small size of the body (length 2.45 mm, maximum width 910 µm near the middle of the body, length: width ratio 1 : 0.37; Fig. 1A), bothriolocolodiscate scolex (for terminology of scolices of caryophyllidean tapeworms – see Figs. 5.1–5.21 in Mackiewicz, 1994), which is 350 µm long and 650 µm wide (Fig. 1C), a defined neck is absent, an external seminal vesicle is well-developed, 79 µm long and 35 µm wide (Fig. 1F), a single gonopore, and uterine loops anterior to the cirrus-sac, which is 165 µm long and 150 µm wide (Fig. 1F). The testicular field spans anteriorly almost from the level of the anterior-most vitelline follicles to the level of the anterior-most loops of the uterus, but does not reach the level of the cirrus-sac (Fig. 1F). Anterior-most vitelline follicles are situated 520 µm posterior to the anterior extremity, i.e., 21% of total body length, 26 µm anterior to anterior-most testes, which start 546 µm posterior to the anterior extremity (22% of total body length). Vitelline follicles are extensive, surround the testes and are present also lateral or laterodorsal to the ovarian arms, thus connecting the prev ovarian field of follicles with postovarian vitelline follicles (Fig. 1F). Intrauterine eggs are 51–55 µm long and 30–35 µm wide.

## 2. *Archigetes* (?) sp. 2 Fig. 1B, E

**Material studied:** One specimen from Nazas shiner, *Notropis nazas* Meek (Cypriniformes: Leuciscidae), Río Nazas in Emilio Carranza, Durango, collected by Rogelio Rosas-Valdéz in November 2008 (CNHE 6797).

**Host:** *Notropis nazas*.

**Distribution:** Mexico (Durango).

### 2.3. Remarks

The tapeworm found in *N. nazas* is also tentatively placed in *Archigetes* based on the shape and small size of its body (2.5 mm; Fig. 1B), shape of the scolex, which is bothriolocolodiscate (Fig. 1E; and dumbbell-shaped ovary (see Mackiewicz, 1994 for generic diagnosis of *Archigetes*). The specimen from *N. nazas* is elongate and slender (Fig. 1B), with the maximum width of 430 µm, which represents only 17% of total length. The scolex is slightly separated from the neck region and is 260 µm long and 320 µm wide (Fig. 1E). Testes are not numerous (their precise number could not be counted), begin 106 µm posterior to anterior-most vitelline follicles (Fig. 1E); posterior extent of the testicular field could not be observed due to damage of the body, but testes apparently reach to the anterior loops of the uterus (Fig. 1B). Cirrus-sac is subspherical, thick-walled, 102 µm long and 88 µm wide. Presence of an external seminal vesicle could not be verified due to the presence of numerous eggs in broken part of the body. Anterior-most vitelline follicles, which are circum-medullary, i.e., in confluent lateral and median fields (Fig. 1B), begin 474 µm from the anterior extremity, i.e., 19% of total body length, anterior to the anterior-most testes (Fig. 1E). Prev ovarian follicles do not reach posteriorly as far as to the ovary (Fig. 1B); postovarian follicles present, reach anteriorly to the posterior end of the ovary. Eggs are very numerous and uterine region occupies a major part of the posterior half of the body (Fig. 1B); intrauterine eggs are 49–53 long and 31–34 µm wide (n = 5; only uncollapsed eggs measured).

Unfortunately, the specimen is in poor condition and its posterior part with the uterus is broken; lateral sides of the scolex are also slightly damaged (Fig. 1E – dotted lines). Numerous eggs also prevent reliable observation of the presence of an external seminal vesicle (if present), which is a typical characteristic of species of *Archigetes*. Tentatively, the specimen from *N. nazas* is designated as *Archigetes* (?) sp. 2 to distinguish it from supposedly congeneric tapeworms from *Notropis caliensis* (*Archigetes* sp. 1 – see above) and *Chirostoma* sp. (*Archigetes* sp. 3 – see below).

## 3. *Archigetes* sp. 3 Fig. 1D

**Material studied:** One specimen from silverside, *Chirostoma humboldtianum* (Valenciennes) (Atheriniformes: Atherinidae), Lago de Zacapu, Michoacán, collected by Berenit Mendoza-Garfias in November 2008 (CNHE 6801).

**Host:** *Chirostoma humboldtianum*.

**Distribution:** Mexico (Michoacán).

### 2.4. Remarks

The specimen from *C. humboldtianum* is in a better condition compared to that found in *Notropis nazas*, which was designated as *Archigetes* (?) sp. 2 (see above). It is placed in *Archigetes* because it corresponds well to its generic diagnosis provided by Mackiewicz (1994), including the presence of a single gonopore and thick-walled external seminal vesicle (Fig. 1D). The tapeworm has oblong body shape, 1.47 mm long and 465 µm wide, i.e., width: length ratio 1 : 0.32 (almost double compared to *Archigetes* sp. 1; Fig. 1D). Scolex is 420 µm wide, without a defined neck. Cirrus-sac is thick-walled, subspherical, 94 µm long and 104 µm wide. Testes relatively few (their precise number not countable reliably), begin posterior to anterior-most vitelline follicles; posteriorly, testes reach just to the anterior limit of the uterus, i.e., far anterior to the cirrus-sac (Fig. 1D). External seminal vesicle is thick-walled, large, oval, oblique, 81 µm long and 52 µm wide. Single gonopore is situated near the ovarian isthmus. Ovary is dumbbell-shaped, 325 µm wide, with ovarian wings 80–100 µm long, i.e., 5–7% of total body length (Fig. 1D). Anterior-most vitelline follicles begin 460 µm from the anterior extremity, i.e., 31% of total body length, 57 µm anterior to anterior-most testes. Vitelline follicles forming one irregular field surrounding testes, i.e., lateral and median, reaching posteriorly as far as to the ovary on one side (Fig. 1D). Postovarian vitelline follicles are well-developed. Uterine loops reach anterior to the cirrus-sac (Fig. 1D). Intrauterine eggs are relatively few (few dozens), 46–49 µm long and 29–30 µm wide (n = 5; only uncollapsed eggs measured).

In North America, only *Archigetes iowensis* Calentine (1962) was reported (Scholz and Oros, 2017). This species was described from *Cyprinus carpio* (type host; adult tapeworms) and the oligochaete *Limnodrilus hoffmeisteri* Claparède (Naididae; progenetic plerocercoids) in Iowa (Calentine, 1962). This species differs from all three morphotypes found in Mexico by the exclusively lateral position of vitelline follicles, i.e., two separate non-confluent lateral fields (versus lateral and median, i.e., confluent, circum-medullary in Mexican worms), and by the presence of conspicuous, deep loculi on the scolex (versus shallow or even indistinct in Mexican specimens – Fig. 1C, D, E).

Three morphotypes of *Archigetes* found in the present study differ from each other in the body shape (much more elongate in *Archigetes* (?) sp. 2), anterior extent of the testes (at almost the same level as the anterior-most vitelline follicles in *Archigetes* sp. 1 versus much more posterior in the other morphotypes), the presence of vitelline follicles lateral to dorsolateral to the ovary (in *Archigetes* sp. 1; absent in the other two morphotypes), and shape and thickness of an external seminal vesicle (widely oval, thick-walled in *Archigetes* sp. 3) (Fig. 1). In fact, morphotypes 2 and 3 are more similar to each other than with *Archigetes* sp. 1, including the shape of the scolex with shallow, almost indistinct lateral loculi, but the single specimen of *Archigetes* (?) sp. 2 is damaged and shape of its body may have been affected but long relaxing before fixation.

