Institute of Parasitology, Biology Centre CAS
Folia Parasitologica 2025, 72: 020
doi: 10.14411/fp.2025.020

Folia Parasitologica
http://folia.paru.cas.cz

Research Article OPEN ACCESS

Some nematodes from fishes of the Lacantún River in the Lacandon rain forest of Chiapas State, southern Mexico, including *Cucullanus potamarii* sp. n. (Cucullanidae) from the endemic catfish *Potamarius usumacintae* (Ariidae)

František Moravec[1], **Guillermo Salgado-Maldonado**[2] and **David González-Solís**[3]

[1] Institute of Parasitology, Biology Centre of the Czech Academy of Sciences, České Budějovice, Czech Republic;

[2] Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City, DF, Mexico;

[3] El Colegio de la Frontera Sur (ECOSUR), Unidad Chetumal, Chetumal, Quintana Roo, Mexico

Abstract: During November of 2007, parasitic nematodes were collected from 161 specimens of 32 freshwater fish species in the Lacantún River of the Lacandon rain forest of Chiapas, southern Mexico. Recent detailed morphological and taxonomic studies of this material revealed the presence of 17 nematode species (12 adult and 5 larval) of nine families, including *Cucullanus potamarii* sp. n. from the intestine of the ariid catfish *Potamarius usumacintae* Betancur-R et Willink, which is endemic to the Usumacinta River basin to which the Lacantún River belongs. This new species is mainly characterised by deirids and the excretory pore located far posterior to the level of the oesophago-intestinal junction, which is an almost unique feature among its congeners. Most parasites are briefly described and illustrated, and problems concerning their morphology, taxonomy, hosts and geographical distribution are discussed. Some findings represent new host and geographical records. *Cucullanus oaxaquensis* Caspeta-Mandujano, Salgado-Maldonado et Martínez-Ramírez, 2010 is considered a junior synonym of *Cucullanus angeli* Cabañas-Carranza et Caspeta-Mandujano, 2007, and *Neocucullanus marcelae* Ramallo, 2012 a *species inquirenda*. Based on absence of relevant morphological differences, *Rhabdochona ictaluri* Aguilar-Aguilar, Rosas-Valdez et Pérez-Ponce de León, 2010 is considered a synonym of *Rhabdochona kidderi* Pearse, 1936.

Keywords: nematode parasite, taxonomy, morphology, zoogeography, Teleostei, Neotropics

The territory of Mexico is very interesting from the zoogeographical point of view and many papers dealing with helminth parasites of freshwater fishes in this country have been published, with emphasis on those carried out in central and southern Mexico. However, considering the diversity of aquatic ecosystems and the large number and diversity of fish species in this country, the present knowledge of the Mexican nematode fauna of inland fishes remains insufficient (Moravec 2000a, Caspeta-Mandujano 2005, Salgado-Maldonado 2006).

During studies on the helminth fauna of fishes of the Lacantún River (Usumacinta River basin) in the famous Lacandon rain forest, Chiapas State, southern Mexico, carried out during November 2007, numerous parasitic nematodes were collected. Preliminary results of their examination were published within broader studies on the helminth fauna of fishes of Chiapas (Salgado-Maldonado et al. 2011a,b). Subsequently, results of more detailed studies of these nematodes assigned to *Rhabdochona* Railliet, 1916 and *Spinitectus* Fourment, 1884, including the evaluation of their morphology, taxonomy and host-parasite relationships, were also published (Moravec et al. 2009, 2012). The remaining nematodes were recently examined in detail, mostly including the use of scanning electron microscopy (SEM), and evaluated. Results of studies of this interesting material are presented herein.

MATERIALS AND METHODS

Fishes were collected using gill nets at the Lacantún River (station El Remolino, 16.238611 N, -90.85 W) (16 fish specimens also from three nearby localities Arroyo El Venado, Lago El Oaxaco and Rio Trendales), all Usumacinta River drainage system, Chiapas State, southern Mexico, during November of 2007. A total of 161 fish specimens belonging to 32 species, 13 families and 9 orders were examined for the presence of helminth parasites (numbers of specimens examined in parentheses):

Lepisosteiformes: Lepisosteidae – *Atractosteus tropicus* Gill (4).

Clupeiformes: Dorosomatidae – *Dorosoma anale* Meek (18), *D. petenense* (Günther) (9).

Characiformes: Bryconidae – *Brycon guatemalensis* Regan (9); Characidae – *Astyanax aeneus* (Günther) (2).

Address for correspondence: František Moravec, Institute of Parasitology, Biology Centre of the Czech Academy of Sciences, Branišovská 31, 370 05, České Budějovice, Czech Republic. E-mail: moravec@paru.cas.cz. ORCID: 0000-0003-1086-1181

Zoobank number for article: urn:lsid:zoobank.org:pub:49E0D078-9BB7-4492-98BE-B7DFF9FE2D81

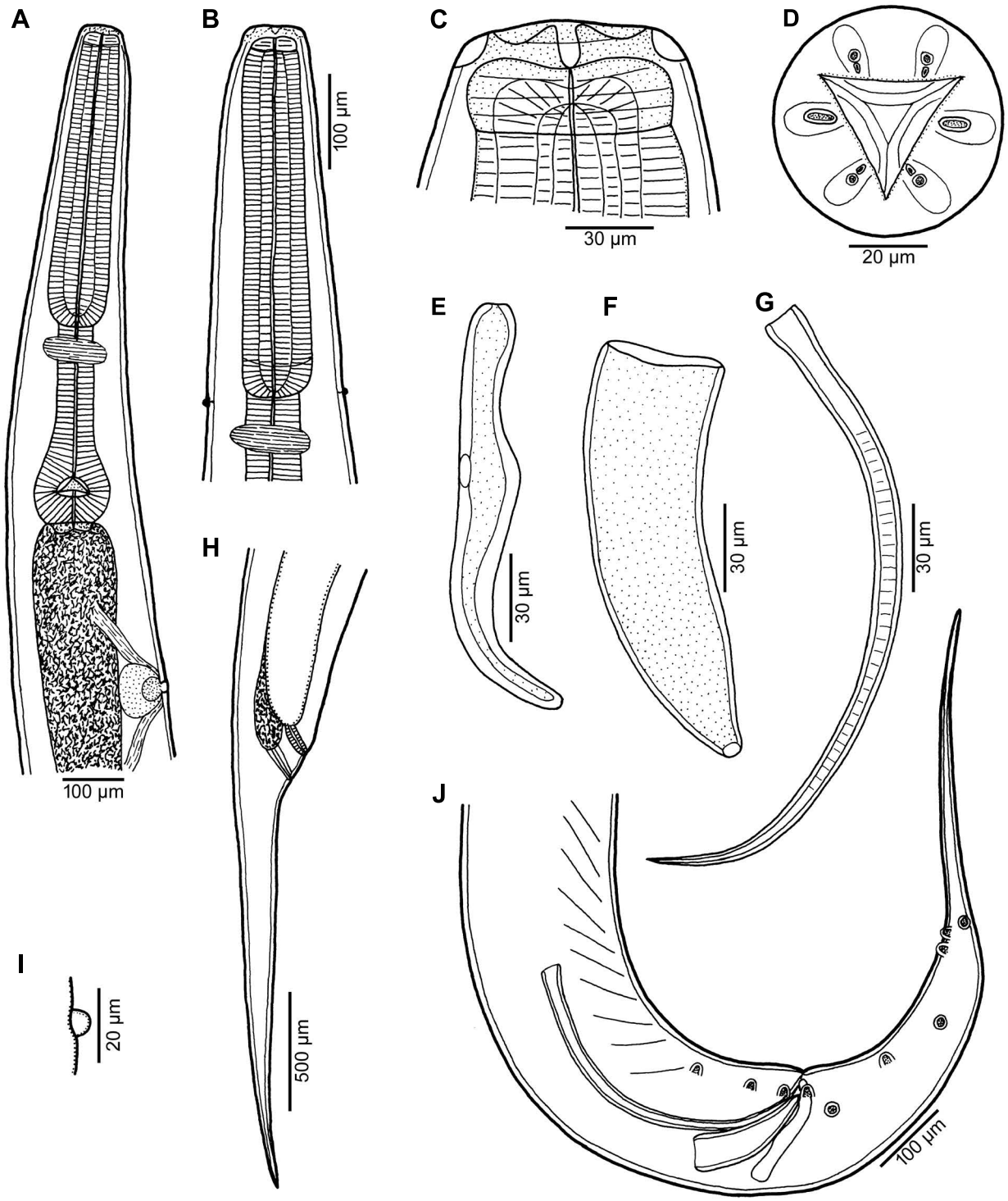

Fig. 1. *Atractis vidali* González-Solís et Moravec, 2002 from *Chuco intermedium* (Günther). **A** – anterior end of male, lateral view; **B** – anterior end of female, dorsoventral view; **C**, **D** – cephalic end of female, lateral and apical views, respectively; **E** – gubernaculum, lateral view; **F** – right spicule, lateral view; **G** – left spicule, lateral view; **H** – posterior end of female, lateral view; **I** – deirid; **J** – posterior end of male, lateral view.

Siluriformes: Ariidae – *Ariopsis* sp. (5), *Cathorops aguadulce* (Meek) (16), *Potamarius usumacintae* Betancur-R et Willink (2), *Potamarius nelsoni* (Evermann et Goldsborough) (4); Ictaluridae – *Ictalurus furcatus* (Valenciennes) (12); Heptapteridae – *Rhamdia guatemalensis* (Günther) (2), *Rhamdia laticauda* (Kner) (5); Lacantuniidae – *Lacantunia enigmatica* Rodiles-Hernández, Hendrickson et Lundberg (2).

Cyprinodontiformes: Poeciliidae – *Poecilia reticulata* Peters (1), *Poecilia sphenops* Valenciennes (8).

Beloniformes: Belonidae – *Strongylura hubbsi* Collette (4).

Perciformes, Eupercaria/misc.: Gerreidae – *Eugerres mexicanus* (Steindachner) (4).

Cichliformes: Cichlidae – *Chuco intermedium* (Günther) (6), "*Cichlasoma*" sp. (1), *Cincelichthys pearsei* (Hubbs) (6),

Maskaheros argenteus (Allgayer) (2), *Mayaheros urophthalmus* (Günther) (6), *Oreochromis mossambicus* (Peters) (1), *Parachromis friedrichsthalii* (Heckel) (1), *Parachromis managuensis* (Günther) (2), *Petenia splendida* Günther (4), *Rheoheros lentiginosus* (Steindachner) (1), *Theraps irregularis* Günther (1), *Thorichthys helleri* (Steindachner) (4), *Thorichthys meeki* Brind (3), *Thorichthys* sp. (5), *Vieja melanurus* (Günther) (3), *Vieja* sp. (1), *Wajpamheros nourissati* (Allgayer) (6).

Gobiiformes: Eleotridae – *Gobiomorus dormitor* Lacepède (1).

Nematodes recovered from the digestive tract were fixed in hot 4% formalin. For light microscopy (LM), they were cleared in glycerine. Drawings were made with the aid of a Zeiss microscope drawing attachment. Specimens used for SEM were postfixed in 1% osmium tetroxide (in phosphate buffer), dehydrated through a graded acetone series, critical-point-dried and sputter-coated with gold; they were examined using a JEOL JSM-7401F scanning electron microscope at an accelerating voltage of 4 kV (GB low mode). All measurements are given in micrometres unless otherwise stated. The specimens were deposited in the Helminthological Collection of the Institute of Parasitology, Biology Centre of the Czech Academy of Sciences, České Budějovice, Czech Republic (IPCAS).

In addition to the newly collected nematodes, two paratypes (male and female) of *Cucullanus mexicanus* Caspeta-Mandujano, Moravec et Aguilar-Aguilar, 2000 deposited in the Helminthological Collection of the Institute of Parasitology, BC CAS, České Budějovice (IPCAS N-767) were studied for comparative purposes. Fish nomenclature follows FishBase (Froese and Pauly 2024).

RESULTS

Adult nematodes

Family Atractidae Railliet, 1917

***Atractis vidali* González-Solís et Moravec, 2002** Figs. 1, 2

Description: Medium-sized, whitish nematodes with finely transversely striated cuticle (Fig. 2 A,D). Lateral alae in form of very narrow cordons present, initiating at region of deirids and extending posteriorly somewhat behind level of cloacal aperture in males and somewhat behind anus in females (Fig. 2E,F). Oral aperture triangular, surrounded by 3 small flat lips (Figs. 1D, 2A–C,E). Cephalic papillae arranged in 2 circles: outer circle formed by 4 small spherical papillae, inner circle by 4 small digital papillae; 2 lateral elongate amphids present (Figs. 1D, 2A–C). Oesophagus consisting of dilated oesophageal corpus, isthmus and bulb containing sclerotised apparatus (Fig. 1A,B). Anterior end of oesophagus triradiate, forming short pharynx (Fig. 1 A–D). Nerve ring slightly posterior to posterior end of corpus; excretory pore at some distance posterior to oesophagus. Deirids small, rounded (Figs. 1B,I, 2D), somewhat anterior to level of nerve ring. Tail of both sexes conical, elongate, slender and sharply pointed.

Male (based on 5 specimens from *Chuco intermedium*; measurements of 5 specimens from *Cincelichthys pearsei* in parentheses): Length of body 5.92–6.69 (6.03–7.60) mm, maximum width 258–299 (272–394). Length of entire oesophagus 912–943 (844–919); length of pharynx 15–18 (15–21), width 72–81 (72–81), of corpus 503 (476–517), width 95–109 (95–109), length of isthmus 231–272 (190–231), width 82–95 (68–82); bulb 150–163 (136–163) long and 136–150 (136–150) wide. Deirids, nerve ring and excretory pore 530–558 (517–544), 558–585 (544–612) and 1.17–1.32 (1.18–1.33) mm, respectively, from anterior extremity. Ten pairs of caudal papillae: 3 preanal, 1 adanal and 6 postanal; all preanal and adanal pairs subventral; second, fourth and fifth postanal pairs subventral; first, third and sixth pairs lateral (Figs. 1J, 2.F,G). Ventral region anterior to preanal papillae with inconspicuous oblique muscle bands (Fig. 1J). Spicules unequal and dissimilar, well sclerotised. Large (left) spicule 489–597 (453–592) long, its proximal end somewhat expanded, 27–33 (24–39) wide; middle part of this spicule finely transversely striated, 15 (15–18) wide; distal end very narrow, sharply pointed (Fig. 1G,J). Small (right) spicule 168–171 (171–186) long, funnel-shaped, with proximal end widely expanded and distal end narrowed (Fig. 1F,J). Length ratio of both spicules 1 : 2.86–3.55 (1 : 2.65–3.46). Gubernaculum well sclerotised, 150–165 (153–162) long, its maximum width at proximal end 18–21 (18–21) in lateral view; distal end of gubernaculum somewhat narrower, ventrally curved, with rounded tip (Fig. 1E,J). Length ratio of gubernaculum and large spicule 1 : 3.04–3.98 (1 : 2.90–3.72). Tail conical, 707–816 (680–816) long, ending in sharp point.

Female (based on 5 gravid specimens from *Ch. intermedium*; measurements of 5 gravid specimens from *C. pearsei* in parentheses): Length of body 6.99–7.62 (6.94–7.82) mm, maximum width 394–422 (490–558). Length of entire oesophagus 935–963 (935–984); length of pharynx 18–24 (18–24), width 75–84 (75–81), length of corpus 530–544 (517–544), width 109–122 (95–109), length of isthmus 218–245 (231–245), width 82–109 (82–95); bulb 150–163 (163–177) long and 150 (163) wide. Deirids, nerve ring and excretory pore 503–571 (530–558), 612–625 (598–639) and 1.33–1.38 (1.27–1.36) mm, respectively, from anterior extremity. Monodelphic. Vulva at short distance, 54–68 (54–68), anterior to anus; vagina short, directed anteriorly from vulva (Fig. 1H). Uterus containing a few developing eggs, size 136 × 82–95, and/or fully formed, 2–3 (3–5) coiled larvae approximately (450–570) long and (54–82) wide. Tail conical, 952–1,006 (925–1,074) long, with sharply pointed tip (Fig. 1H).

Hosts: *Chuco intermedium* (Günther), Northern checkmark cichlid, total body length (TBL) 12–23 cm, and *Cincelichthys pearsei* (Hubbs), Pantano cichlid, TBL 29 cm (both Cichlidae).

Site of infection: Intestine.

Locality: Lacantún River (Usumacinta River basin), Chiapas State, southern Mexico (collected 18 and 19 November 2007).

Prevalence and intensity: *Ch. intermedium*: 1 fish infected/6 fish examined; *ca*. 4,000 nematodes. *C. pearsei*: 1 fish infected/6 fish examined; *ca*. 2,000 nematodes.

Deposition of voucher specimens: IPCAS N-784.

Comments: *Atractis* Dujardin, 1845 is one of six genera of the cosmocercoid family Atractidae which contains species parasitising fishes. Other atractid genera with repre-

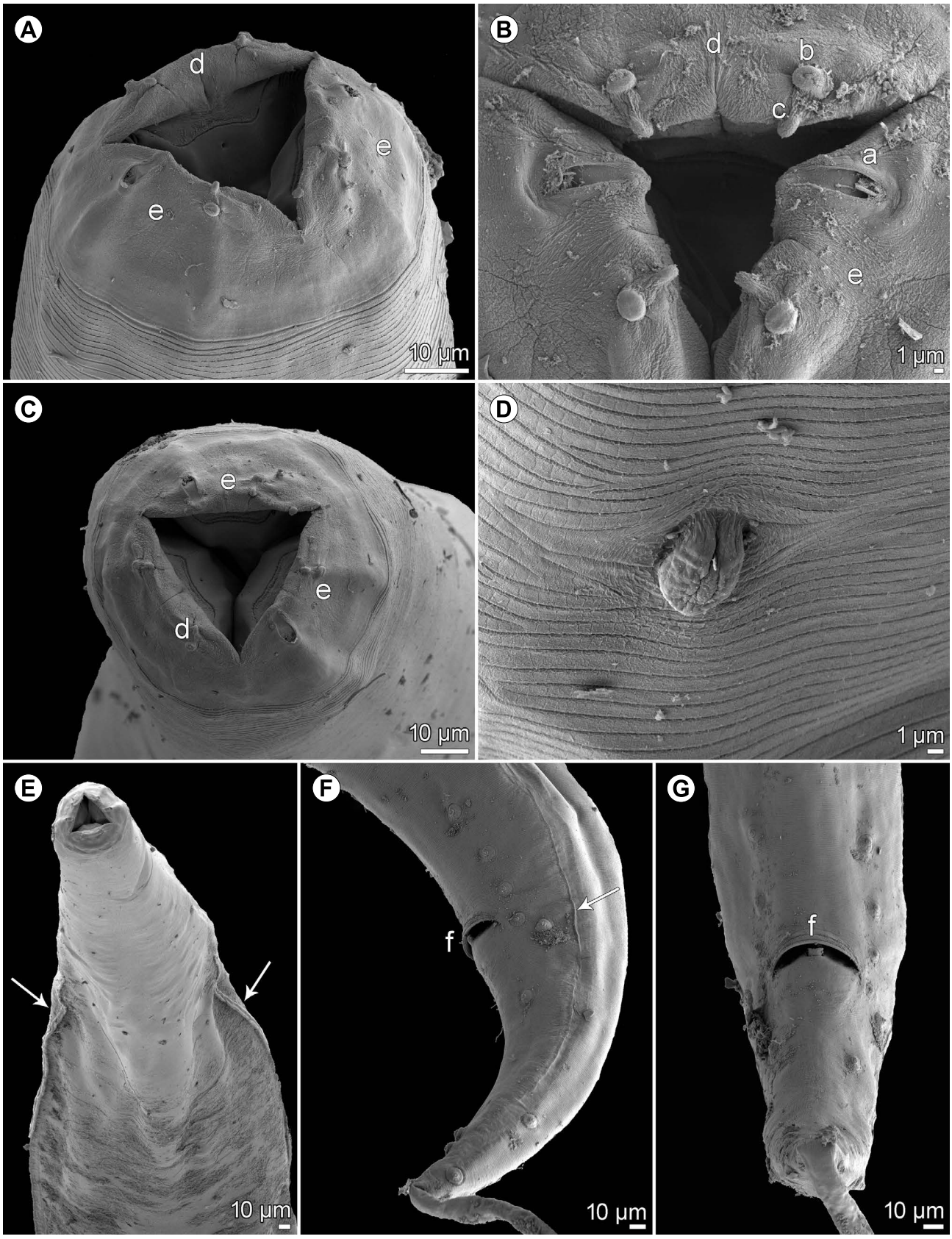

Fig. 2. *Atractis vidali* González-Solís et Moravec, 2002 from *Chuco intermedium* (Günther), scanning electron micrographs. **A** – cephalic end, subapical view; **B** – region of lips, apical view; **C** – cephalic end, apical view; **D** – deirid; **E** – anterior end of body, ventral view (arrows indicate lateral alae); **F** – region of male cloacal aperture, lateral view (arrow indicates lateral ala); **G** – same, ventral view. *Abbreviations*: a – amphid; b – cephalic papilla of outer circle; c – cephalic papilla of inner circle; d – dorsal lip; e – subventral lip; f – cloacal aperture.

sentatives in fishes are *Klossinemella* Costa, 1961, *Labeonema* Puylaert, 1970, *Monhysterides* Baylis et Daubney, 1922, *Orientatractis* Petter, 1966 and *Rondonia* Travassos, 1920 (see González-Solís and Moravec 2002, 2004, Anderson et al. 2009).

The genus *Atractis* includes many species parasitic in reptiles (turtles and lizards) and one is known from amphibians (toads), whereas only two species were described from freshwater fishes in southern Mexico: *Atractis bravoae* (Osorio-Sarabia, 1984) from *Amphilophus istlanus* (Jordan et Snyder) (Cichlidae) in Michoacán and *Atractis vidali* González-Solís et Moravec, 2002 from *Ch. intermedium* (type host) and *C. pearsei* (both Cichlidae) in Campeche and Chiapas (Osorio-Sarabia 1984, González-Solís and Moravec 2002).

The former species (*A. bravoae*) was originally inadequately described by Osorio-Sarabia (1984) as *Laurotravassoxyuris bravoae*, being reported from the cichlid *Am. istlanus* and the atherinopsid *Atherinella balsana* (Meek). Subsequently, its type specimens from *Am. istlanus* were re-examined by Moravec (2000b), who had transferred *L. bravoae* to *Atractis*; nevertheless, some female paratypes of the type series proved to belong to a different family, Cosmocercidae, being probably identical to *Raillietnema kritscheri* Moravec, Salgado-Maldonado et Pineda-López, 1993. Specimens of *A. bravoae* from *Ath. balsana* were not deposited and could not be re-examined. Without any reference, Caspeta-Mandujano (2005) reported the ictalurid catfish *Ictalurus balsanus* (Jordan et Snyder) as a host of *A. bravoae* in its type locality, but this information seems to be doubtful, because *I. balsanus* is endemic to Morelos State (Froese and Pauly 2024).

Although both *A. bravoae* and *A. vidali* are parasites of cichlids, they clearly differ in the characteristics of spicules, which are similar in shape and almost equal in length in *A. bravoae* and markedly dissimilar in shape and length in *A. vidali*. The morphology and measurements of the present specimens, as well as their host species from the same river basin show that they belong to *A. vidali*. Nevertheless, the present SEM study of *A. vidali* shows that, in contrast to the original description, the cuticle of this species is not smooth but finely transversely striated and the body of these nematodes has narrow lateral alae described here for the first time.

The morphology of *Atractis* spp. somewhat resembles that of *Rondonia rondoni* Travassos, 1920, a parasite of freshwater characiform, siluriform and some other fishes in South America (e.g., Moravec et al. 1992a, Moravec 1998, Cavalcante et al. 2017), but representatives of these two genera differ substantially from each other based on the vaginal opening (into vulva and separate from anus in *Atractis vs* into rectum forming cloaca in *Rondonia*) (Anderson et al. 2009).

Atractis spp. as well as other atractid nematodes are ovoviviparous and their third-stage larvae develop within the uterus of the female; these are freed in the digestive tract of the host, where they complete the life cycle without passing out into the external environment (Petter 1966). Apparently, this is the reason why the atractid nematodes are often found in fish hosts in huge numbers, as confirmed by the present findings of *A. vidali* in *Ch. intermedium* and *C. pearsei*, in which the intensity of infection reached about 4,000 and 2,000 nematodes per fish, respectively. Mass infections in fish hosts were previously recorded for *R. rondoni* in Brazil and Argentina, where thousands (maximum 120,000) of these nematodes in one fish individual were reported by different authors (Moravec 1998).

***Orientatractis chiapasensis* González-Solís et Moravec, 2004** Figs. 3, 4

Description: Small-sized, whitish nematodes with finely transversely striated cuticle (Fig. 4D). Cephalic end blunt, posterior end with conspicuously slender, long, pointed tail. Narrow lateral alae present, initiating near mouth and extending posteriorly to about mid-length of tail (Fig. 4E,F). Oral aperture of irregular shape, from roughly triangular to almost circular, surrounded by 4 lip-like formations and bearing 4 (2 dorsal and 2 subventral) large oval submedian cephalic papillae of outer circle, 4 (2 dorsal and 2 subventral) very small oval papillae of inner circle and 2 lateral amphids; each of 4 submedian lip-like formations armed with 1 Y-shaped, well-sclerotised piece whose distal portion consists of 2 horns extending outward and downward (Figs. 3A–D, 4A–C); cuticle immediately posterior to each pair of sclerotised horns forms another, non-sclerotised single horn. Deirids small, knob-like, situated somewhat anterior to end of oesophageal corpus (Fig. 3B). Oesophagus consisting of almost cylindrical corpus with weakly outlined short pharynx, isthmus and bulb containing sclerotised apparatus. Nerve ring encircling isthmus near its anterior end. Excretory pore slightly posterior to level of mid-way between nerve ring and posterior end of oesophagus (Fig. 3A). Intestine straight, narrow. Tail of both sexes slender, long, sharply pointed.

Male (based on 2 specimens): Length of body 3.05–3.13 mm, maximum width 109–136. Length of lip-like formations 9–12. Size of buccal cavity 9–12 × 9–12. Length of sclerotised horns 9. Length of entire oesophagus 393; length of pharynx 15, width 18–24, of corpus 153–162, width 18–24, length of isthmus 147–165, width 24–30; bulb 60–69 long and 54–60 wide. Deirids, nerve ring and excretory pore 125–189, 108–225 and 225–270, respectively, from anterior extremity. Caudal papillae 9 pairs, of which 4 pairs preanal (all subventral) and 5 pairs postanal (3 pairs subventral and 2 pairs lateral); in addition, 1 small median unpaired papilla present on anterior cloacal lip (Fig. 3E). Spicules unequal and dissimilar, well sclerotised. Large (left) spicule 264–300 long, small (right) spicule 63–87 long; length ratio of spicules 1 : 3.0–4.8; proximal ends of spicules somewhat expanded, cup-shaped, distal ends sharply pointed (Fig. 3F,G). Gubernaculum simple, rod-like in lateral view, well sclerotised, 54–60 long, its maximum width 6; distal end of gubernaculum somewhat narrower (Fig. 3E,H). Tail slender, 462–816 long.

Female (based on 5 gravid specimens): Length of body 3.08–4.10 mm, maximum width 140–223. Lip-like formations 12–15 long. Size of buccal capsule 12–15 × 12–15. Length of sclerotised horns 12. Length of entire oesophagus 426–455; length of pharynx 15, width 24, of corpus 165–170, width 24–27, length of isthmus 173–186, width 24–30; bulb 73–84 long and 60–80 wide.

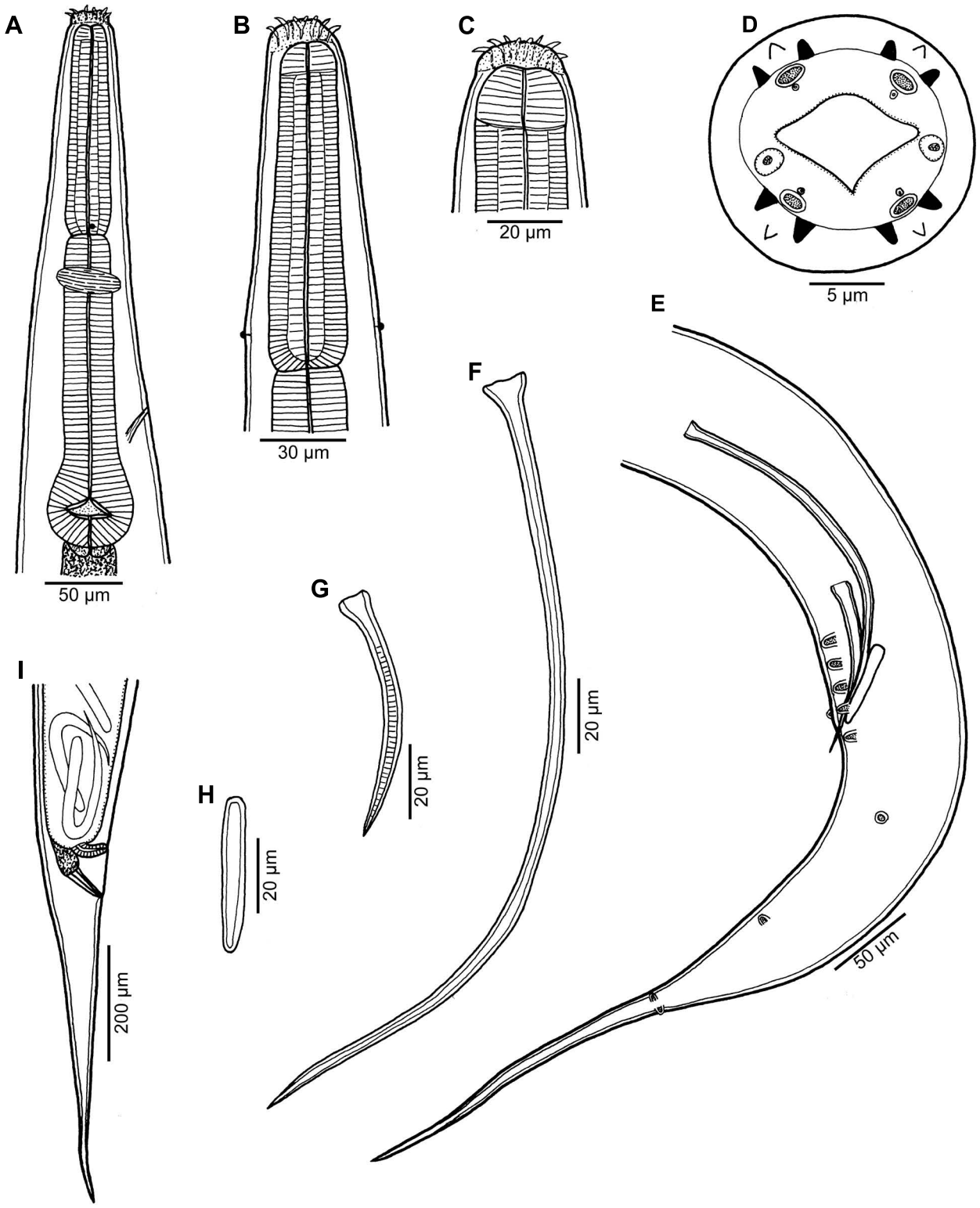

Fig. 3. *Orientatractis chiapasensis* González-Solís et Moravec, 2004 from *Chuco intermedium* (Günther). **A**, **B** – anterior end of female, lateral and dorsoventral views, respectively; **C**, **D** – cephalic end, lateral and apical views, respectively; **E** – posterior end of male, lateral view; **F** – long (left) spicule, lateral view; **G** – short (right) spicule, lateral view; **H** – gubernaculum, lateral view; **I** – posterior end of female, lateral view.

Deirids, nerve ring and excretory pore 158–198, 178–243 and 250–287, respectively, from anterior extremity. Monodelphic. Vulva at short distance, 89–132, anterior to anus; vagina short, directed anteriorly from vulva (Figs. 3I, 4E). Uterus containing few developing eggs and/or fully formed larvae (Fig. 3I). Ovary short, reflexed, situated some distance posterior to oesophagus. Length of tail 550–590.

Host: *Chuco intermedium* (Günther) (Cichlidae), Northen check-mark cichlid, TBL 12 cm.