The occurrence of three morphotypes of *Archigetes*, which may represent three new species, indicates that the actual diversity of species of this genus is much higher in North America than previously thought (Scholz and Oros, 2017). This assumption is supported by the fact that Scholz et al. (2021) reported two putative new species of *Archigetes* from *Ictiobus* spp. in Mississippi. They differ conspicuously in their morphology from *A. iowensis* as well as all three morphotypes found in endemic leuciscids and atherinopsids in Mexico.

*Archigetes* sp. 3 from *C. humboldtianum* represents the first record of



any caryophyllidean tapeworm from atheriniform fish. Caryophyllideans occur mainly in siluriform and cypriniform fishes, with few records from cichlids (Cichliformes) and elephant fishes (Mormyriiformes) in Africa (Scholz et al., 2021). The present finding may represent an accidental infection of a silverside or it results from a host switching of a species of *Archigetes* from cypriniform to atheriniform fish host.

4. *Isoglaridacris brevicollis* sp. n. Fig. 2A–F

Synonym: *Isoglaridacris* sp. of Pérez-Ponce de León et al. (2010).

**Material studied:** four specimens from *Catostomus nebuliferus*, Rio Covadonga, Peñon Blanco, Durango, collected by Rogelio Aguilar-Aguilar (CNHE 6761, 6802; IPCAS C-885); ten spec. from *Catostomus bernardini* Girard, Rio Bavispe, Sonora, collected by Rogelio Rosas-Valdéz in November 2008 (CNHE 6796); two spec. from *Moxostoma astrinum* Bean, Atengo, Jalisco, collected by Rogelio Rosas-Valdéz in November 2008 (CNHE 6799).

Description (based on whole mounts of four specimens, including

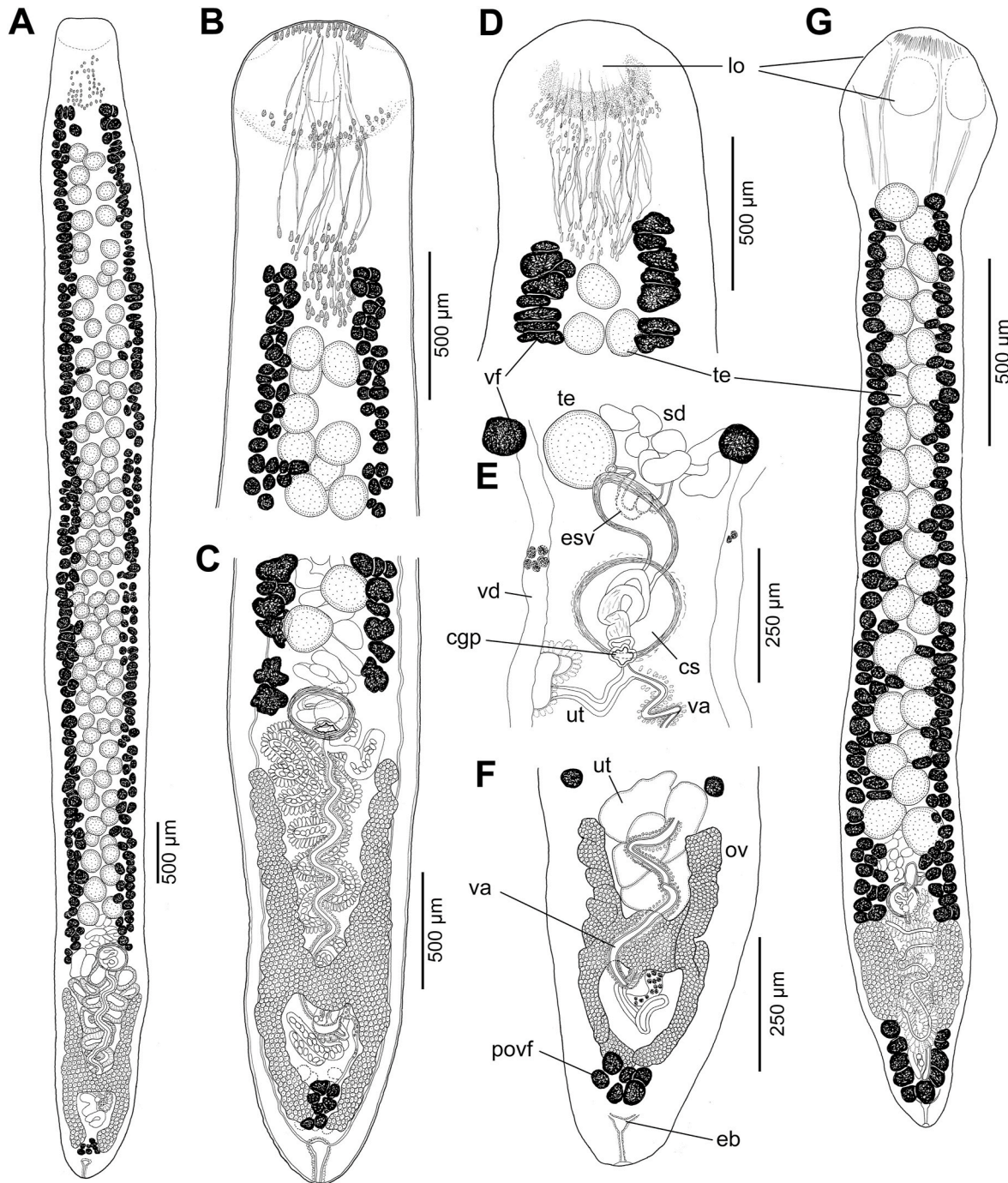


Fig. 2. *Isoglaridacris brevicollis* sp. n. from *Catostomus nebuliferus*, Durango (CNHE xxxx; IPCAS C-xxxx) (A–D), *Catostomus bernardini*, Sonora, Mexico (CNHE 6796) (E), and *Moxostoma astrinum*, Jalisco (CNHE 6799) (F); *Pseudoglaridacris confusa* (Hunter, 1929) from *Ictiobus meridionalis*, Oaxaca (G). A – total view, ventrally; B – anterior end; C – posterior end, ventrally; D – slightly contracted scolex; E – cirrus-sac with external seminal vesicle, ventrally; F – ovary with joined posterior wings, dorsally (uterine loops are omitted at level of ovarian isthmus and more posteriorly); G – total view, dorsally. Abbreviations: cs – cirrus-sac; eb – excretory bladder; esv – external seminal vesicle; lo – loculi; ov – ovary; povf – postovarian vitelline follicles; sd – sperm duct (*vas deferens*); te – testes; ut – uterus; va – vagina; vd – vitelline duct; vf – vitelline follicles.



one contracted; measurements in micrometres unless otherwise stated): Caryophyllidea, Capingentidae (as emended by Scholz et al., 2021; formerly in the Caryophyllaeidae *sensu* Mackiewicz, 1994). Body elongate, robust, 10.0–12.6 mm long, with maximum width 798–1054 mm at anterior third or middle of body (length: width ratio 1 : 0.07–0.09); width of body at level of cirrus-sac 713–837, at level of ovarian isthmus 615–701.