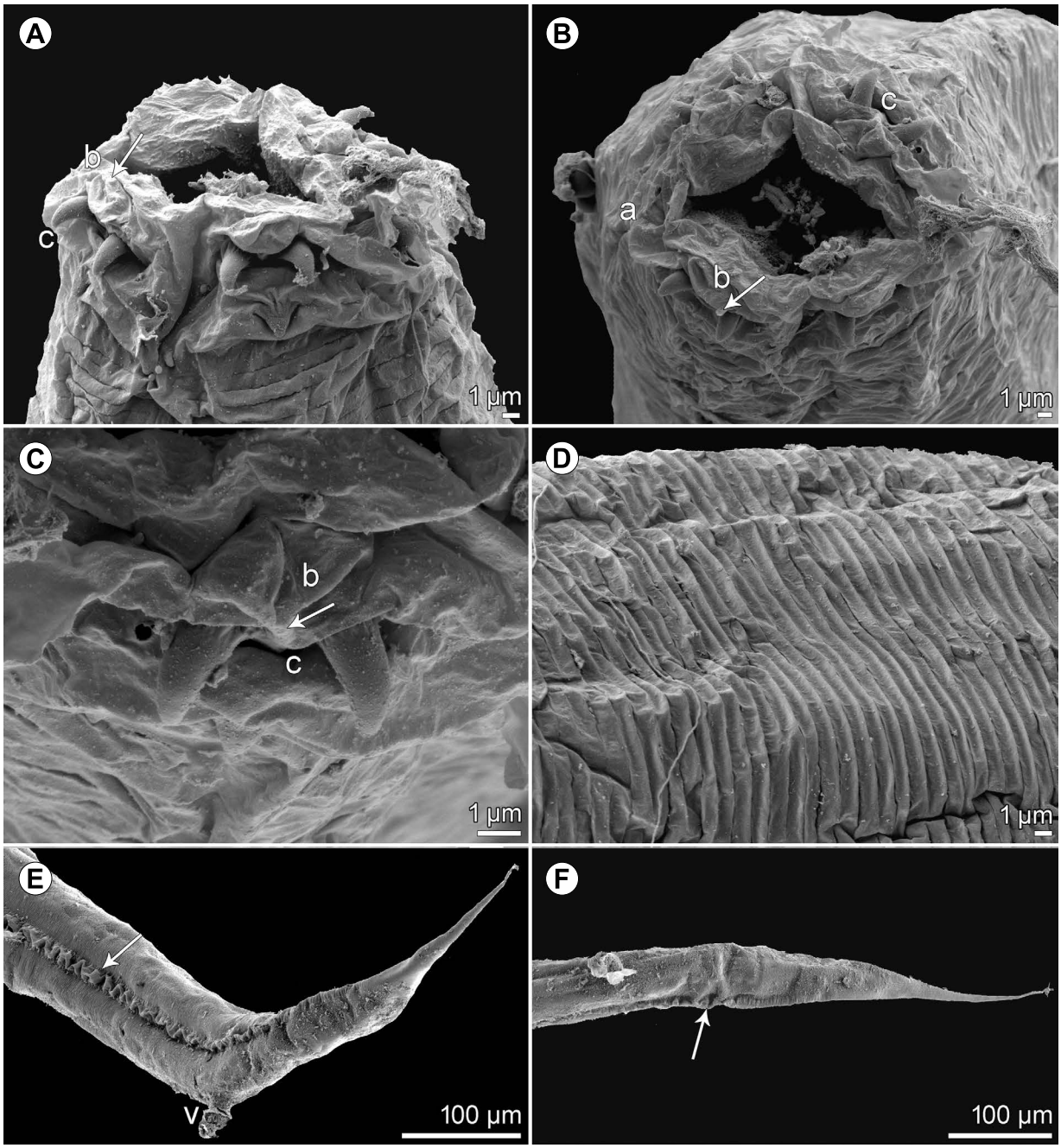

Fig. 4. *Orientatractis chiapasensis* González-Solís et Moravec, 2004 from *Chuco intermedium* (Günther), scanning electron micrographs. **A**, **B** – cephalic end, subapical and apical views, respectively; **C** – pair of cephalic horns, sublateral view; **D** – striation of cuticle in post-oesophageal region; **E**, **F** – posterior end of female, lateral and dorsal views, respectively (arrows indicate lateral alae). *Abbreviations*: a – amphid; b – cephalic papilla of outer circle and close small cephalic papilla of inner circle (see arrow); c – submedian pair of cephalic horns; v – vulva.

Site of infection: Intestine.

Locality: Lacantún River (Usumacinta River basin), Chiapas State, southern Mexico (collected 17 November 2007).

Prevalence and intensity: 1 fish infected/6 fish examined; 198 nematodes.

Deposition of voucher specimens: IPCAS N-807.

Comments: González-Solís and Moravec (2004) described two morphologically similar species of *Orientatractis*, both intestinal parasites of cichlids (Cichlidae) in Mexico and Nicaragua: *Orientatractis campechensis* González-Solís et Moravec, 2004 from *Vieja bifasciata* (Steindachner) (type host) in Campeche and *C. pearsei* in Chiapas (both Mexico); and *Orientatractis chiapasensis* González-Solís et Moravec, 2004 from *Ch. intermedium* (type host) in Mexico (Chiapas) and *Tomocichla tuba* (Meek) in Nicaragua. The present specimens were identified as *O. chiapasensis* mainly based on the rod-like gubernaculum, cup-shaped proximal ends of spicules and the fish host, which is the type host of this nematode species.

González-Solís and Moravec (2004) also mentioned the lengths of spicules as a differential feature between *O. campe-*

chensis (left spicule 400–510 μm) and *O. chiapasensis* (left spicule 200–250 μm). However, the left spicule in the present specimens was up to 300 μm long, which may be associated with the fact that the present males were somewhat larger than those used for the original species description.

Orientatractis comprises nematodes parasitic in fishes, amphibians and reptiles (chelonians). Currently, this genus includes 11 valid species, of which five are intestinal parasites of freshwater fishes (see Jesus et al. 2023): *O. campechensis* and *O. chiapasensis* from cichlids in southern Mexico and Nicaragua; *Orientatractis moraveci* Cavalcante, Silva, Santos, Chagas-Moutinho et Santos, 2017 from pimelodid catfishes in South America (Brazil); *Orientatractis mekongensis* Moravec, Kamchoo et Pachanawan, 2015 from pangasiid catfishes in South Asia (Thailand); and *Orientatractis brycini* González-Solís et Mariaux, 2017 from upside-down catfishes in Africa (Gabon) (González-Solís and Moravec 2004, Moravec et al. 2015, Cavalcante et al. 2017, González-Solís and Mariaux 2017).

In addition to *O. campechensis* and *O. chiapasensis* from Mexico, the only other congeneric species parasitising fishes in the Neotropical Region is *O. moraveci* reported from *Pimelodus blochii* Valenciennes (Pimelodidae) of the Xapuri and Acre Rivers (Amazon River basin), Acre State, western Brazil (Cavalcante et al. 2017). This species can be differentiated from *O. chiapasensis* mainly by the length of the larger spicule (161–198 μm *vs* 204–300 μm) and the length of the male tail (225–270 μm *vs* 460–816 μm) (Cavalcante et al. 2017).

In having the mouth surrounded by sclerotised formations (pieces), species of *Orientatractis* are similar to those of *Klossinemella*, including the type species *Klossinemella iheringi* (Travassos, Artigas et Pereira, 1928) parasitising mainly characiform and siluriform fishes in Brazil and Argentina and three other species from turtles (Moravec and Thatcher 1997, Moravec 1998). Whereas species of *Orientatractis* possess four bicornuate sclerotised pieces and four single horns around the mouth, those of *Klossinemella* are characterised by the mouth armed with eight Y-shaped sclerotised structures and four single horns (Moravec and Thatcher 1997, González-Solís and Moravec 2004, Moravec et al. 2015, González-Solís and Mariaux 2017, Cavalcante et al. 2017, Jesus et al. 2023).

The present finding of *O. chiapasensis* represents only the second record of this parasite since its original description.

Family Cosmocercidae Railliet, 1916

***Raillietnema kritscheri* Moravec, Salgado-Maldonado et Pineda-López, 1993** Fig. 5

Description (based on specimens from *C. pearsei*): Small, whitish nematodes. Cuticle finely transversely striated (Fig. 5A,B,D). Narrow lateral alae present, initiating at level of about mid-length of oesophagus and extending posteriorly to some distance anterior to cloacal opening in males and to level of anus in females (Fig. 5C,E–G). Somatic papillae indistinct. Cephalic end rounded. Oral aperture triangular; 3 small flat lips present, each provided with broad cuticular membrane (lamella) on inner margin. Four submedian cephalic papillae, 2 on dorsal lip and 1 on each of subventral lip; 2 large oval lateral amphids present (Fig. 5A). Oesophagus with anterior, well-developed and relatively long pharynx; posterior oesophageal bulb with sclerotised apparatus. Nerve ring at mid-length of oesophagus, excretory pore somewhat anterior to level of bulb. Tail of both sexes conical and pointed.

Male (based on 5 specimens): Length of body 2.39–3.36 mm, maximum width 136–190. Length of entire oesophagus 620–722; length of pharynx 42–54, width 21–30, of corpus 449–530, width 33–48, length of isthmus 36–48, width 33–39; bulb 81–105 long and 90–105 wide. Nerve ring and excretory pore 299–340 and 435–571, respectively from anterior extremity. Preanal region with 2 subventral rows of 5 pairs of large caudal papillae; anterior lip of cloaca with 3 pairs of small papillae and 1 larger unpaired median papilla. One pair of large lateral caudal papillae present approximately at level of cloacal aperture. Mid-region of tail with 2 pairs of large subventral papillae. One pair of small papillae located two-thirds of distance from cloaca to tail tip. Terminal portion of tail with 2 pairs of papillae located close together (Fig. 5B,C,H). Spicules short, equally long, somewhat ventrally bent, well sclerotised, with pointed distal tips; spicules 105–126 long and 12–15 wide. Gubernaculum well sclerotised, 57–66 long and 12–18 wide in lateral view. Length ratio of gubernaculum and spicules 1 : 1.7–2.1. Tail conical, 177–245 long, ending in sharp point (Fig. 5C,H).

Female (based on 5 gravid specimens): Length of body 3.60–4.28 mm, maximum width 231–286. Length of entire oesophagus 759–813; length of pharynx 51–60, width 30–39, length of corpus 558–612, width 51–60, length of isthmus 33–45, width 48–60; bulb 105–108 long and 120–129 wide. Nerve ring and excretory pore 340–381 and 517–694, respectively, from anterior extremity. Uterus amphidelphic; ovaries short, posterior ovary anterior to level of vulva. Vulva distinctly postequatorial, 2.37–2.87 mm, at 66–68% from anterior body end. Vulval lips may be somewhat elevated. Vagina directed anteriorly from vulva. Eggs thin-walled, oval, with uncleaved content, size 163–190 × 136–150; maximum number of eggs in uterus 4–5. Tail conical, 231–299 long, with sharply pointed tip; pair of small lateral phasmids present some distance anterior to tail tip (Fig. 5D,F,G).

Hosts: *Cincelichthys pearsei* (Hubbs), Pantano cichlid, TBL 12–29 cm; and *Chuco intermedium* (Günther), Northern checkmark cichlid, TBL 12 cm (both Cichlidae).

Site of infection: Intestine.

Locality: Lacantún River (Usumacinta River basin), Chiapas State, southern Mexico (collected 18–20 November 2007).

Prevalence and intensity: *C. pearsei*: 4 fish infected/6 fish examined; 56 to *ca*. 2,000 nematodes per fish. *Ch. intermedium*: 1 fish infected/6 fish examined; 10 nematodes in one infected fish specimen.

Deposition of voucher specimens: IPCAS N-596.

Comments: The morphology and measurements of the present specimens are very similar to those of *R. kritscheri*

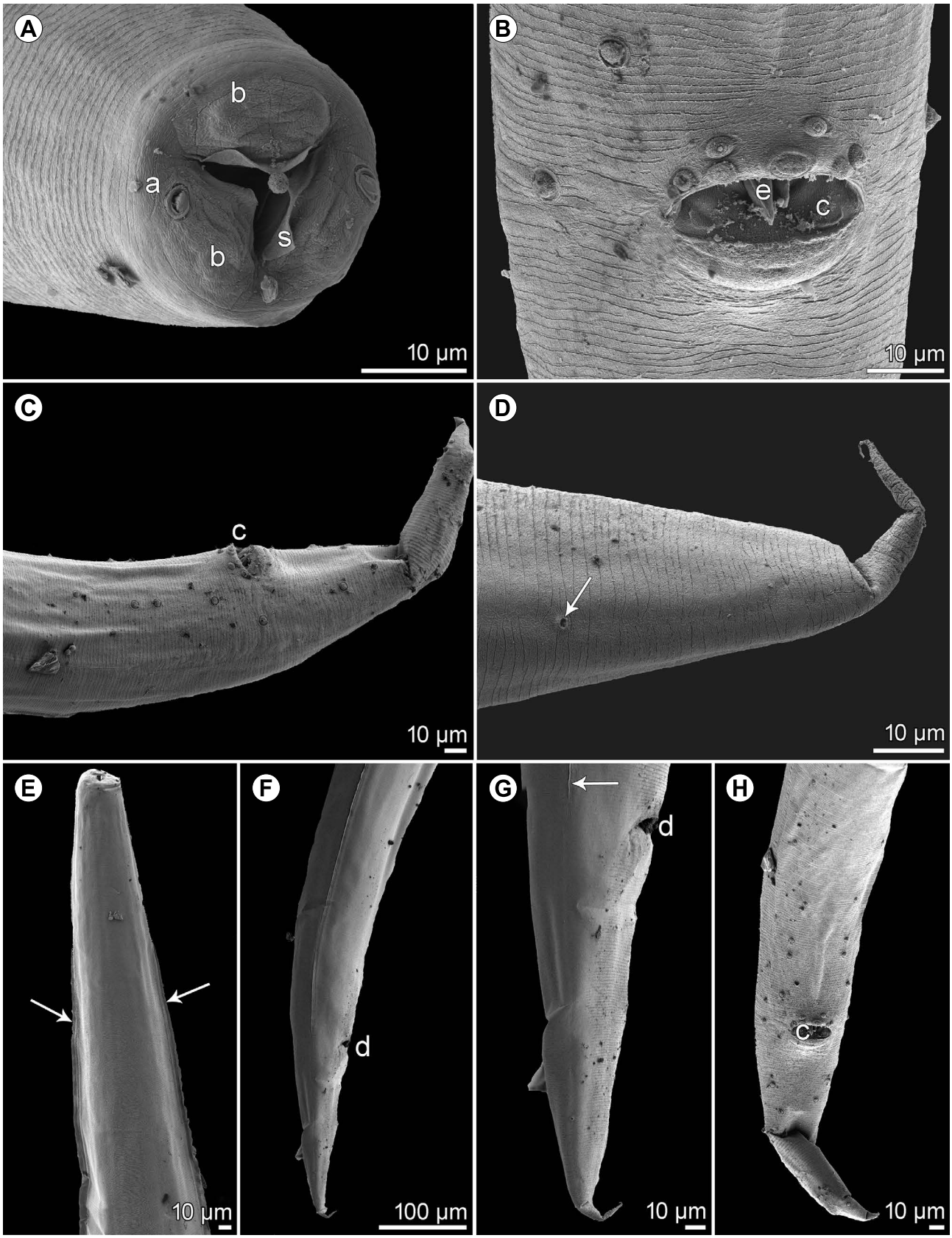

Fig. 5. *Raillietnema kritscheri* Moravec, Salgado-Maldonado et Pineda-López, 1993 from *Cincelichthys pearsei* (Hubbs), scanning electron micrographs. **A** – cephalic end, apical view; **B** – region of cloaca, ventral view; **C** – posterior end of male, lateral view; **D** – posterior portion of female tail, lateral view (arrow indicates phasmid); **E** – anterior end of body, ventral view (arrows indicate lateral alae); **F** – posterior end of female, lateral view; **G** – female tail, lateral view (arrow indicates lateral ala); **H** – posterior end of male, ventral view. *Abbreviations*: a – amphid; b – cephalic papilla; c – cloaca; d – anus; e – spicula; s – lamela (cuticular membrane).

described by Moravec et al. (1993a) and, therefore, they are considered to belong to this species. *Railletnema kritscheri* has been known as a parasite of cichlids in southern Mexico (Campeche, Chiapas, Tabasco), being previously reported from *C. pearsei* (type host) and *Vieja melanurus* (see Moravec et al. 1993a, Moravec 1998), later also from endemic cichlids *Chiapaheros grammodes* (Taylor et Miller), *Vieja breidohri* (Werner et Stawikowski) and *Vieja hartwegi* (Taylor et Miller) from the upper Grijalva River in southeastern Chiapas, the river which joins the branch of the Usumacinta River in Tabasco (all three last-named cichlids are endemic to the Grijalva River basin) (Paredes-Trujillo et al. 2020).