Scolex widely rounded, 540–611 wide, with central pair of shallow loculi; lateral loculi very shallow or indistinguishable (Fig. 2A, B, D); apical disc absent, anterior edge of scolex slightly convex (Fig. 2B, D) or almost blunt (Fig. 2A). Neck indistinct, body at level of first vitelline follicles 570–652 wide. Inner longitudinal muscles well-developed. Osmoregulatory canals form 8 main longitudinal, anastomosed canals. Excretory bladder elongate, with widened proximal and long, narrow distal (terminal) part, 158–208 long and 72–88 wide. Excretory pore terminal.

Testes medullary, subspherical to widely oval, 123–273 long and 114–193 wide, arranged in 2 longitudinal rows and 2 layers; testes numbering 154–180 (mean 168; n = 4). Anterior-most testes begin 1015–1, 618 posterior to anterior extremity, i.e., 9–13% of total body length, 201–324 posterior to anterior-most vitelline follicles. Posteriorly, testes reach anterior to cirrus-sac, slightly anterior to posterior-most preovarian vitelline follicles (Fig. 2C). Cirrus-sac thick-walled, subspherical, wider than long, 200–256 long and 230–287 wide; width of cirrus-sac represents 32–34% of body width at level of cirrus-sac. External seminal vesicle thick-walled, pyriform, 177–207 long and 93–123 wide. Gonopore single, situated 137–266 anterior to ovarian wings.

Ovary inverted A-shaped, with long and narrow ovarian wings, posterior wings approaching to each other (Fig. 2A, C) or overlapping one another (Fig. 2F), but never connected posteriorly. Ovarian arms 1168–1631 long, i.e., 11–13% of total body length, and 160–231 wide near isthmus. Maximum width of ovary at level of anterior-most ovarian wings 534–652; width at level of ovarian isthmus 461–568. Ratio of length of ovarian wings to length of uterus area 1 : 0.86–1.09. Vagina tubular, slightly sinuous; seminal receptacle absent (Fig. 2F).

Vitelline follicles medullary, variable in shape and size, 72–212 long and 42–143 wide. Preovarian vitelline follicles numerous, begin anterior to first testes, 691–1420 posterior to anterior edge of scolex, i.e., 7–11% of total body length. Posteriorly, preovarian vitelline follicles do not reach to ovary (finish at distance of 151–238 from ovary; Fig. 2C). Postovarian vitelline follicles relatively few (estimated as 15–30 follicles), forming small, compact group near posterior extremity, between posterior ovarian wings (Fig. 2A, C) or slightly more posterior (Fig. 2F).

Uterus coiled, forming a few loops posterior to ovarian isthmus; anteriorly, loops reach to level of cirrus-sac, never more anteriorly (Fig. 2C). Uterine glands well-developed, absent only in most distal and proximal parts of uterus (Fig. 2C). Uterus area 1440–1500 long, i.e., 12–15% of total body length. Eggs operculate, without fully formed oncosphere *in utero*; intrauterine eggs in whole mounts 36–41 long and 23–26 wide (n = 11).

## 2.5. Taxonomic summary

*Type-host*: *Catostomus nebuliferus* (Cypriniformes: Catostomidae).

*Additional hosts*: *Catostomus bernardini* and *Moxostoma austrinum* (Cypriniformes: Catostomidae).

*Type-locality*: Rio Covadonga, Peñon Blanco, Durango, Mexico (24.7912° N, 104.0334° W).

*Distribution*: Mexico (Durango, Jalisco, Sonora).

*Type-material*: Holotype (CNHE 6802) and two paratypes (CNHE 6761); one paratype (IPCAS C-885).

*Representative DNA sequences*: Not available.

## 2.6. Differential diagnosis

The new species is placed in *Isoglaridacris* Mackiewicz, 1965 based on the following morphological characteristics (see Mackiewicz, 1994 for generic diagnosis): gonopore single, external seminal vesicle present, ovary in shape of inverted letter A or nearly so, uterus does not loop anterior to the cirrus-sac, and vitelline follicles usually in lateral rows only. *Isoglaridacris brevicollis* n. sp. differs from other 12 species of *Isoglaridacris* in the shape of the scolex, which is round (versus wedge-shaped in most species), and the absence of a defined neck (neck region is not clearly separated from an indistinct, very short neck – Fig. 2A, B, D) (versus neck always distinct, often very long – see Table 1 in Williams, 1975).

*Isoglaridacris brevicollis* n. sp. is most similar to *Isoglaridacris hexacotyle* (syn. *Monobothrium hexacotyle* Linton, 1897), which was described from *Catostomus* sp. from the Gila and Salt River in Arizona by Linton (1897). This species was redescribed by Mackiewicz (1968), based on tapeworms from *Catostomus clarki* and *C. insignis* from Utah and *Catostomus* sp. from Colorado. The new species can be differentiated from *I. hexacotyle* mainly by the shape of the scolex, which is wedge-shaped to hexagonal in the latter species, with a pair of well-developed, deep median loculi and two pairs of shallow, but distinct lateral loculi (see Figs. 1–3 of *I. hexacotyle* in Mackiewicz, 1968), and an indistinct neck, wider or as wide as the scolex in the new species (Fig. 2A, B, D), versus well-defined, always narrower than the scolex in *I. hexacotyle* (see Figs. 1–3 in Mackiewicz, 1968).

*Isoglaridacris* was erected by Mackiewicz (1965) to accommodate his new species *Isoglaridacris bulbocirrus* Mackiewicz (1965) from *Catostomus commersonii* (Lacépède), *C. catostomus* (Forester) and *Hypentelium nigricans* (Lesueur) (see Mackiewicz, 1965). Currently, it includes 12 species, with three taxa occurring in *Catostomus* spp., namely *I. bulbocirrus*, *Isoglaridacris calentinei* Mackiewicz (1974) from *C. columbianus* (Eigenmann and Eigenmann) and *C. macrocheilus* Girard, and *Isoglaridacris hexacotyle* (Linton, 1897) from *Catostomus clarki*, *C. insignis* and *Catostomus* sp. (Williams, 1975; Scholz and Oros, 2017).

In addition to a different shape of the scolex and the presence of a well-defined neck, *I. bulbocirrus* can be easily distinguished from the new species by an extraordinarily large cirrus-sac and a much longer distance of the anterior-most testes from the first vitelline follicles (see Figs. 1–7 in Mackiewicz, 1965). *Isoglaridacris calentinei* differs by a different shape of the scolex and the absence of postovarian vitelline follicles (Mackiewicz, 1974).