The present SEM examination of *R. kritscheri* enabled a more detailed study of the cephalic structures and male caudal papillae and, for the first time, showed the presence of lateral alae in this species.

Representatives of the cosmocercid genus *Raillietnema* Travassos, 1927 are mostly parasites of amphibians and reptiles (Baker 1987), only two congeneric species were reported from freshwater fishes: *R. kritscheri* from cichlids in Mexico (Moravec et al. 1993a) and *Raillietnema synodontisi* Vassiliadès, 1973 from upside-down catfishes (*Synodontis* spp.) in Africa and from aquarium breedings in former Czechoslovakia (present Czech Republic) (Vassiliadès 1973, Moravec and Řehulka 1987). However, based on a re-examination of its type specimens, *R. synodontisi* was subsequently transferred to the atractid genus *Labeonema* (see Koubková et al. 2008). This was later followed by subsequent authors (e.g., Moravec and Jirků 2017, Moravec 2019).

Although species of *Raillietnema* and *Labeonema* are presently listed in two different families of the Cosmocercoidea, their general morphologies are very similar, and the only intergeneric difference should be the presence of two ovaries in *Raillietnema* and the absence of the posterior ovary in *Labeonema* (see Moravec and Van As 2004, Koubková et al. 2008, Anderson et al. 2009). Nevertheless, in the phylogenetic analysis of the Cosmocercoidea by Pereira et al. (2015b), *Labeonema* was considered to be very similar to *Raillietnema*.

Subsequent phylogenetic analyses of 18S rDNA sequences of cosmocercoid nematodes by Cavalcante et al. (2017) also nested *Labeonema synodontisi* (Vassiliadès, 1973) with *Raillietnema* sp. According to these authors, the molecular data and previous morphological studies of *L. synodontisi* indicate that this species should be returned to *Raillietnema*. Moreover, Koubková et al. (2008) considered *L. synodontisi* to be probably identical to *Labeonema intermedium* Puylaert, 1970, which is the type species of *Labeonema*. If this is the case, then *Labeonema* would become a junior synonym of *Raillietnema*.

As mentioned above, the posterior ovary in *R. kritscheri* is located approximately at the level of vagina, as it is illustrated for *Raillietnema* in fig. 6.6 of Anderson et al. (2009), i.e., anterior to the posterior branch of uterus, which looks like a sac without an ovary. Similar location of the posterior ovary as in *R. kritscheri* was described by Moravec and Řehulka (1987) for *R. synodontisi*. However, since the posterior ovary is somewhat reduced compared with the anterior ovary, and is partly overlapped by the uterus, it is not easy to observe it in these tiny nematodes.

The presence of the posterior ovary in *Raillietnema* and *Labeonema* is also indicated by the location of the vulva near the middle of body and the anteriorly directed vagina, in contrast to the vaginal opening into the rectum forming a cloaca or into the vulva located near the anus in typically monodelphic atractids such as species of *Atractis*, *Orientatractis* or *Rondonia* (see above). In our opinion, future histological studies will confirm synonymy of *Labeonema* with *Raillietnema* and, consequently, the allocation of all these nematodes in the Cosmocercidae.

Family Cucullanidae Cobbold, 1864

***Cucullanus angeli* Cabañas-Carranza et Caspeta-Mandujano, 2007** Figs. 6–8

New syn. *Cucullanus oaxaquensis* Caspeta-Mandujano, Salgado-Maldonado et Martínez-Ramírez, 2010

Description: Medium-sized nematodes with whitish, elongate body. Lateral alae absent. Cephalic end slightly asymmetrical in lateral view. Oral aperture dorsoventrally elongate, surrounded by raised narrow membraneous ala (collarette) supported by row of *c.* 60 minute rod-like basal teeth approximately 10 long (Figs. 6C, 7A,B). Four submedian cephalic double papillae and pair of lateral amphids present (Figs. 6C, 7A,B). Oesophagus muscular, expanded at anterior end to form bulbous pseudobuccal capsule (oesophastome), slightly asymmetrical in lateral view; posterior part of oesophagus also expanded, approximately as wide as oesophastome in lateral view (Fig. 6A,B). Oesophagus opens into intestine through large valve. Nerve ring encircles oesophagus at 42–49% of its length. Deirids small, conical, at short distance anterior to oesophago-intestinal junction (Figs. 6A,B, 7C). Postdeirids not found. Excretory pore located just posterior to posterior end of oesophagus (Fig. 6A,B). Tail of both sexes conical and sharply pointed at tip.

Male (based on 4 specimens from *C. pearsei*): Length of body 7.44–8.72 mm, maximum width 258–408; width at level of oesophastome 163–204, at middle of oesophagus 231–245. Length of entire oesophagus 734–830, representing 8–10% of whole body length; length of oesophastome 258–286, its width 136–150; minimum width of oesophagus 82–95; maximum width of posterior part of oesophagus 136–163. Distance of nerve ring from anterior extremity 354–394, representing 46–48% of oesophageal length. Deirids and excretory pore 625–694 and 854–938, respectively, from anterior end of body. Posterior end of body curved ventrally. Ventral sucker present (Fig. 6I,J). Cloacal region not elevated. Median, transversely oval cuticular elevation present anterior to cloacal opening (Figs. 6G–J, 7D–F, 8C). Spicules equal, 612–734 long, representing 7–9% of body length (Fig. 6J). Gubernaculum well sclerotised, 108–114 long, rod-like in lateral view (Fig. 6G,J) and Y-shaped in ventral view. Caudal papillae 10 pairs: 5 pairs of subventral preanal papillae and 5 pairs of postanal papillae (3 subventral and 2 dorsolateral); first sub-

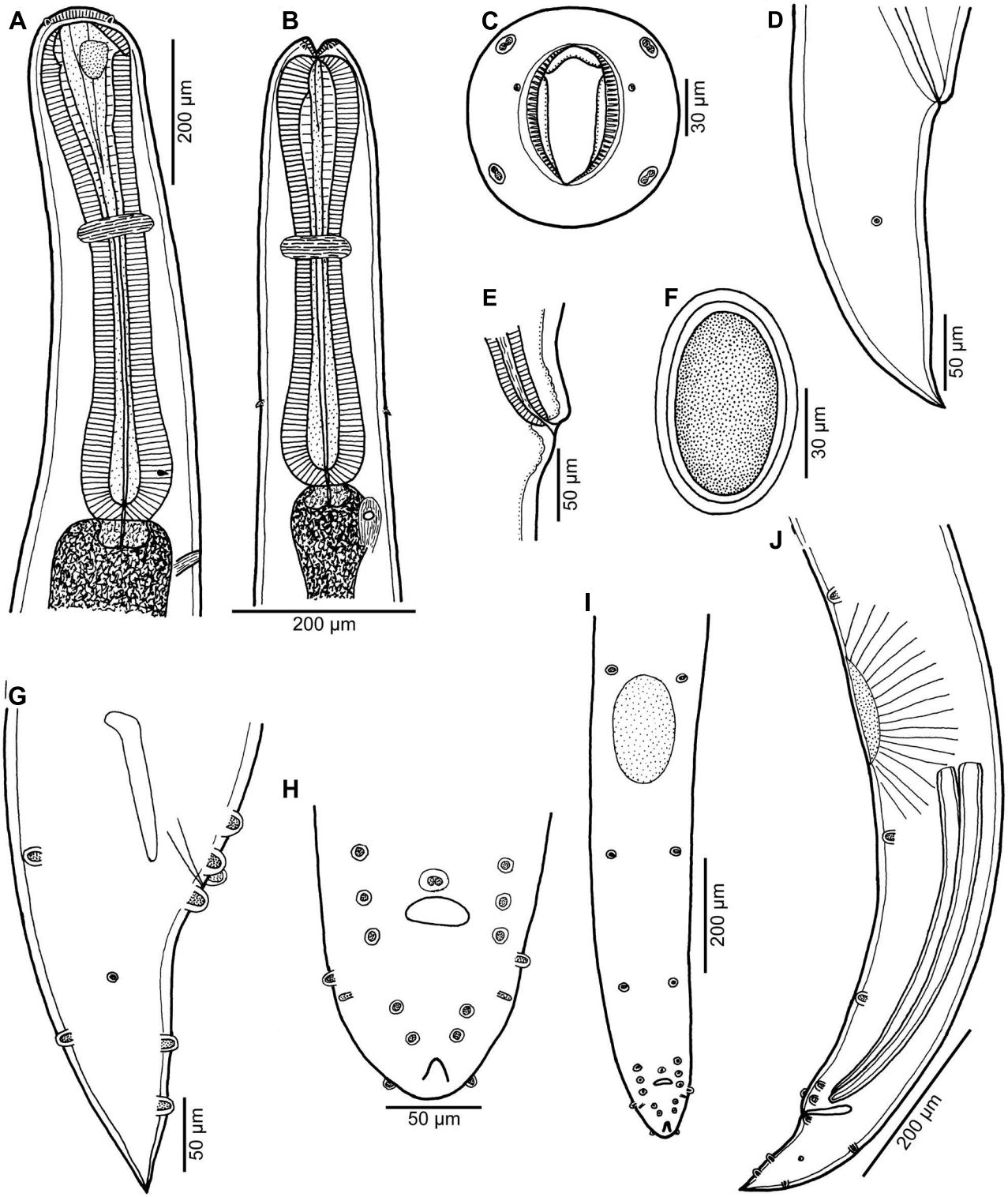

Fig. 6. *Cucullanus angeli* Cabañas-Carranza et Caspeta-Mandujano, 2007 from *Cincelichthys pearsei* (Hubbs). **A** – anterior end of female, lateral view; **B** – anterior end of male, dorsoventral view; **C** – cephalic end, apical view; **D** – female tail, lateral view; **E** – vulva, lateral view; **F** – egg; **G**, **H** – tail of male, lateral and ventral views, respectively; **I**, **J** – posterior end of male, ventral and lateral views, respectively. (**C**, **H**, **I** – based on SEM micrographs.)

ventral pair of postanals slightly posterior to level of cloacal aperture, second subventral pair of postanals slightly posterior to mid-length of tail and posterior-most pair of subventrals somewhat anterior to tail tip; postanals of dorsolateral pairs approximately at levels of first and second pairs of subventrals (Figs. 6G–J, 7E,F, 8A–C). Pair of small lateral phasmids somewhat anterior to level of second pair of subventral postanal papillae (Fig. 6H,I). Length of tail 177–190 (Figs. 6G–J, 7E–F, 8A–C).

Female (based on 10 ovigerous specimens from *C. pearsei*; measurements of 2 specimens with immature eggs from *Theraps irregularis* in parentheses). Length of body

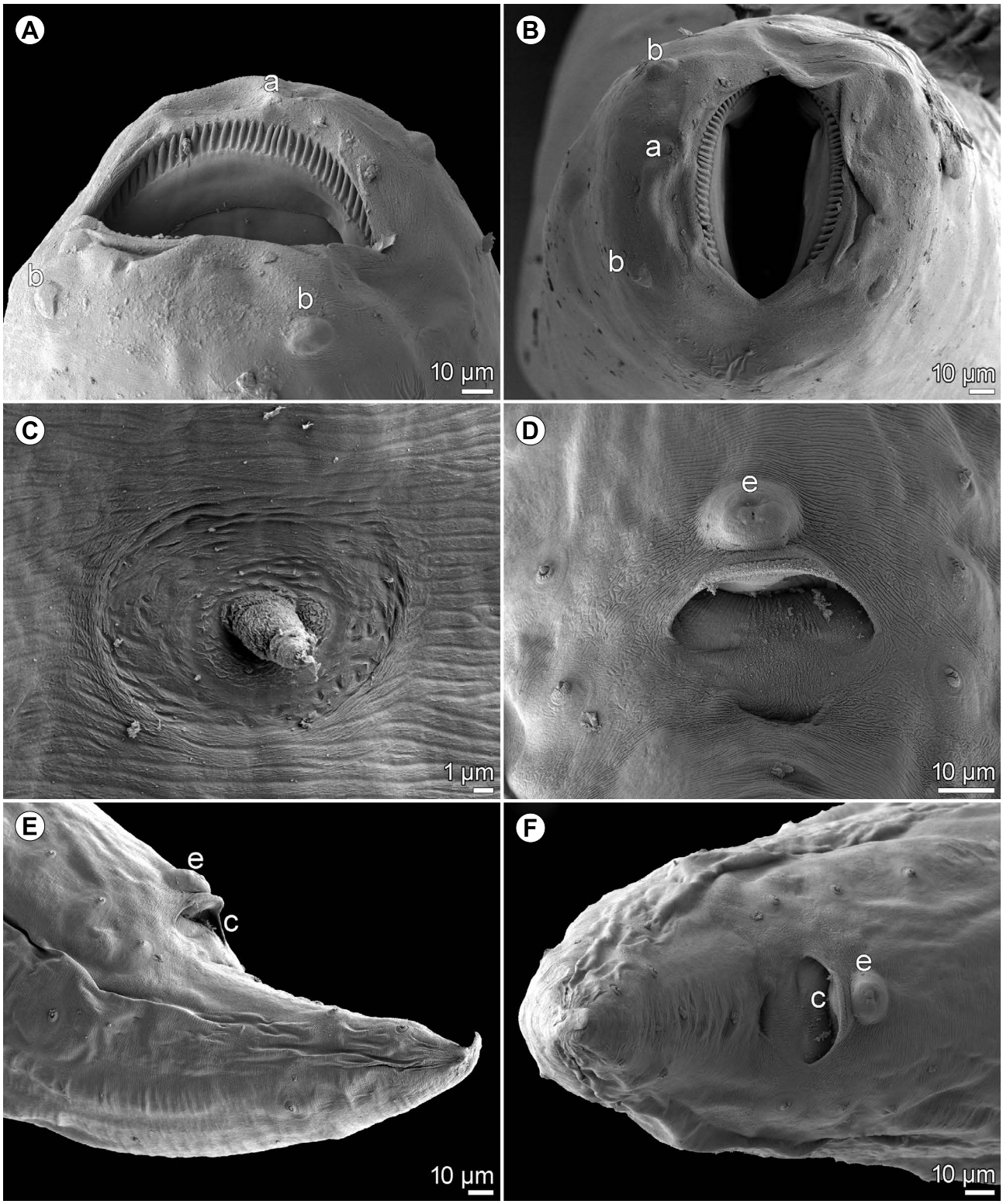

Fig. 7. *Cucullanus angeli* Cabañas-Carranza et Caspeta-Mandujano, 2007 from *Cincelichthys pearsei* (Hubbs), scanning electron micrographs. **A**, **B** – cephalic end, sublateral and apical views, respectively; **C** – deirid; **D** – region of cloaca, ventral view; **E**, **F** – male tail, lateral and ventral views, respectively. *Abbreviations*: a – amphid; b – cephalic papilla; c – cloaca; e – median precloacal papilla-like formation.

9.03–13.60 (9.11–9.15) mm, maximum width 299–503 (313–381); width at level of oesophastome 190–245 (177–218), at middle of oesophagus 190–313 (218–272). Length of entire oesophagus 898–1,074 (802–938), representing 8–10% (9–10%) of whole body length; length of oesophastome 286–367 (299–326), its width 163–190 (150–177); minimum width of oesophagus 109–136 (82–95); maximum width of posterior part of oesophagus 163–218 (150–177). Distance of nerve ring from anterior extremity 381–462 (394–408), representing 42–49% (43–49%) of oesophageal length. Deirids and excretory pore 775–925 (721–775) and 952–1,156 (911–1,047), respectively, from

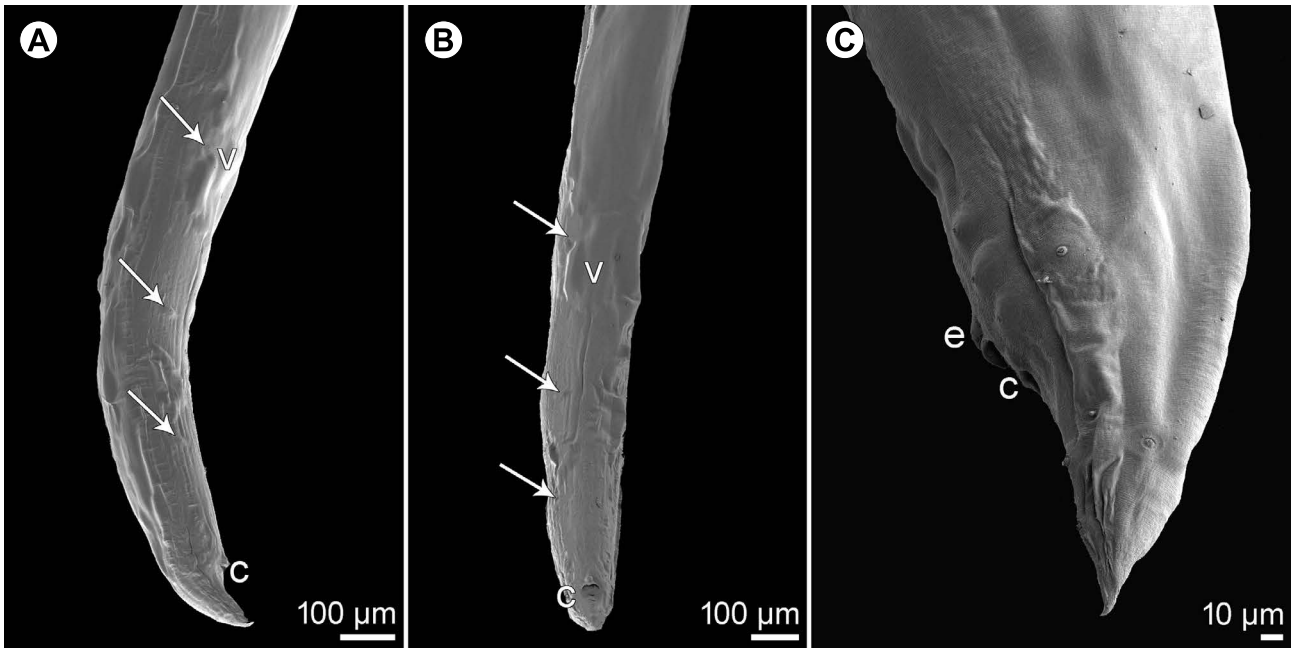

Fig. 8. *Cucullanus angeli* Cabañas-Carranza et Caspeta-Mandujano, 2007 from *Cincelichthys pearsei* (Hubbs), scanning electron micrographs of posterior end of male. **A**, **B** – posterior end of body, lateral and ventral views, respectively (arrows indicate papillae of first three preanal pairs); **C** – tail of male (another specimen), lateral view. *Abbreviations*: c – cloaca; e – median precloacal papilla-like formation; **v** – ventral sucker.

anterior end of body. Vulva postequatorial, 5.54–8.16 (5.18–5.64) mm from anterior extremity, at 59–63% (57–62%) of body length; vulval lips slightly elevated (Fig. 6E). Vagina directed anteriorly from vulva. Uterus didelphic, amphidelphic. Fully developed eggs elongate-oval, thin-walled, size 90–105 × 42–57 (-), with uncleaved contents (Fig. 6F). Length of tail 204–258 (190); phasmids situated approximately at its middle (Fig. 6D).

Hosts: *Cincelichthys pearsei* (Hubbs), Pantano cichlid, TBL 25 cm; and *Theraps irregularis* Günther, Arroyo cichlid, TBL not available (both Cichlidae).

Site of infection: Intestine.

Locality: Lacantún River (Usumacinta River basin), Chiapas State, southern Mexico (collected 20 November 2007).

Prevalence and intensity: *C. pearsei*: 2 fish infected/6 fish examined; 4 and 11 nematodes. *T. irregularis*: 2 nematodes found in the only fish examined.

Deposition of voucher specimens: IPCAS N-1289.

Comments: At present the genus *Cucullanus* Müller, 1777 includes more than a hundred of species (Pereira et al. 2015a) that are intestinal parasites mostly of freshwater, brackish-water and marine fishes throughout the world. Because of their rather uniform morphology and often inadequate descriptions, these parasites are usually dealt with according to their host groups or their zoogeographical region (Petter 1974a, Moravec et al. 1997, Moravec and Justine 2017, 2020).

To date, only five species of *Cucullanus* have been described from freshwater fishes of the family Cichlidae: *Cucullanus angeli* Cabañas-Carranza et Caspeta-Mandujano, 2007 and *C. oaxaquensis* Caspeta-Mandujano, Salgado-Maldonado et Martínez-Ramírez, 2010 from *Ch. intermedium* (Günther) and *Thorichthys helleri* (Steindachner), respectively, in southern Mexico; *Cucullanus tucunarensis* Lacerda, Takemoto, Marchiori, Martins et Pavanelli, 2013 and *Cucullanus opisthoporus* Pereira et Luque, 2016 from *Cichla piquiti* Kullander et Ferreira, and from *Cichla melaniae* Kullander et Ferreira and *Cichla pinima* Kullander et Ferreira, respectively, in Brazil; and *Cucullanus tilapiae* Moravec, 2019 from *Tilapia sparrmanii* Smith in Africa (Botswana) (Cabañas-Carranza and Caspeta-Mandujano 2007, Caspeta-Mandujano et al. 2010, Lacerda et al. 2013, Pereira and Luque 2016, Moravec 2019).

The general morphology of the present specimens is very similar to that of *C. angeli*, a species reported by Cabañas-Carranza and Caspeta-Mandujano (2007) from the same Mexican locality (Lacantún River). Nevertheless, a major difference is in the lengths of spicules; the spicules of *C. angeli* were originally described as 107–175 µm long, whereas those of the present specimens measure 612–734 µm. However, the length of spicules given in the description of *C. angeli* is evidently erroneous. It can be determined from the accompanying line drawing and its scale bar (fig. 5) in the paper by Cabañas-Carranza and Caspeta-Mandujano (2007) that in fact the spicules of *C. angeli* were about 860 µm long, i.e., similar to those in the present specimens. Therefore, the present nematodes are identified as *C. angeli*. The finding of *C. angeli* in *C. pearsei* and *T. irregularis* represent new host records for this parasite.

In the paper describing *C. oaxaquensis*, Caspeta-Mandujano et al. (2010) write that this species can be easily distinguished from similar *C. angeli* based on the length of spicules; however, the spicule length of *C. oaxaquensis* (575–825 µm) is in fact very similar to that in *C. angeli* (see above). Of other reported interspecific differences allegedly found in *C. oaxaquensis*, the "two small papillae"

near the female tail tip and the "small terminal sclerotised structure" on the tail tip were evidently based on artifacts, as visible in SEM micrographs (figs. 12, 14 and 17) in the paper of Caspeta-Mandujano et al. (2010). A roughly granular (reported as "net-like") superficial sculpture on eggs in *C. oaxaquensis* was observed using SEM (fig. 13 in Caspeta-Mandujano et al. 2010), but the eggs of *C. angeli* have not yet been studied using this technique; it may well be that such egg sculpture may occur in both species. Moreover, a markedly granular surface on eggs was also observed in *C. tilapiae* (see Moravec 2019) and possibly occurs in some other congeners. Consequently, we consider *C. oaxaquensis* a junior synonym of *C. angeli*.

Accordingly, *C. angeli* appears to be a specific parasite of Cichlidae distributed in the Usumacinta and Coatzacoalcos Rivers drainage systems, southern Mexico, from where it was recorded in four host species, *Ch. intermedium*, *C. pearsei*, *T. helleri* and *T. irregularis*. In addition, Paredes-Trujillo et al. (2020) reported this nematode in three cichlid species, *C. grammodes*, *V. breidohri* and *V. hartwegi*, from the upper Grijalva River in southeastern Chiapas; all these three fish hosts are endemic to the Grijalva River basin.

Cucullanus tucunarensis and *C. opisthoporus*, two species reported from Brazil, differ from other species of *Cucullanus* from cichlids, as well as from all other congeners, in possessing a terminal caudal appendage covered with small spines on its ventral surface. From *C. angeli* they also differ by the absence of a ventral sucker in the male. The African species *C. tilapiae*, whose male is not known, can be distinguished from *C. angeli* by deirids located slightly posterior to the level of oesophago-intestinal junction (*vs* at a short distance anterior to this junction).

***Cucullanus mexicanus* Caspeta-Mandujano, Moravec et Aguilar-Aguilar, 2000** Figs. 9, 10

Description: Medium-sized nematodes with whitish, elongate body; anterior end of body not narrowed in region of nerve ring. Lateral alae absent. Cephalic end slightly asymmetrical in lateral view. Oral aperture dorsoventrally elongate, surrounded by raised narrow membraneous ala (collarette) supported by row of *c.* 70 minute basal teeth approximately 4 long (Figs. 9C, 10A,B). Four submedian cephalic double papillae and pair of lateral amphids present (Figs. 9C, 10A,B). Oesophagus muscular, expanded at anterior end to form short bulbous pseudobuccal capsule (oesophastome) slightly asymmetrical in lateral view; posterior part of oesophagus also expanded, approximately as wide as oesophastome in lateral view (Fig. 9A). Oesophagus opens into intestine through large valve. Nerve ring encircles oesophagus at 35–37% of its length. Deirids small, pointed, with broad basal part, situated approximately in mid-way between nerve ring and posterior end of oesophagus (Figs. 9A,D, 10G). Postdeirids not found. Excretory pore located short distance anterior to posterior end of oesophagus (Fig. 9A). Tail of both sexes conical, pointed at tip.

Male (based on 3 specimens): Length of body 10.02–13.40 mm, maximum width 231–286; width at level of oesophastome 163–190, at middle of oesophagus 190. Length

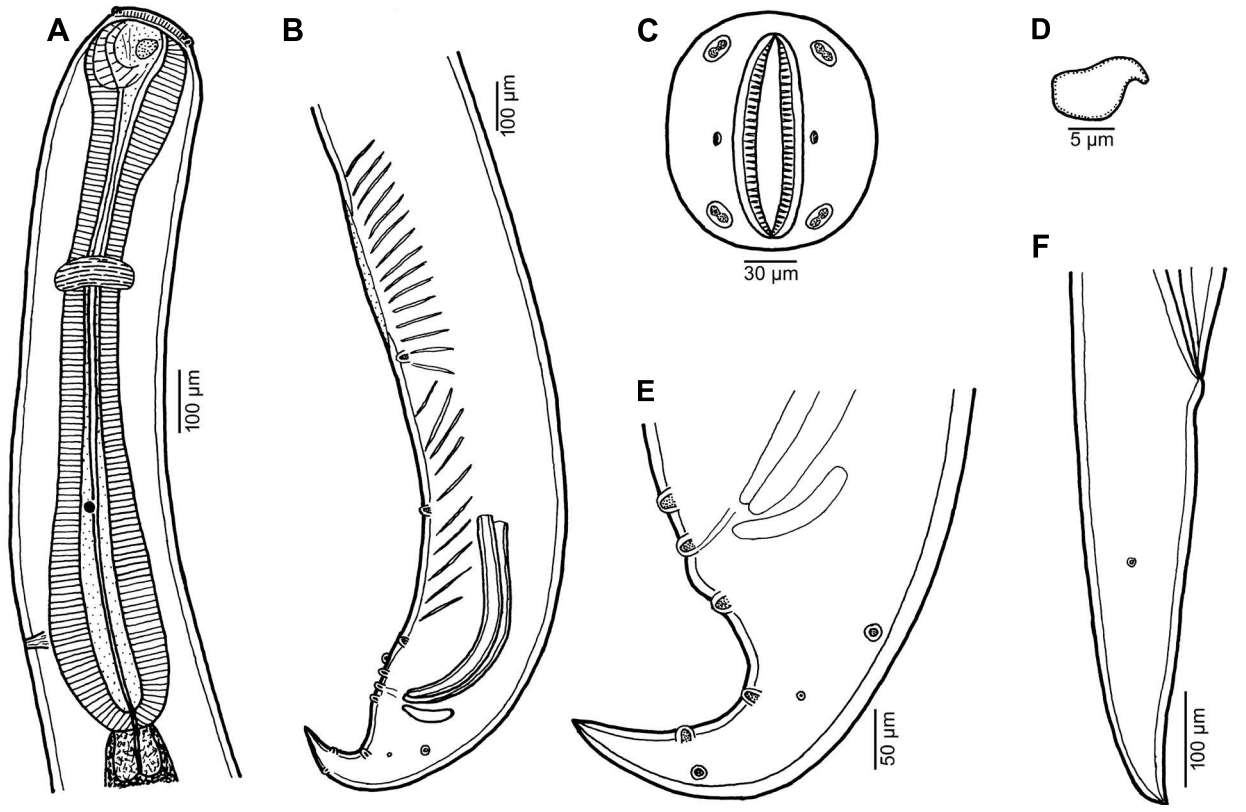

Fig. 9. *Cucullanus mexicanus* Caspeta-Mandujano, Moravec et Aguilar-Aguilar, 2000 from *Rhamdia laticauda* (Kner). **A** – anterior end of male, lateral view; **B** – posterior end of male, lateral view; **C** – cephalic end, apical view; **D** – deirid; **E** – tail of male, lateral view; **F** – tail of nongravid female, lateral view. (C, D – based on SEM micrographs).

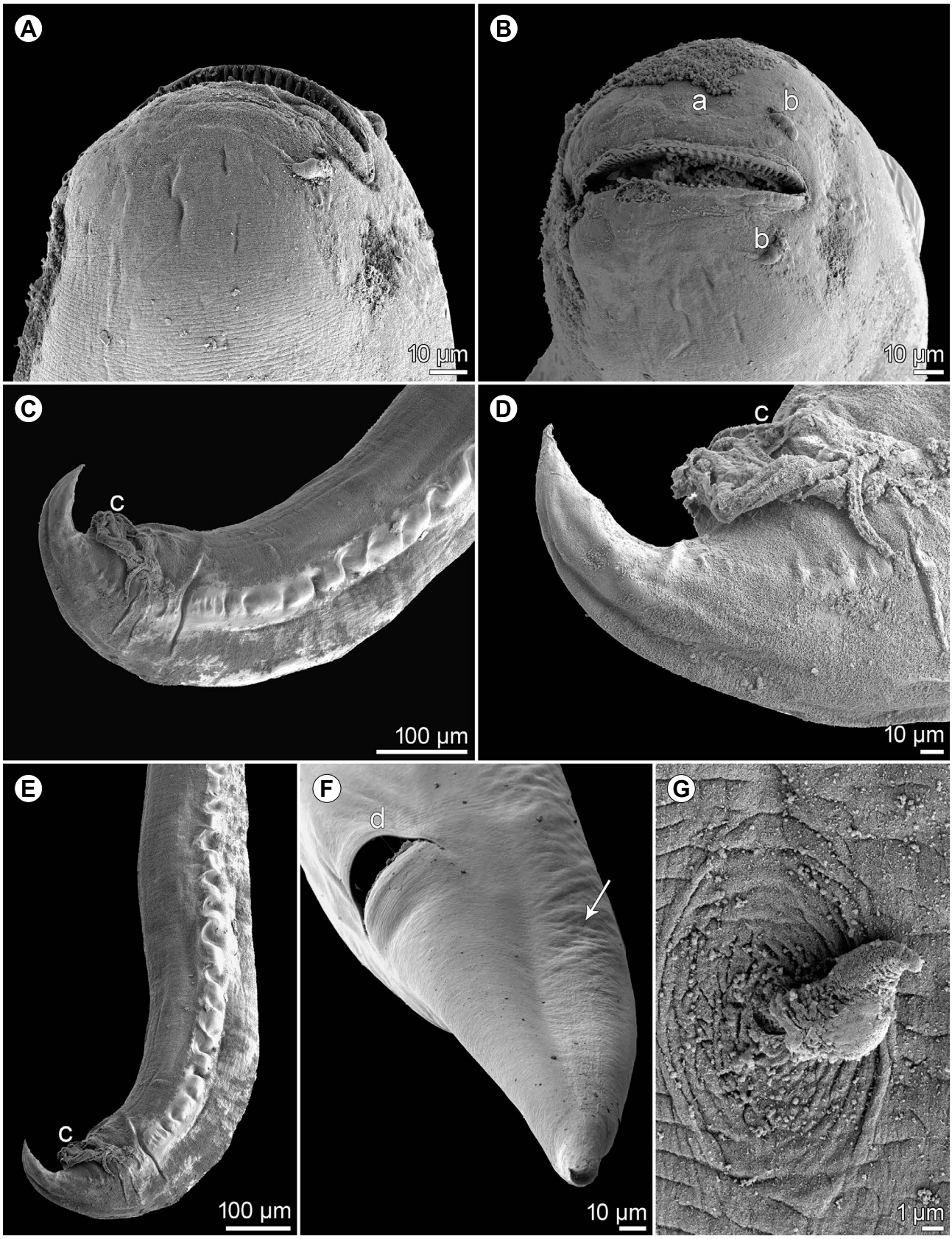

Fig. 10. *Cucullanus mexicanus* Caspeta-Mandujano, Moravec et Aguilar-Aguilar, 2000 from *Rhamdia laticauda* (Kner), scanning electron micrographs. **A**, **B** – cephalic end, lateral and apical views, respectively; **C** – posterior end of male, lateral view; **D** – tail of male, lateral view; **E** – Posterior end of male (lower magnification), lateral view; **F** – tail of female, ventrolateral view (arrow indicates phasmid); **G** – deirid. *Abbreviations*: a – amphid; b – cephalic papilla; c – cloaca; d – anus.