Additionally to the scolex shape and presence of the neck, the remaining nine species can be differentiated from the new species as follows: (i) *Isoglaridacris agminis* Williams et Rogers, 1972 from *Erimyzon sucetta* (Lacépède) has a single median row of testes (Williams and Rogers, 1972) versus double in *I. brevicollis* n. sp., and much fewer testes (28–40 versus 154–180); (ii) *Isoglaridacris chetekensis* Williams (1977) and *Isoglaridacris wisconsinensis* Williams (1977) from *Moxostoma macrolepidotum* (Lesueur) and *Hypentelium nigricans*, respectively, differ by the presence of a single median row of preovarian vitelline follicles well separated from lateral rows of follicles (Williams, 1977) versus absent in the new species; (iii) *Isoglaridacris erraticus* Williams (1975) and *Isoglaridacris etowani* Williams (1975) from *Moxostoma* cf. *poecilurum* (Jordan) and *Hypentelium etowanum* (Jordan), respectively, can be differentiated by a more posterior position of the testes compared to the position of the first vitelline follicles (Williams, 1975) versus short distance between the anterior-most testes and vitelline follicles in the new species; *I. erraticus* also differs in a more posterior extent of the testes, which may reach to the ovary (versus anterior to the cirrus-sac in *I. brevicollis* n. sp.); (iv) *Isoglaridacris folius* Fredericson et Ulmer, 1965 from *Moxostoma erythrurum* (Rafinesque) differs by the greater posterior extent of preovarian vitelline follicles, which reach the level of the ovary (Fredericson and Ulmer, 1965) versus last follicles at a distance from the ovary in the new species, and a more posterior position of the cirrus-sac, with the gonopore between ovarian wings (versus the gonopore situated

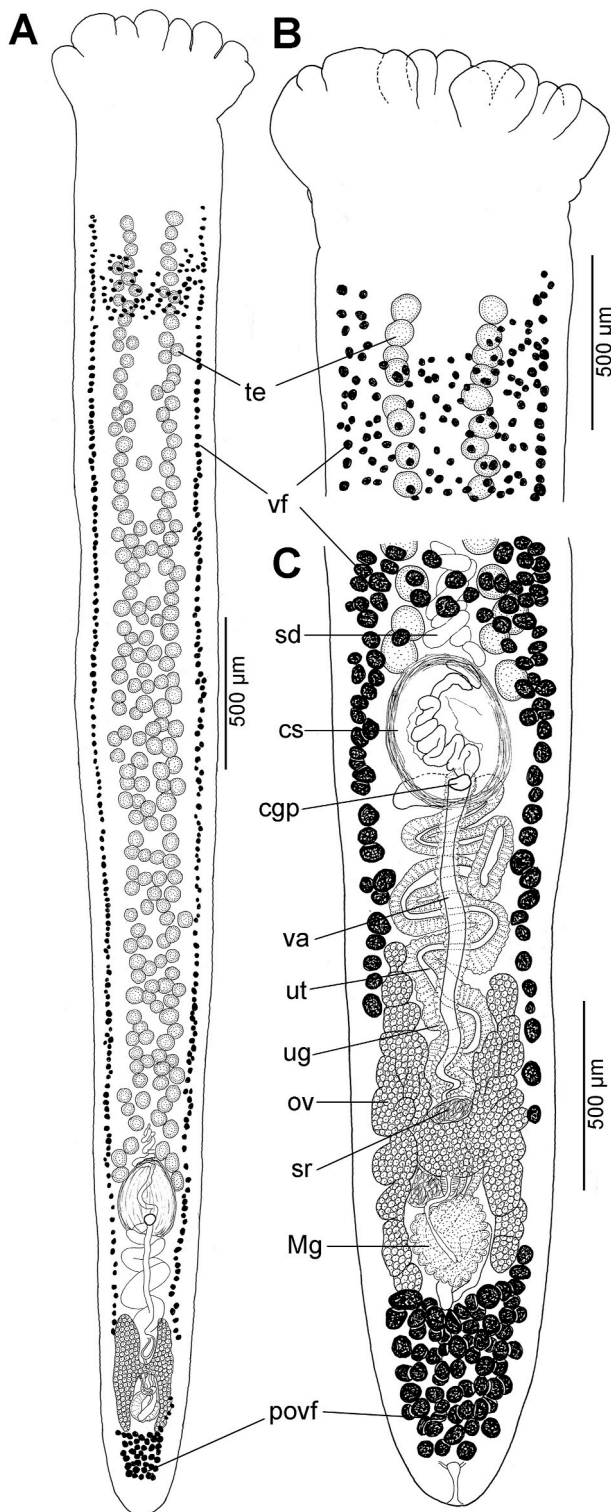


Fig. 3. *Khawia japonensis* (Yamaguti, 1934) from *Cyprinus carpio*, Durango. A – total view, ventrally (CNHE 6516; median preovarian vitelline follicles omitted except for anterior-most follicles); B – anterior end; C – posterior end, ventrally (both CNHE 6516). Abbreviations: cgp – common genital pore; cs – cirrus-sac; Mg – Mehlis' gland; ov – ovary; povf – postovarian vitelline follicles; sd – sperm duct (*vas deferens*); sr – seminal receptacle; te – testes; ug – uterine glands; ut – uterus; va – vagina; vf – vitelline follicles.

at a distance anterior to the ovary in the new species); (v) *Isoglaridacris jonesi* Mackiewicz (1972) from *Moxostoma duquesni* (Lesueur) and *M. erythrurum* does not possess postovarian vitelline follicles (Mackiewicz, 1972), which are present in *I. brevicollis* n. sp.; (vi) *Isoglaridacris longus* Fredericson et Ulmer, 1965 from *Moxostoma macrolepidotum* has a much longer preovarian uterus area and preovarian vitelline follicles reach much more anteriorly (see Fig. 12 in Fredericson and Ulmer, 1965); (vii) *Isoglaridacris multivitellaria* Amin (1986) from *E. sucetta* has extensive postovarian vitelline follicles (Amin, 1986) versus just a few (a dozen) follicles in the new species, with the ovary situated more anteriorly in *I. multivitellaria* compared to that of *I. brevicollis* n. sp.

## 2.7. Remarks

Description of the new species was based on four specimens from *Catostomus nebuliferus*. Supposedly conspecific tapeworms were found in *Catostomus bernardini* and *Moxostoma austrinum* from Sonora and Jalisco. Unfortunately, these specimens are in poor condition, being partly decomposed and deformed. For this reason, their measurements were not used for the original description. Molecular data are not available for the new species to assess its relationships to other species of *Isoglaridacris*. However, morphological similarity with *I. hexacotyle*, which also parasitises species of *Catostomus* and has been reported from the southern part of the USA (Arizona), i.e., close to the distribution area of the new species, indicates that these species may be closely related.

## 5. *Pseudoglaridacris confusa* Hunter (1929), Oros et al. (2018), Fig. 2G

Synonym: *Glaridacris confusa* Hunter (1929).

Material studied: One specimen from *Ictiobus meridionalis* (Günther) (Catostomidae: Ictiobinae), Rio Papaloapan at Tuxtepec, Oaxaca, Mexico, collected by Anindo Choudhury in November 2008 (CNHE 6798); vouchers from *I. meridionalis*, Papaloapan River at Tlacotalpan, Veracruz, Mexico, collected by Tomáš Scholz and Guillermo Salgado-Maldonado on 26 September 2000 (CNHE 10836, IPCAS C-363/1, NHMUK, 2017.10.25.7–8, USNM 1460982–1460983; see Oros et al., 2018).

Type host: Smallmouth buffalo, *Ictiobus bubalus* (Rafinesque) (Catostomidae: Ictiobinae).

Host in Mexico: Usumacinta buffalo, *Ictiobus meridionalis*.

Morphological descriptions: Hunter (1929), Calentine and Williams (1967), Orcutt et al. (2017), Oros et al. (2018).

Type locality: Rock River, Illinois (USA).