of entire oesophagus 857–884, representing 6–9% of whole body length; length of oesophastome 136–177, its width 109–136; minimum width of oesophagus 54–68; maximum width of posterior part of oesophagus 136–150. Distance of nerve ring from anterior extremity 313–340, representing 37–39% of oesophageal length. Deirids and excretory pore 558–571 and 721–775, respectively, from anterior end of body. Posterior end of body curved ventrally. Ventral sucker present, weakly developed (Figs. 9B, 10E). Cloacal region not elevated. Spicules equal, 348–360 long, representing 3–4% of body length (Fig. 9B). Gubernaculum weakly sclerotised, 60–81 long, rod-like in lateral view (Fig. 9B,E) and Y-shaped in ventral view. Caudal papillae 10 pairs: 5 pairs of subventral preanal papillae and 5 pairs of postanal papillae (3 subventral and 2 dorsolateral); first subventral pair of postanals slightly posterior to level of cloacal aperture, second subventral pair of postanals slightly posterior to mid-length of tail and posterior-most pair of subventrals somewhat anterior to tail tip; postanals of dorsolateral pairs approximately at levels of first and third pairs of subventrals (Figs. 9B,E, 10C–E). Pair of small lateral phasmids somewhat anterior to level of second pair of subventral postanal papillae (Figs. 9B,E). Length of tail 245–258 (Figs. 9B,E, 10C–E).

Female (based on 1 nongravid specimen): Length of body 17.68 mm, maximum width 340; width at level of oesophastome 163, at middle of oesophagus 218. Length of entire oesophagus 1.05 mm, representing 6% of whole body length; length of oesophastome 163, its width 150; maximum width of posterior part of oesophagus 163. Distance of nerve ring from anterior extremity 367, representing 35% of oesophageal length. Deirids and excretory pore not located. Vulva postequatorial, 10.04 mm from anterior extremity, at 57% of body length. Vagina directed anteriorly from vulva. Uterus didelphic, amphidelphic; empty. Tail elongate, slender, 354 long; small lateral phasmids situated approximately at mid-length of tail (Figs. 9F, 10F).

Host: *Rhamdia laticauda* (Kner) (Heptapteridae), Filespine chulín, TBL 15 cm.

Site of infection: Intestine.

Locality: Lacantún River (Usumacinta River basin), Chiapas State, southern Mexico (collected 16 and 18 November 2007).

Prevalence and intensity: 2 fish infected/4 fish examined; 3 and 1 nematodes.

Deposition of voucher specimens: Not deposited (paratypes IPCAS N-767).

Comments: To date, the only species of *Cucullanus* reported from catfishes of the family Heptapteridae is *Cucullanus mexicanus*, a parasite of the freshwater catfish *Rhamdia guatemalensis*, described from the brooks in Oaxaca, southern Mexico (Caspeta-Mandujano et al. 2000, Caspeta-Mandujano 2005). In contrast to other congeners, this species was characterised by the presence of a conspicuously elongate ventral sucker in the posterior region of the male (Caspeta-Mandujano et al. 2000).

The present specimens from *R. laticauda* are somewhat larger than those of *C. mexicanus* desribed by Caspeta-Mandujano et al. (2000), but their morphology is more or less in agreement with the original description of the species. It should be highlighted that the female nematodes studied by Caspeta-Mandujano et al. (2000) had only immature eggs. In addition to morphological and biometrical similarity of both these nematode forms, it is necessary to consider that these were collected from congeneric hosts from nearby regions (Oaxaca and Chiapas) in southern Mexico. Re-examination of the paratypes (male and female) of *C. mexicanus* deposited in the Helminthological Collection of the Institute of Parasitology, BC CAS indicated their conspecificity with the present nematodes, which are considered to belong to this species. The original description of *C. mexicanus* was based solely on LM examination, so that the present SEM study is the first one for this species.

The present finding of *C. mexicanus* infecting *R. laticauda* in Chiapas represents new host and geographical records.

***Cucullanus potamarii* sp. n.** Figs. 11–13

ZooBank number for species:
urn:lsid:zoobank.org:act:BD2D8410-8786-4F2C-A948-FC1490A551CD

Description: Medium-sized nematodes with whitish, elongate body; anterior end of body somewhat narrowed in region of nerve ring. Lateral alae absent. Cephalic end slightly asymmetrical in lateral view. Oral aperture dorsoventrally elongate, surrounded by raised narrow membraneous ala (collarette) supported by row of *c.* 140 minute basal teeth (Figs. 11C, 12A,B). Four submedian cephalic double papillae and pair of lateral amphids present (Figs. 11C, 12A,B). Oesophagus muscular, expanded at anterior end to form short bulbous pseudobuccal capsule (oesophastome) slightly asymmetrical in lateral view; posterior part of oesophagus also expanded, approximately as wide as oesophastome in lateral view (Fig. 11 A,B). Oesophagus opens into intestine through large valve. Nerve ring encircles oesophagus at 30–35% of its length. Deirids small, pointed with broad basal part, situated somewhat posterior to level of oesophago-intestinal junction (Figs. 11B,F, 12D). Postdeirids not found. Excretory pore located far posterior to level of deirids (Fig. 11B). Tail of both sexes conical, pointed at tip.

Male (based on 2 specimens; holotype; measurements of paratype in parentheses): Length of body 17.76 (19.22) mm, maximum width 408 (435); width at level of oesophastome 367 (340), at middle of oesophagus 286 (286). Length of entire oesophagus 1.77 (1.77) mm, representing 10% (11%) of whole body length; length of oesophastome 380 (313), its width 286 (299); minimum width of oesophagus 122 (122); maximum width of posterior part of oesophagus 272 (272). Distance of nerve ring from anterior extremity 571 (530), representing 32% (30%) of oesophageal length. Deirids and excretory pore 1.80 (1.93) mm and 2.58 (2.60) mm, respectively, from anterior end of body. Posterior end of body curved ventrally. Ventral sucker present (Figs. 11G, 12F,G, 13C–F). Cloacal region conspicuously protruded, with broad distal end forming curved rim (Figs. 11G,H,J, 12F,G, 13A,B,D). Small median, papilla-like elevation present anterior to cloacal opening (Fig. 11J). Spicules equal, 300 (342) long, repre-

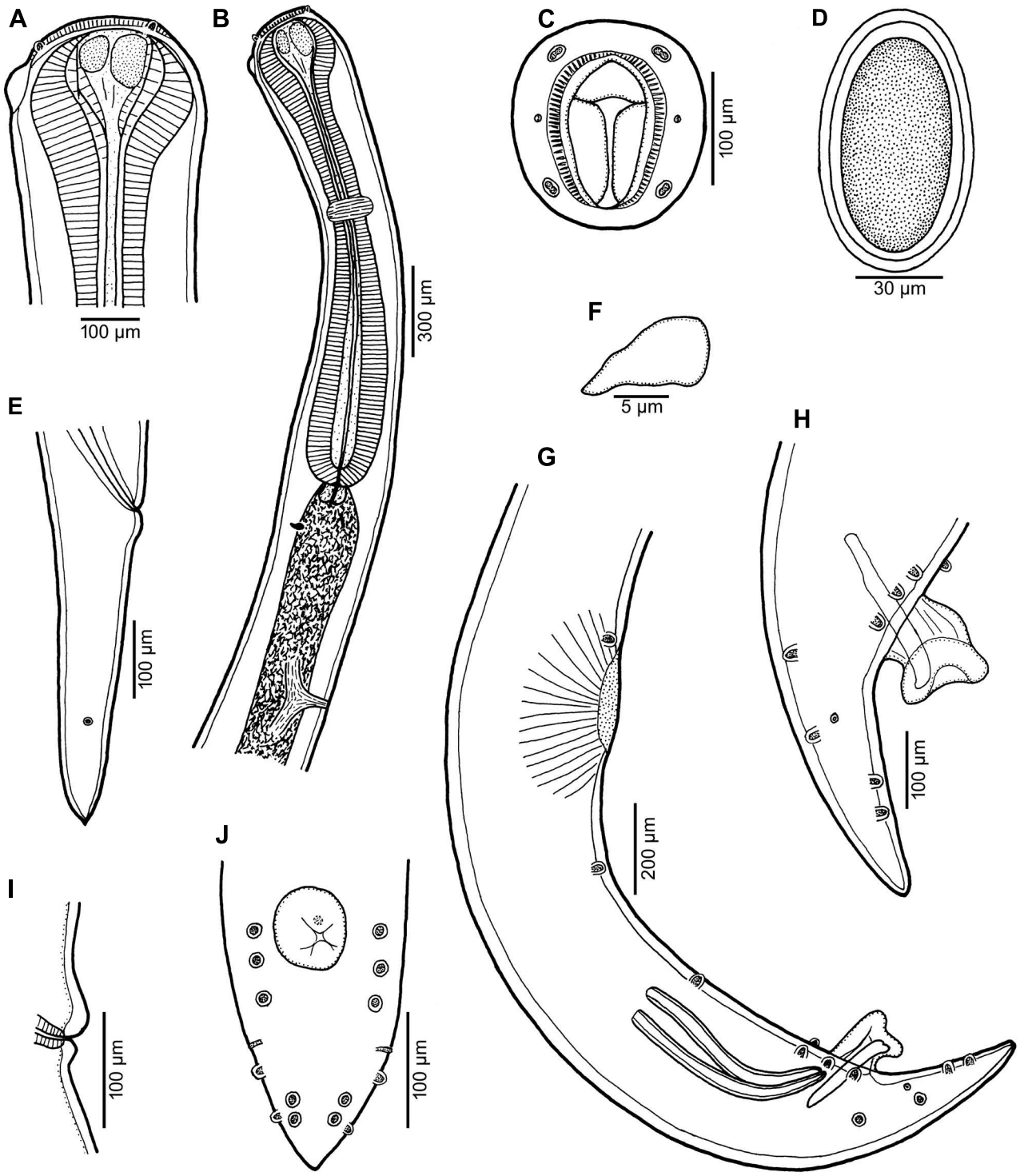

Fig. 11. *Cucullanus potamarii* sp. n. from *Potamarius usumacintae* Betancur-R et Willink. **A** – anterior end of male, lateral view; **B** – anterior portion of male body, lateral view; **C** – cephalic end, apical view; **D** – egg; **E** – tail of gravid female, lateral view; **F** – deirid; **G** – posterior end of male, lateral view; **H** – male tail, lateral view; **I** – vulva, lateral view; **J** – tail of male, ventral view. C, F, J – based on SEM micrographs).

senting 1.7% (1.8%) of body length (Fig. 11G). Gubernaculum well sclerotised, 245 (231) long, rod-like in lateral view (Fig. 11G,H) and Y-shaped in ventral view. Caudal papillae 10 pairs: 5 pairs of subventral preanal papillae, 1 pair of subventral adanal papillae and 4 pairs of postanal papillae (2 subventral and 2 dorsolateral); first dorsolateral pair of postanals just posterior to level of cloacal aperture, second dorsolateral pair of postanals near mid-length of tail; papillae of both subventral postanal pairs situated in posterior half of tail (Figs. 11 G,H,J). Pair of lateral phasmids just anterior to level of second dorsolateral pair of postanal papillae (Figs. 11 G,H,J, 13A,B). Length of tail 408 (422) (Figs. 11G,H,J, 12F,G, 13A,B,E,F).

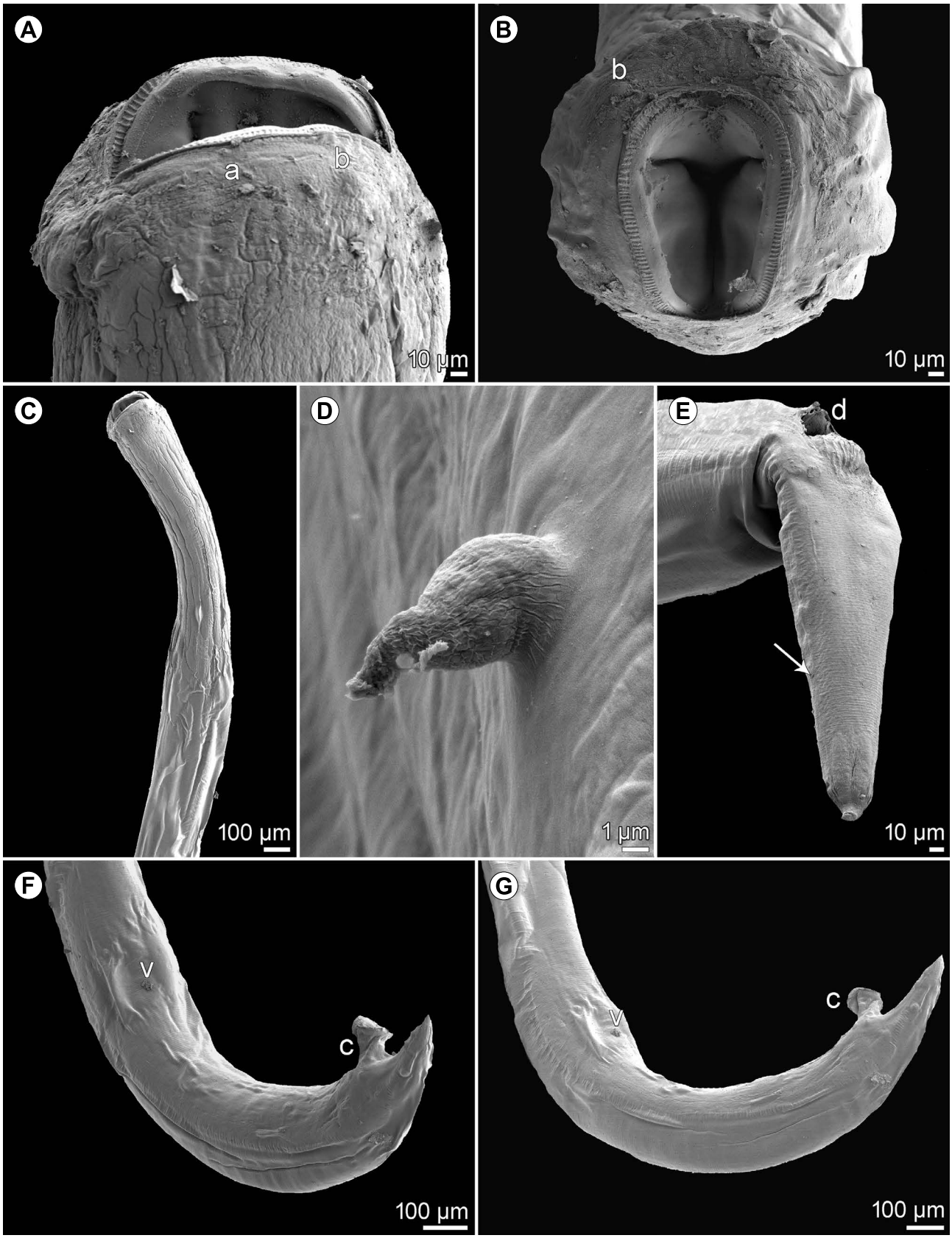

Fig. 12. *Cucullanus potamarii* sp. n. from *Potamarius usumacintae* Betancur-R et Willink, scanning electron micrographs. **A**, **B** – cephalic end sublateral and apical views, respectively; **C** – anterior end of body, lateral view; **D** – deirid; **E** – tail of female, ventrolateral view (arrow indicates phasmid); **F**, **G** – posterior end of male (two different specimens), ventrolateral views. *Abbreviations*: a – amphid; b – cephalic papilla; c – cloaca; d – anus; **v** – ventral sucker.

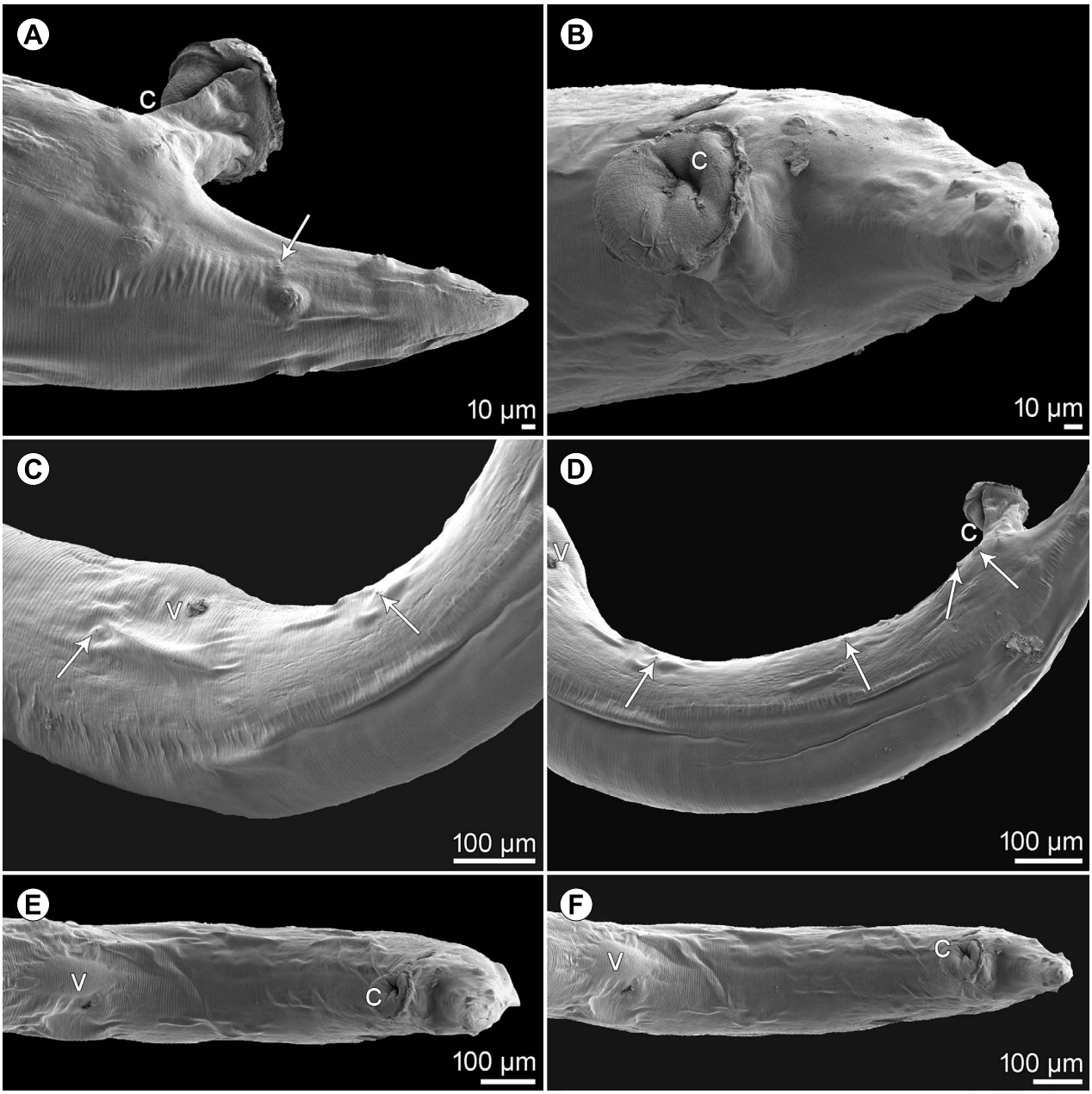

Fig. 13. *Cucullanus potamarii* sp. n. from *Potamarius usumacintae* Betancur-R et Willink, scanning electron micrographs of male. **A**, **B** – tail, lateral and ventral views, respectively (arrow indicates phasmid); **C** – region of ventral sucker, ventrolateral view (arrow indicates subventral preanal papilla); **D** – region between ventral sucker and cloaca, lateral view (arrows indicate subventral preanal papillae); **E**, **F** – posterior end of body (two different specimens), ventral views. *Abbreviations*: c – cloaca; **v** – ventral sucker.

Female (based on 1 ovigerous specimen, allotype): Length of body 15.23 mm, maximum width 313; width at level of oesophastome 286, at middle of oesophagus 245. Length of entire oesophagus 1.51 mm, representing 10% of whole body length; length of oesophastome 326, its width 326; minimum width of oesophagus 109; maximum width of posterior part of oesophagus 204. Distance of nerve ring from anterior extremity 530, representing 35% of oesophageal length. Deirids and excretory pore 1.65 mm and 2.12 mm, respectively, from anterior end of body. Vulva postequatorial, 9.52 mm from anterior extremity, at 63% of body length; vulval lips somewhat elevated (Fig. 11I). Vagina directed anteriorly from vulva. Uteri opposed. Fully developed eggs elongate-oval, thin-walled, size 84–105 × 51–54, with uncleaved contents (Fig. 11D). Tail elongate, slender, 435 long; phasmids situated approximately at 2/3 of its length (Figs. 11E, 12E).

Type host: *Potamarius usumacintae* Betancur-R et Willink (Ariidae), Usumacinta sea catfish, TBL 51 cm.

Site of infection: Intestine (its anterior portion).

Type locality: Lacantún River (Usumacinta River basin), Chiapas State, southern Mexico (collected 20 November 2007).

Prevalence and intensity: 1 fish infected/2 fish examined; 3 nematodes.

Deposition of type specimens (mounted on SEM stub): IPCAS N-1290.

Etymology: The species name of this nematode relates to the generic name of the type host.

Comments: Only seven species of *Cucullanus* have been described from catfishes of the family Ariidae: *Cucullanus arii* Yamaguti, 1954 and *Cucullanus armatus* Yamaguti, 1954, each from *Arius* sp. off Borneo, Indonesia; *Cucullanus bagre* Petter, 1974 from *Bagre bagre* (Linnaeus) off French Guiana (reported also from this host species off Brazil and from *Ariopsis assimilis* (Günther) off Mexico); *C. baylisi* Bharatha-Lakshmi, 2000 from *Netuma thalassina* (Rüppel) off India; *Cucullanus costaricensis* López-Caballero, Osorio-Sarabia et García-Prieto, 2009 from *Bagre pinnimaculatus* (Steindachner) in Costa Rica; *Cucullanus laurotravassosi* Petter et Le Bel, 1992 from *Arius* sp. in Australia; and *Cucullanus quadrii* Bilqees et Fatima, 1980 from *N. thalassina* off Pakistan (Yamaguti 1954, Petter 1974b, Bilqees and Fatima 1980, Petter and Le Bel 1992, Bharatha-Lakshmi 2000, Aguirre-Macedo et al. 2007, López-Caballero et al. 2009, Pereira et al. 2015a).

Of these, only *C. costaricensis* and *C. laurotravassosi* occur in fresh waters of Costa Rica and Australia, respectively, whereas all the remaining five species were reported from marine environments, largely in Asia. It is necessary to note that the fish host of *C. potamarii* sp. n., i.e., *P. usumacintae*, is an exclusively freshwater fish (as all its congeners), which is endemic to the Usamacinta River basin (Froese and Pauly 2024).

Based on the general morphology, *C. potamarii* sp. n. is similar to species of *Cucullanus* described from ariid hosts in America (*C. bagre* and *C. costaricensis*) and that from Australia (*C. laurotravassosi*) (see also Pereira et al. 2015a), differing from them mainly in the location of deirids, that are distinctly posterior to the level of the oesophago-intestinal junction (*vs* some distance anterior to oesophago-intestinal junction). The excretory pore of *C. bagre* is far posterior to the posterior end of oesophagus, resembling thus the new species, whereas that of *C. costaricensis* is allegedly placed at a short distance posterior to the nerve ring, i.e., anterior to the level of deirids. However, considering that the excretory pore is often difficult to observe in cucullanids and its location in relation to deirids as described for *C. costaricensis* is unusual in these nematodes, the information about the position of the excretory pore in *C. costaricensis* needs to be verified. In contrast to the new species, the excretory pore of *C. laurotravassosi* was reported to be "close to the deirids" (Petter and Le Bel 1992), i.e., slightly anterior to the oesophago-intestinal junction.

The location of deirids and the excretory pore far posterior to the end of the oesophagus as in *C. potamarii* sp. n. is very rare among all *Cucullanus* spp. and, in fact, this feature was previously reported only for *Cucullanus rhamphichthydis* Moravec, Kohn et Fernandes, 1997 (described solely from females), a parasite of *Rhamphichthys rostratus* (Linnaeus) (Rhamphichthyidae, Gymnotiformes) in the Paraná River, Brazil (Moravec et al. 1997) and for *C. opisthoporus* Pereira et Luque, 2016 parasitising *Cichla* spp. (Cichlidae, Cichliformes) in the Amazon River basin Brazil (Pereira and Luque 2016).

However, in contrast to the new species, specimens of *C. rhamphichthydis* are smaller (body length 9–12 *vs* 15–19 mm), their oesophastome is funnel-shaped (*vs* approximately spherical) and smaller (258 × 177–190 *vs* 313–380 × 286–326 μm), the entire oesophagus is shorter (1.17–1. 35 *vs* 1.51–1.77 mm long) and also the female tail is shorter (313–326 *vs* 435 μm long). Moreover, hosts of both species belong to different fish orders (Gymnotiformes *vs* Siluriformes). *Cucullanus opisthoporus* differs clearly from *C. potamarii* sp. n. in having no ventral sucker in the male, much longer spicules (793–1,180 μm *vs* 300–342 μm) and the presence (*vs* absence) of numerous minute spines on the tail tip of both sexes. These species also differ in the orders of their fish hosts (Cichliformes *vs* Siluriformes) and in the geographical region (Brazil *vs* Mexico).

Cucullanus potamarii sp. n. is the fourth known valid species of *Cucullanus* parasitising freshwater fishes in Mexico, in addition to *C. angeli* (syn. *C. oaxaquensis*), *Cucullanus caballeroi* Petter, 1977 and *C. mexicanus*.

***Neocucullanus neocucullanus* Travassos, Artigas et Pereira, 1928** Figs. 14–16

Syns.: *Cucullanus interrogativus* Travassos, Artigas et Pereira, 1928; *Neocucullanus multipapillatus* Petter, 1989

Description: Larger-sized nematodes. Body whitish, elongate, slightly narrower in region between posterior end of pseudobuccal capsule and posterior end of oesophagus (Fig. 14A,B). Lateral cervical alae absent. Cephalic end rounded in lateral view (Figs. 14A, 15A). Oral aperture dorsoventrally elongate, surrounded by raised narrow membraneous ala (collarette) supported by row of *c.* 100 minute basal teeth (Figs. 14C, 15A–D). Four submedian cephalic double papillae and pair of lateral amphids present (Figs. 14C, 15A–C). Oesophagus muscular, expanded at its anterior portion to form bulbous pseudobuccal capsule (oesophastome); posterior part of oesophagus also expanded, slightly broader than oesophastome in lateral view (Fig. 14A). Six large rounded oesophageal lobes, 3 on each side, visible in mouth in apical view (Figs. 14C, 15C). Oesophagus opens into intestine through large valve. Nerve ring encircles oesophagus at distance representing 37–44% of oesophageal length. Deirids small, rounded, situated at posterior half of distance between nerve ring and posterior end of oesophagus (Figs. 14A, B). Postdeirids absent. Excretory pore slightly posterior to level of deirids (Fig. 14A). Tail of both sexes short, conical to broadly rounded, bearing small terminal cuticular spike (Figs. 14D–F,I, 16A–D,F).

Male (based on 6 specimens): Length of body 9.86–19.53 mm, maximum width 245–639; width at level of cloaca 245–666. Length of entire oesophagus 1.05–1.32 mm, representing 9–11 (9)% of body length; length of oesophastome 326–394, its width 150–231; minimum width of oesophagus 68–136; maximum width of posterior part of oesophagus 190–245. Distance of nerve ring from anterior extremity 449–517, representing 37–43% of oesophageal length. Deirids and excretory pore 680–870 and 707–966, respectively, from anterior end of body. Posterior end of body curved ventrally. Ventral sucker present, well developed (Fig. 14E,F). Spicules broad, non-alate, equal, 435–517 long and 24–60 wide (Fig. 14D,F). Gubernaculum absent. Thirteen pairs of caudal papillae: 8 pairs of subventral preanal papillae, 1 pair of adanal papillae and 4 pairs

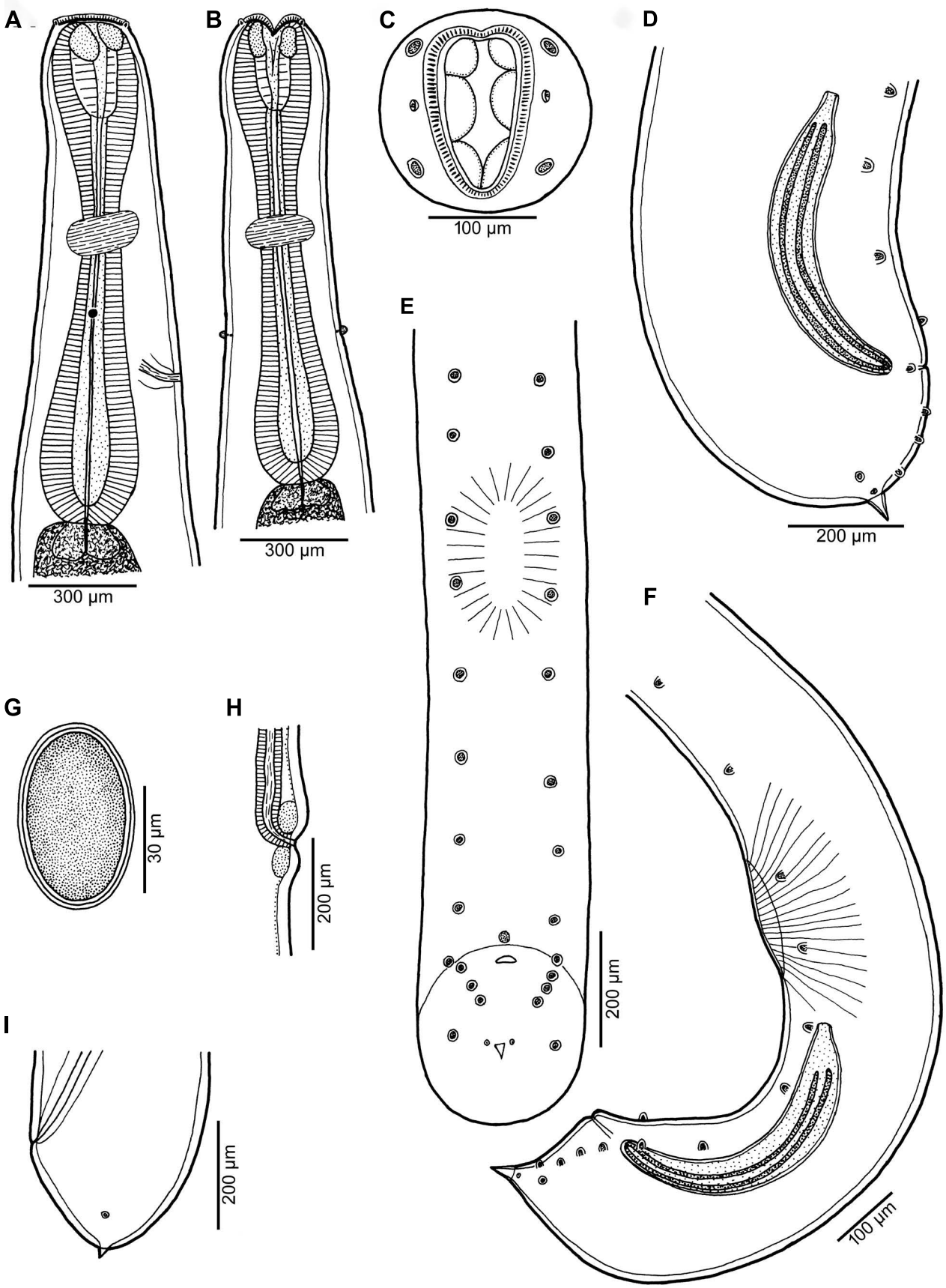

Fig. 14. *Neocucullanus neocucullanus* Travassos, Artigas et Pereira, 1928 from *Brycon guatemalensis* Regan. **A**, **B** – anterior end of male, lateral and dorsoventral views, respectively; **C** – cephalic end, apical view; **D** – posterior end of larger male, lateral view; **E** – distribution of caudal papillae in male, ventral view (constructed based on SEM micrographs); **F** – posterior end of body of smallest male, lateral view; **G** – egg; **H** – vulva, lateral view; **I** – tail of female, lateral view.