Distribution in Mexico: Oaxaca, Veracruz.

## 2.8. Remarks

The specimen found in *I. meridionalis* corresponds to *P. confusa* as characterised by Mackiewicz (1976) in its morphology, including the low numbers of testes (31; 24–27 testes in specimens from Veracruz), anterior-most testes always anterior to anterior-most vitelline follicles (posteriorly, testes reach the level of the external seminal vesicle – Fig. 2G), small size of the body (total length 2.9 mm; 1.2–2.1 mm in immature worms from Veracruz), postovarian vitelline follicles forming a U or V shape and touching the ovary, and a relatively large postgonoporal distance (20% of total body length; 19–25% in specimens from Veracruz).

This species was described as *Glaridacris confusa* by Hunter (1929) from *Ictiobus bubalus* in the Rock River in Illinois (type locality) and the Mississippi River in Iowa. Oros et al. (2018) transferred the species to *Pseudoglaridacris* Oros, Uhrovič et Scholz et al., 2018 as *P. confusa* n. comb. Hunter (1929) reported 25–35 testes in two rows in worms 3–7 mm long and illustrated specimens with the testes extending more anteriorly than the vitelline fields and the H-shaped ovary in contact with postovarian vitelline follicles that form a broad U- or V-shape. However, Orcutt et al. (2017) questioned the reliability of



morphological and biometrical characteristics used to differentiate this species from *Pseudoglaridacris laruei* (Lamont, 1920) (syn. *Glaridacris laruei* Lamont, 1920) by Mackiewicz (1976).

*Pseudoglaridacris confusa* has been reported from several buffaloes, such as bigmouth buffalo (*Ictiobus cyprinellus* [Valenciennes]), Usumacinta buffalo (*Ictiobus meridionalis*), and black buffalo (*Ictiobus niger* [Rafinesque]), but also in a number of other suckers, e.g., quillback, *Carpionodes cyprinus* (Lesueur), white sucker, *Catostomus commersonii*, largescale sucker, *C. macrocheilus* Girard, and greater redhorse, *Moxostoma valenciennesi* Jordan. Such a broad range of fish hosts is unusual among North American caryophyllideans (Scholz and Kuchta, 2017; Kuchta et al., 2020) and should be verified using molecular data.

*Pseudoglaridacris confusa* has a wide distribution area that includes Canada (Ontario and Québec), Mexico (Oaxaca and Veracruz), and the United States (Arizona, Connecticut, Idaho, Iowa, Mississippi, New York, North Dakota, Oklahoma and Wisconsin) (Hoffman, 1999; Oros et al., 2018). However, the actual range of definitive hosts and distribution of *P. confusa* should be confirmed because differentiation between this species and *P. laruei* (Lamont, 1920) can be problematic (Orcutt et al., 2017).

In Mexico, *P. confusa* was reported (as *G. confusa*) from an unidentified 'bagre' (a catfish) from the Papaloapan River at Tuxtepec, Oaxaca, Mexico by Bravo-Hollis and Caballero-Deloya (1973). This catfish was apparently accidental or postcyclic host because Nearctic caryophyllideans do not occur in catfishes (Scholz and Kuchta, 2017; Scholz et al., 2021). Usumacinta buffalo is a Neotropical member of the otherwise Nearctic genus and occurs southwards up to Central America (Guatemala – Froese and Pauly, 2021).

Family Caryophyllaeidae Leuckart, 1878 (as emended by Scholz et al., 2021).

### 5. *Khawia japonensis* (Yamaguti, 1934) Hsü, 1935 Fig. 3

Synonyms: *Caryophyllaeus japonensis* Yamaguti (1934); *Bothrioscolex japonensis* (Yamaguti, 1934) Szidat, 1937; *Khawia iowensis* Calentine et Ulmer, 1961; *Khawia cyprini* Li, 1964

Material studied: Seven specimens misidentified as *Khawia sinensis* Hsü, 1935 from *Cyprinus carpio*, Presa Francisco Zarco, Durango, Mexico, collected by David Hernández in June and November 2008 (CNHE 6515, 6516; IPCAS C-348) (see Pérez-Ponce de León et al., 2010).

Type host: *Cyprinus carpio* Linnaeus (Cypriniformes: Cyprinidae).

Distribution in Mexico: Durango, Tamaulipas.

Morphological description: Yamaguti (1934 – as *Caryophyllaeus japonensis*), Calentine and Ulmer (1961 – as *K. iowensis*), Protasova et al. (1990), Scholz et al. (2001, 2011a).

### 2.9. Remarks

Tapeworms found by the present authors in common carp correspond in their morphology to *K. japonensis* as redescribed by Scholz et al. (2011a). All specimens were immature except a single worm bearing just two eggs in the uterus. The worms were 4.8–10.7 mm long and 0.64–1.23 mm wide at the level of the scolex or at the first third of the body. The scolex is cuneifimbriate, 0.64–1.01 mm wide (Fig. 3A and B). Anterior-most testes arrange in two longitudinal row, confluent more posteriorly; posterior-most testes anterior or anterolateral to the cirrus-sac (Fig. 3A, C). Anterior-most vitelline follicles begin at the same level as first testes and reach posteriorly as far as to the ovary, with a few follicles present lateral to the ovarian wings, but not continuous with postovarian follicles (Fig. 3A, C).

*Khawia japonensis* was described as *Caryophyllaeus japonensis* from the common carp, *Cyprinus carpio*, in Japan and occurred originally in East Asia (Yamaguti 1934; Protasova et al., 1990; Scholz et al., 2001, 2011a). With the import of common carp throughout the world, the parasite was introduced to North America (described there as *Khawia iowensis* by Calentine and Ulmer, 1961) and more recently to Europe

(Scholz et al. 2011b, 2018).

Scholz et al. (2011a) considered *K. japonensis* to be a specific parasite of *C. carpio*, even though Hoffman (1999) reported non-cyprinid fishes such as bigmouth buffalo, *Ictiobus cyprinellus*, white sucker, *Catostomus commersonii* (Cypriniformes: Catostomidae), and black bullhead, *Ameiurus melas* (Rafinesque) (Siluriformes: Ictaluridae) as hosts of this parasite in North America. However, these fishes are apparently incidental hosts or other caryophyllidean tapeworms were misidentified.

In North America, *K. japonensis* occurs in Canada (Manitoba and Ontario) and USA (California, Illinois, Iowa, Kansas, Minnesota, Nebraska, North Dakota, Oklahoma, Oregon, South Dakota, Tennessee, Wisconsin – Scholz et al., 2018). The only previous record of *K. japonensis* (as *K. iowensis*) from Mexico was listed in an Appendix 1 by Pérez-Ponce de León and Choudhury (2005) from unspecified cyprinids from the Rio Grande basin in Mexico. However, no other details about this record were provided. The present specimens confirm the occurrence of *K. japonensis* in northern Mexico and most likely represent the southernmost record of the parasite (25.270833 S, 103.773056 W).

*Khawia japonensis* is distinguished from congeneric species, including *Khawia sinensis* Hsü, 1935, another parasite of common carp, by the shape of its body, with almost the same width throughout its length, a cuneifimbriate scolex slightly wider than the neck region, the first testes beginning very close posterior to the scolex, usually anterior to the first vitelline follicles (Fig. 3A, B), and a few vitelline follicles present lateral to the preovarian uterine loops, with a few isolated follicles lateral to the ovarian arms (Fig. 3A, C). Unlike *K. sinensis*, which is considerably larger (up to 12 cm) and has a wider distribution area (Oros et al., 2009), the pathogenicity and veterinary importance of *K. japonensis* for cultured carp are not known.

### 3. Discussion

The present paper is the first systematic survey of caryophyllidean tapeworms in Mexico. Even though the number of species found is rather low, some records are important from the taxonomic (a new species described), zoogeographical (records from the southernmost part of the Nearctic region) and host association (first record of a caryophyllidean in atheriniform fish) points of view. Overall, the cestode fauna of Mexican teleosts is depauperate, especially when compared with the extraordinarily rich fauna of fish trematodes and monogeneans (Salgado-Maldonado, 2006; Pérez-Ponce de León and Choudhury, 2010). The most frequent cestode parasites of freshwater fish in Mexico are larvae (metacestodes) of gryporhynchids (Cyclophyllidea) (Scholz and Salgado-Maldonado, 2001), whose adults parasitise fish-eating birds (Ortega-Olivares et al., 2014; Ortega-Olivares and García-Varela, 2019). In contrast, adult tapeworms are relatively rare (Salgado-Maldonado, 2006). As discussed by Pérez-Ponce de León and Choudhury (2010), while the number of studies describing the helminth parasite fauna of freshwater fishes in Mexico increased, the rate of discovery of different species (including new species) has slowed for cestodes. Actually, irrespective of the fact that caryophyllidean tapeworms are not abundant in freshwater fishes in Mexico, their study had been long neglected, and only isolated reports of unidentified species had been published, until we conducted the present study. Instead, in the Nearctic part of Mexico, several species of proteocephalids (Onchoproteocephalidea) occur in freshwater fish, especially members of the newly erected subfamily Essexiellinae (formerly placed in the Corallobothriinae – see Hoffman, 1999) in ictalurid catfishes (Siluriformes) (Scholz et al., 2020), whereas bothriocephalideans are represented by just a few species, especially the invasive Asian fish tapeworm, *Schyzocotyle acheilognathi* (Yamaguti, 1934) (syn. *Bothriocephalus acheilognathi*) (Kuchta et al., 2018; Pérez-Ponce de León et al., 2018).

The present study provides the first data on the occurrence of species of two lytocestid genera (*Archigetes* and *Isoglaridacris*), which have an Holarctic (*Archigetes*) and Nearctic (*Isoglaridacris*) distribution (Scholz and Oros, 2017). In addition to a new species of species-rich

*Isoglaridacris*, the most intriguing finding is the first report of a caryophyllidean cestode in atheriniform fish. Caryophyllideans occur almost exclusively in cypriniform and siluriform fish, with just a few species found in mormyriiform and cichliform fishes (Scholz and Oros, 2017; Scholz et al., 2021).

Catostomids (commonly known as suckers) reach their southernmost distributional range in the Usumacinta River basin comprising south-eastern Mexico and northern Guatemala. At least 18 species of suckers allocated in six genera (*Carpioides* Rafinesque, *Catostomus* Lesueur, *Cycleptus* Lesueur, *Ictiobus* Rafinesque, *Moxostoma* Rafinesque, and *Xyrauchen* Abbott) have been reported in Mexican freshwaters (Miller et al., 2005; Lyons et al., 2020). However, studies on the diversification of the southern group of *Moxostoma* (previously known as *Scartomyzon* Baird & Girard) showed that the group consisted of six differentiated forms, three still undescribed (Clements et al., 2012; Pérez-Rodríguez et al., 2016), raising the number of catostomids to 21. Of these, only four have been studied for helminths, i.e., *Catostomus bernardini*, *C. nebuliferus*, *Ictiobus meridionalis* and *Moxostoma austrinum*. From them, only two helminths were recovered, representing part of the core parasite fauna of catostomids, i.e., the caryophyllidean *P. confusa* and the trematode *Lissorhis fairporti* Magath, 1917 (see Pérez-Ponce de León and Choudhury, 2005). Considering the relatively narrow host specificity of many North American caryophyllideans towards catostomids (Scholz and Kuchta, 2017; Kuchta et al., 2020) we predict the occurrence of more unknown species of endemic caryophyllideans in Mexican freshwaters; these may include not only tapeworms associated to catostomids, but also to cyprinids and other unrelated fish groups.

Cyprinoids including families Cyprinidae and Leuciscidae are also a Nearctic fish group that reaches its southernmost distribution range in Mexico, where as many as 77 native species have been reported (Miller and Smith, 1986; Miller et al., 2005; Lyons et al., 2020). The only previous report of a caryophyllidean tapeworm in native cyprinoids occurring in Mexico is that of Mendoza-Garfias et al. (1996) from the Patzcuaro chub, *Algansea lacustris* Steindachner, a native species endemic to Lake Patzcuaro in Central Mexico. The species was reported as Caryophyllidea gen. sp. from a single fish specimen sampled in 360 hosts examined throughout a year. Pérez-Ponce de León and Choudhury (2005) re-examined the specimen and determined that it might represent a new species of *Edlintonia* Mackiewicz (1970) based on the distribution and host association pattern, although more specimens are required to confirm that hypothesis. Interestingly, cyprinoids are not the principal hosts of caryophyllideans in the Nearctic region (in contrast to the Palaearctic region – see Kuchta et al., 2020; Scholz et al., 2021). Only four caryophyllideans occur in cyprinoids (Cyprinidae and Leuciscidae) in North America: *Edlintonia ptychocheila* Mackiewicz, 1970 in *Ptychocheilus* Agassiz and in *Myocheilus* Richardson, *Bialovarium nocomis* Fischthal, 1953 in *Nocomis* Kirtland, *Hypocaryophyllaeus gilae* Fischthal, 1953 in *Gila* Baird and Girard, and *Pliovittellaria wisconsinensis* Fischthal, 1951 in *Notemigonus* Rafinesque, not considering three species in non-native *Cyprinus carpio*, namely *Archigetes iowensis*, *Atractolytocestus huronensis* Anthony, 1958 and *Khawia iowensis* (syn. of *K. japonensis*) (Hoffman, 1999). Our study added three putative new species of *Archigetes* parasitising endemic leuciscids in Mexico.

Finally, the cestode *Khawia japonensis* represents an invasive species. When reported for the first time (as *K. sinensis* by Pérez-Ponce de León et al., 2010), it was not considered that the record corresponded to a species that was introduced in Mexican freshwaters with common carp imported for commercial purposes. As discussed above, *K. japonensis* is a specific parasite of *C. carpio* throughout the world. It is widely known that other species of helminths were introduced to Mexico along with carps, such as the Asian fish tapeworm *Schyzocotyle acheilognathi*, and the trematode *Centrocestus formosanus* (Nishigori, 1924), and they may represent a serious threat to the aquacultural activity.

## Declaration of competing interest

There is no conflict of interest in the submitted manuscript entitled “Caryophyllidean tapeworms (Cestoda), Nearctic parasites of fish in Mexico, including description of a new species of *Isoglaridacris* and the first report of *Khawia japonensis*, an invasive parasite of common carp (*Cyprinus carpio*).”

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## References

- Aguilar-Aguilar, R., Contreras-Medina, R., Salgado-Maldonado, G., 2003. Parsimony analysis of endemism (PAE) of Mexican hydrological basins based on helminth parasites of freshwater fishes. *J. Biogeogr.* 30, 1861–1872.
- Amin, O.M., 1986. Caryophyllidae (Cestoda) from lake fishes in Wisconsin with a description of *Isoglaridacris multivittellaria* sp. n. from *Erimyzon succetta* (Castostomidae). *Proc. Helminthol. Soc. Wash.* 53, 48–58.
- Bravo-Hollis, M., Caballero-Deloya, J., 1973. Catálogo de la Colección Helmintológica del Instituto de Biología. Instituto de Biología, Universidad Nacional Autónoma de México, Publicaciones Especiales 2, 138.
- Calentine, R.L., 1962. *Archigetes iowensis* sp. n. (Cestoda: Caryophyllidae) from *Cyprinus carpio* L. And *Limnodrilus hoffmeisteri* Claparède. *J. Parasitol.* 48, 513–524.
- Calentine, R.L., Ulmer, M.J., 1961. *Khawia iowensis* n. sp. Cestoda: Caryophyllidae from *Cyprinus carpio* L. In Iowa. *J. Parasitol.* 47, 795–805.
- Calentine, R.L., Williams, D., 1967. Larval development of *Glaridacris confusa* (Cestoda: Caryophyllidae). *J. Parasitol.* 53, 692–693.
- Clements, M.D., Bart Jr., H.L., Hurley, D.L., 2012. A different perspective on the phylogenetic relationships of the Moxostomatini (Cypriniformes: Catostomidae) based on cytochrome- b and growth hormone intron sequences. *Mol. Phylogenet. Evol.* 63, 159–167.
- Choudhury, A., García-Varela, M., Pérez-Ponce de León, G., 2017. Parasites of freshwater fishes and the Great American Biotic Interchange: a bridge too far? *J. Helminthol.* 91, 174–196.
- Frederickson, L.H., Ulmer, M.J., 1965. Caryophyllid cestodes from two species of redbone (*Moxostoma*). *Proc. Iowa Acad. Sci.* 72, 444–461.
- Froese, R., Pauly, D. (Eds.), 2021. FishBase. World Wide Web electronic publication version (1/2021). [www.fishbase.org](http://www.fishbase.org).
- Hoffman, G.L., 1999. Parasites of North American Freshwater Fishes, second ed. Cornell University Press, Ithaca, New York, p. 539.
- Hunter III, G.W., 1929. New Caryophyllidae from north America. *J. Parasitol.* 15, 185–192.
- Kuchta, R., Choudhury, A., Scholz, T., 2018. Asian fish tapeworm: the most successful invasive parasite in freshwaters. *Trends Parasitol.* 34, 511–523.
- Kuchta, R., Rehulková, E., Francová, K., Scholz, T., Šimková, A., 2020. What do we know about parasites of cypriniform fishes? Diversity of monogeneans and tapeworms across two continents. *Int. J. Parasitol.* 50, 771–786.
- Linton, E., 1897. Notes on cestode parasites of fishes. *Proc. U. S. Natl. Mus.* 20, 423–456.
- Lyons, T.J., Maíz-Tomé, L., Tognelli, M., Daniels, A., Meredith, C., Bullock, R., Harrison, I. (Eds.), 2020. The Status and Distribution of Freshwater Fishes in Mexico. IUCN and ABQ BioPark, Cambridge, UK and Albuquerque, New Mexico, USA, p. 91.
- Mackiewicz, J.S., 1965. *Isoglaridacris bulboicirrus* gen. et sp. n. (Cestoidea: Caryophyllidae) from *Catostomus commersoni* in North America. *J. Parasitol.* 51, 377–381.
- Mackiewicz, J.S., 1968. *Isoglaridacris hexacotyle* comb. n. (Cestoidea: Caryophyllidae) from catostomid fishes in southwestern North America. *Proc. Helminthol. Soc. Wash.* 35, 193–196.
- Mackiewicz, J.S., 1972. Two new species of caryophyllid tapeworms from catostomid fishes in Tennessee. *J. Parasitol.* 58, 1075–1081.
- Mackiewicz, J.S., 1974. *Isoglaridacris calentinei* n. sp. (Cestoidea: Caryophyllidae) from catostomid fish in western United States. *Trans. Am. Microsc. Soc.* 93, 143–147.
- Mackiewicz, J.S., 1976. *Glaridacris vogei* n. sp. (Cestoidea: Caryophyllidae) from catostomid fishes in western North America. *Trans. Am. Microsc. Soc.* 95, 92–97.



- Mackiewicz, J.S., 1994. Order Caryophyllidea van Beneden in Carus, 1863. In: Khalil, L. F., Jones, A., Bray, R.A. (Eds.), Keys to the Cestode Parasites of Vertebrates. CAB International, Wallingford, pp. 21–43.
- Martínez-Aquino, A., Salgado-Maldonado, G., Aguilar-Aguilar, R., Cabañas-Carranza, G., Mendoza-Palmero, C., 2007. Helminth parasites of *Characodon audax* and *Characodon lateralis* (Pisces: Goodeidae), two endemic freshwater fish species from the state of Durango, Mexico. Southwest. Naturalist 52, 125–130.
- Mendoza-Garfias, B., García-Prieto, L., Pérez-Ponce de León, G., 1996. Helminths de la “acúmara” *Algansea lacustris* en el Lago de Pátzcuaro, Michoacán, México. An. Inst. Biol., Univ. Nac. Autón. Méx., Ser. Zool. 67, 77–88.
- Miller, R.R., Minckley, W.L., Norris, S.M., 2005. Freshwater Fishes of México. The University of Chicago Press, Chicago, p. 652.
- Miller, R.R., Smith, M.L., 1986. Origin and geography of the fishes of central Mexico. In: Hocutt, C.H., Wiley, E.O. (Eds.), The Zoogeography of North American Freshwater Fishes. Wiley-Interscience Publications, New York, pp. 487–519.
- Orcutt, G., Shaffer, J., Barger, M.A., 2017. Evaluation of key taxonomic characters distinguishing *Glaridacris confusus* and *Glaridacris laruei* (Cestoda: Caryophyllaeidae). Comp. Parasitol. 84, 180–186.
- Oros, M., Scholz, T., Hanzelová, V., 2009. Tapeworm *Khawia sinensis*: review of the introduction and subsequent decline of a pathogen of carp, *Cyprinus carpio*. Vet. Parasitol. 164, 217–222.
- Oros, M., Uhrovič, D., Scholz, T., 2018. A new classification of *Glaridacris* Cooper, 1920 (Cestoda: Caryophyllidae), parasites of suckers (Catostomidae) in North America, including erection of *Pseudoglaridacris* n. gen. J. Parasitol. 104, 60–69.
- Ortega-Olivares, M.P., García-Preto, L., García-Varela, M., 2014. Gryporhynchidae (Cestoda: Cyclophyllidae) in Mexico: species list, hosts, distribution and new records. Zootaxa 3795, 101–125.
- Ortega-Olivares, M.P., García-Varela, M., 2019. Phylogenetic relationships of the family Gryporhynchidae (Cestoda: Cyclophyllidae) inferred through SSU and LSU rDNA sequences. J. Helminthol. 93, 763–771.
- Pérez-Ponce de León, G., Choudhury, A., 2002. Adult endohelminth parasites of ictalurid fishes (Osteichthyes: Ictaluridae) in México: empirical evidence for biogeographical patterns. Comp. Parasitol. 69, 10–19.
- Pérez-Ponce de León, G., Choudhury, A., 2005. Biogeography of helminth parasites of freshwater fishes in Mexico: the search for patterns and processes. J. Biogeogr. 32, 645–659.
- Pérez-Ponce de León, G., Choudhury, A., 2010. Parasite inventories and DNA-based taxonomy: lessons from helminths of freshwater fishes in a megadiverse country. J. Parasitol. 96, 236–244.
- Pérez-Ponce de León, G., Lagunas-Calvo, O., García-Prieto, L., Briosio-Aguilar, R., Aguilar-Aguilar, R., 2018. Update on the distribution of the co-invasive *Schizocotyle acheilognathi* (= *Bothriocephalus acheilognathi*), the Asian fish tapeworm, in freshwater fishes of Mexico. J. Helminthol. 92, 279–290.
- Pérez-Ponce de León, G., Mendoza-Garfias, B., Rosas-Valdez, R., Choudhury, A., 2013. New host and locality records of freshwater fish helminth parasites in river basins north of the Transmexican Volcanic Belt: another look at biogeographical patterns. Rev. Mex. Biodivers. 84, 556–562.
- Pérez-Ponce de León, G., Rosas-Valdez, R., Aguilar-Aguilar, R., Mendoza-Garfias, B., Mendoza-Palmero, C., García-Prieto, L., Rojas-Sanchez-Aline, Briosio-Aguilar, R., Perez-Rodríguez, R., Domínguez-Domínguez, O., 2010. Helminth parasites of freshwater fishes, Nazas River basin, northern Mexico. Checklist 6, 26–35.
- Pérez-Rodríguez, R., Domínguez-Domínguez, O., Mar-Silva, F., Doadrio, I., Pérez-Ponce de León, G., 2016. The historical biogeography of the southern group of the sucker genus *Moxostoma* (Teleostei: Catostomidae) and the colonization of central Mexico. Zool. J. Linn. Soc. 177, 633–647.
- Pineda-López, R., Carballo-Cruz, V., Fukugauchi-Suárez de Real, M.G., García-Magaña, L., 1985. Metazoarios parásitos de peces de importancia comercial de la región de Los Ríos, Tabasco, México. Usumacinta, Investigación Científica en la Cuenca del Usumacinta. Gobierno del Estado de Tabasco Secretaría de Educación Cultura y Recreación. Villahermosa Tabasco, México, pp. 196–270.
- Protasova, E., Kuperman, B., Roytman, V., Poddubnaya, L., 1990. Caryophyllidae of the Fauna of the USSR. Nauka, Moscow, p. 238 (In Russian).
- Rosas-Valdez, R., Choudhury, A., Pérez-Ponce de León, G., 2004. Phylogenetic analysis of genera of Corallobothriinae (Cestoda: Proteocephalidae) from North American ictalurid fishes using partial sequences of the 28S ribosomal gene. J. Parasitol. 90, 1123–1127.
- Rosas-Valdez, R., Pérez-Ponce de León, G., 2008. Composición taxonómica de los helmintos parásitos de ictalúridos y heptaptéridos (Osteichthyes: Siluriformes) de México, con una hipótesis de homología biogeográfica primaria. Rev. Mex. Biodivers. 79, 473–499.
- Salgado-Maldonado, G., 2006. Checklist of helminth parasites of freshwater fishes from Mexico. Zootaxa 1324, 1–357.
- Scholz, T., Barčák, D., Oros, M., 2018. The occurrence of the non-native tapeworm *Khawia japonensis* (Yamaguti, 1934) (Cestoda) in cultured common carp in the Czech Republic confirms its recent expansion in Europe. Biol. Rec. 7, 303–308.
- Scholz, T., Barčák, D., Waeschenbach, A., McAllister, C.T., Choudhury, A., 2020. Tapeworms (Cestoda) of ictalurid catfishes (Siluriformes) in North America: redescription of type species of two genera and proposal of *Essexiellinae* n. subfam. J. Parasitol. 106, 444–463.
- Scholz, T., Binh, T.T., Dezfúli, B.S., 2011b. *Khawia japonensis* (Cestoda: Caryophyllidae): another invasive parasite of carp, *Cyprinus carpio* L., imported to Europe. J. Fish. Dis. 34, 943–949.
- Scholz, T., Brabec, J., Králová-Hromadová, I., Oros, M., Bazsalovicsová, E., Ermolenko, A., Hanzelová, V., 2011a. Revision of *Khawia* spp. (Cestoda: Caryophyllidae), parasites of cyprinid fish, including a key to their identification and molecular phylogeny. Folia Parasitol. 58, 197–223.
- Scholz, T., Kuchta, R., 2017. A digest of fish tapeworms. Vie Milieu 67, 43–58.
- Scholz, T., Oros, M., 2017. Caryophyllidae van Beneden in Carus, 1863. In: Caira, J.N., Jensen, K. (Eds.), Planetary Biodiversity Inventory (2008–2016): Tapeworms from Vertebrate Bowels of the Earth. The University of Kansas, Natural History Museum, Special Publication No. 25, pp. 47–64.
- Scholz, T., Rosas-Valdez, R., Pérez-Ponce de León, G., Choudhury, A., de Chambrier, A., 2003. Taxonomic status of *Choanoscolex lamothei* García-Prieto, 1990 (Cestoda: Proteocephalidae) using morphological and molecular evidence. J. Parasitol. 89, 1212–1219.
- Scholz, T., Salgado-Maldonado, G., 2001. Metacestodes of the family dilepididae (Cestoda: Cyclophyllidae) parasitising fishes in Mexico. Syst. Parasitol. 49, 23–40.
- Scholz, T., Shimazu, T., Olson, P.D., Nagasawa, K., 2001. Caryophyllidean tapeworms (Platyhelminthes: Eucestoda) from freshwater fishes in Japan. Folia Parasitol. 48, 275–288.
- Scholz, T., Waeschenbach, A., Oros, A., Brabec, J., Littlewood, D.T.J., 2021. Phylogenetic reconstruction of early diverging tapeworms (Cestoda: Caryophyllidae) reveals ancient radiations in vertebrate hosts and biogeographic patterns. Int. J. Parasitol. 51, 263–277.
- Williams, D.D., 1977. *Isoglaridacris chetekensis* sp. n. and *I. wisconsinensis* sp. n. (Cestoda: Caryophyllidae) from red Cedar river, Wisconsin catostomid fishes. Proc. Helminthol. Soc. Wash. 44, 91–95.
- Williams, E.H., 1975. Two new species of *Isoglaridacris* (Cestoidea: Caryophyllidae) from Alabama. Trans. Am. Microsc. Soc. 94, 340–346.
- Williams, E.H., Rogers, O.A., 1972. *Isoglaridacris agminis* sp. n. (Cestoda: Caryophyllidae) from the lake chubsucker, *Erimyzon succetta* (Lacépède). J. Parasitol. 58, 1082–1084.
- Yamaguti, S., 1934. Studies on the helminth fauna of Japan. Part 4. Cestodes of fishes. Jpn. J. Zool. 6, 1–112.