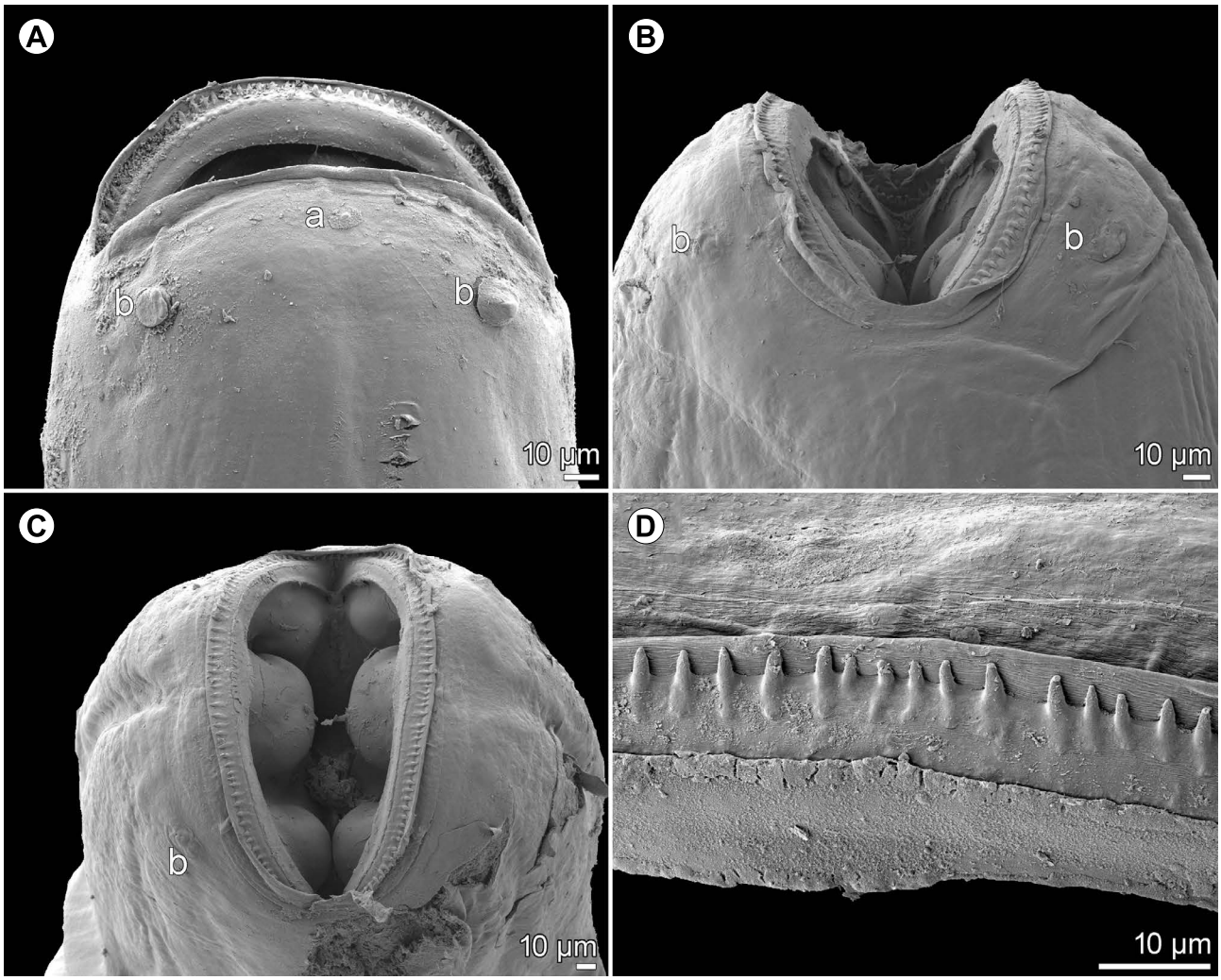

Fig. 15. *Neocucullanus neocucullanus* Travassos, Artigas et Pereira, 1928 from *Brycon guatemalensis* Regan, scanning electron micrographs. **A**, **B** – cephalic end, lateral and dorsoventral views, respectively; **C** – cephalic end, apical view; **D** – detail of peribuccal teeth. *Abbreviations*: a – amphid; b – cephalic papilla.

of postanal papillae (3 subventral and 1 lateral); 1 median papilla-like elevation present anterior to cloacal aperture (Figs. 14 D–F, 16A–E). Pair of minute phasmids located laterally close to base of caudal spike (Figs. 14D–F, 16D). Length of tail including terminal spike 150–272; spike 24–41 long (Figs. 14 D–F, 16 A–D).

Female (based on 3 ovigerous specimens): Length of body 27.57–28.76 mm, maximum width 449–571; width at level of anus 190–394. Length of entire oesophagus 1.33–1.41 mm, representing 7–9% (7%) of body length; length of oesophastome 408–503, its width 218–231; minimum width of oesophagus 95–122; maximum width of posterior part of oesophagus 231–299. Distance of nerve ring from anterior extremity 517–584, representing 37–44% of oesophageal length. Deirids and excretory pore 897–993 and 911–1,020, respectively, from anterior end of body. Vulva postequatorial, 15.05–15.98 mm from anterior extremity, at 53–56% of body length; vulval lips slightly elevated (Fig. 14H). Vagina directed anteriorly from vulva. Uterus didelphic, amphidelphic. Fully developed eggs elongate-oval, thin-walled, size 51–60 × 30–42, with uncleaved contents (Fig. 14G). Length of tail including terminal spike 204–272; spike 15–18 long; pair of small phasmids situated laterally at short distance anterior to caudal terminal spike (Figs. 14I, 16F).

Host: *Brycon guatemalensis* Regan (Bryconidae), Machaca; TBL 21–36 cm.

Site of infection: Intestine.

Locality: Lacantún River (Usumacinta River basin), Chiapas State, southern Mexico (collected 15 and 16 November 2007).

Prevalence and intensity: 5 fish infected/8 fish examined; 1–6 (mean 3) nematodes per fish.

Deposition of voucher specimens: IPCAS N-1288.

Comments: *Neocucullanus neocucullanus*, the type species of *Neocucullanus* Travassos, Artigas et Pereira, 1928, was described by Travassos et al. (1928) from an unidentified characiform fish (reported as Characidae gen. sp.) in the Paraná River basin of Brazil. Subsequently, the same species was reported from Brazil (States of Minas Gerais, Mato Grosso and São Paulo) by several authors from *Brycon* sp., *Brycon hilarii* (Valenciennes), *Salminus brasiliensis* (Cuvier) and *S. hilarii* Valenciennes (all Bryconidae, Characiformes) (see Luque et al. 2011). Caspeta-Mandujano et al. (2005) recorded it from *Brycon guate-*

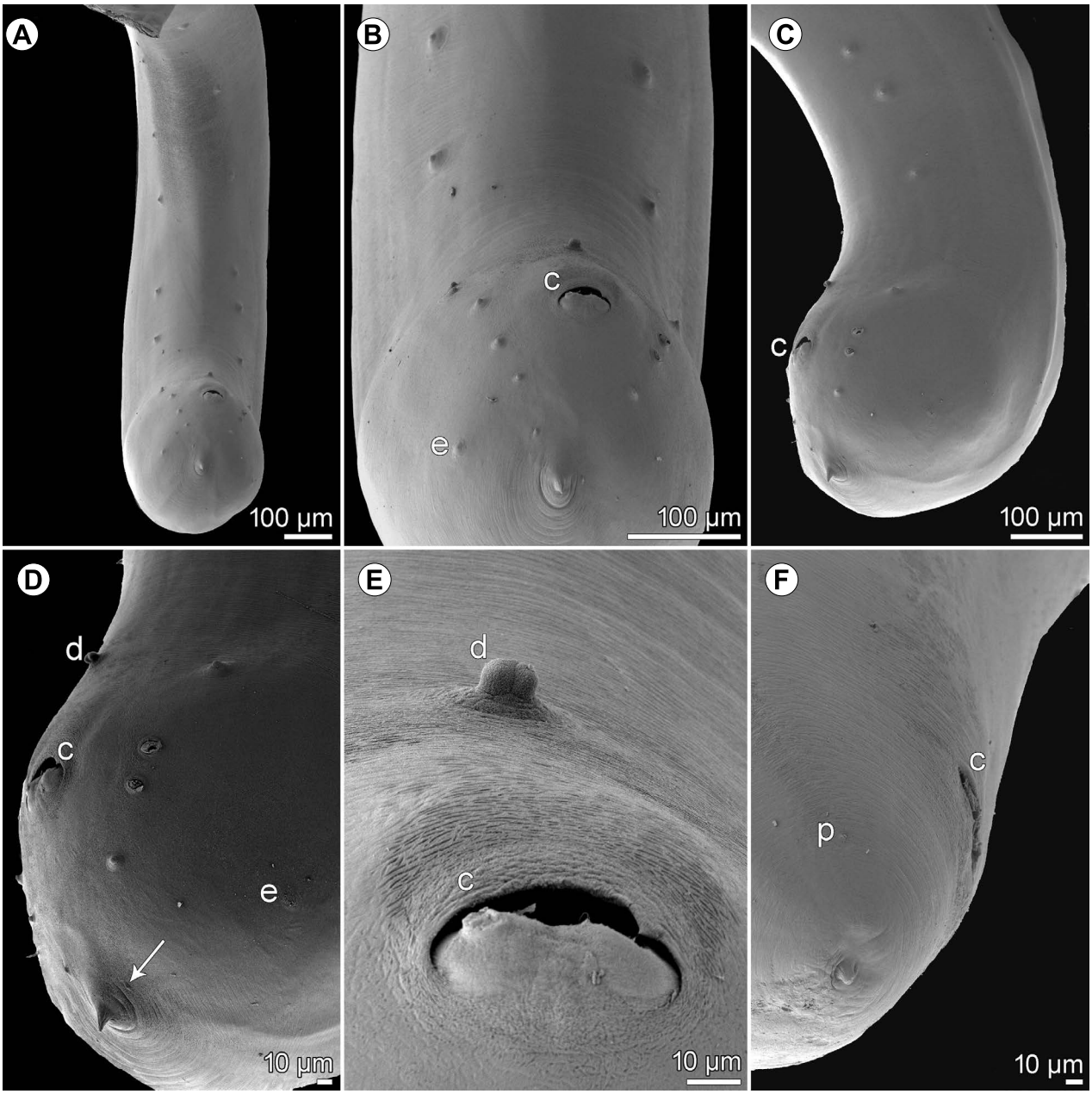

Fig. 16. *Neocucullanus neocucullanus* Travassos, Artigas et Pereira, 1928 from *Brycon guatemalensis* Regan, scanning electron micrographs. **A** – posterior end of male, ventral view; **B** – same, enlarged region of cloaca in ventral view; **C** – posterior end of male, lateral view; **D** – tail of male, lateral view (arrowhead indicates phasmid); **E** – precloacal median papilla-like elevation and cloacal aperture, ventral view; **F** – tail of female, sublateral view. *Abbreviations*: c – cloacal aperture; d – precloacal median papilla-like elevation; e – lateral postanal papilla; p – phasmid.

malensis in the Usumacinta River, southerm Mexico. From the same host species in Chiapas it is also reported from the Lacantún River by Salgado-Maldonado et al. (2011b).

Petter (1989) described another congeneric species, *N. multipapillatus*, from *Brycon microlepis* (Valenciennes) (= syn. of *B. hilarii*) of the Paraná River basin in Paraguay and considered *Cucullanus interrogativus* Travassos, Artigas et Pereira, 1928 from Brazil to represent juvenile forms of *N. neocucullanus*. Nevertheless, based on the morphological similarity between *N. multipapillatus* and *N. neocucullanus*, Moravec (1998) questioned the validity of the former species. Subsequently, *N. multipapillatus* was formally synonymised with *N. neocucullanus* by Saraiva et al. (2006), which is accepted here.

Small differences were found in the present material when compared with other taxonomic studies of *N. neocucullanus*. These differences are mainly in the number and distribution of caudal papillae, which may be difficult to observe in LM. Even though Caspeta-Mandujano et al. (2005) and Saraiva et al. (2006) studied the species using SEM, some inconsistencies persist. According to the original description of *N. neocucullanus* by Travassos et al. (1928), there are 13 pairs of caudal papillae in the males, whereas Petter (1989) and Saraiva et al. (2006) reported 15 and 14 pairs, respectively. The present data are

in agreement with the original description of the species and with the observations of Caspeta-Mandujano et al. (2005), reporting 13 pairs of papillae (8 preanal, 1 adanal and 4 postanal) in *N. neocucullanus*. Petter (1989) reported the presence of a small gubernaculum in *N. multipapillatus* (= *N. neocamallanus*), but no sclerotised gubernaculum was observed in *Neocucullanus neocucullanus* Travassos, Artigas et Pereira, 1928 by Travassos et al. (1928), Caspeta-Mandujano et al. (2005), Saraiva et al. (2006) and in the present study. The shape of spicules in the present specimens was similar to that illustrated by Petter (1989).

The present data show that *N. neocucullanus* is a parasite of fishes belonging to the characiform family Bryconidae, being distributed from Paraguay and southern Brazil to southerm Mexico (Chiapas).

Ramallo (2012) described a new species of *Neocucullanus*, *Neocucullanus marcelae* Ramallo, 2012, from *Salminus brasiliensis* in the Paraná River basin, Argentina (Province of Salta). She distinguished it from *N. neocamallanus* mainly by the excretory pore allegedly located near the anterior end of body (far anterior to the level of nerve ring and deirids), long spicules (over 1.60 mm) and a different number (15 subventral pairs and 2 single median papillae) and distribution of male caudal papillae. However, the low-quality SEM micrographs and the respective line drawings indicate that some of these taxonomic features are apparently based on artifacts (e.g., the excretory pore is never anterior to the nerve ring in cucullanids) or inaccurate observations (presence of a ventral median postanal papilla?). Therefore, we consider *N. marcelae* to be a *species inquirenda*. Since the host species (*S. brasiliensis*) and the river drainage system are identical for both *N. marcelae* and *N. neocucullanus*, the former species may well prove to be conspecific with the latter one. Nevertheless, the length and shape of the spicules of *N. marcelae* as reported by Ramallo (2012) are very different from those in *N. neocamallanus*, resembling rather the spicules in other cucullanid genera, so that the generic misidentifcation of these nematodes cannot be excluded.

Family Camallanidae Railliet et Henry, 1915

Procamallanus (*Spirocamallanus*) *rebecae* (Andrade-Salas, Pineda-López et García-Magaña, 1994) Moravec, Mendoza-Franco, Vargas-Vázquez et Vivas-Rodríguez, 1995

Syn.: *Spirocamallanus rebecae* Andrade-Salas, Pineda-López et García-Magaña, 1994

The present specimens of *P.* (*S.*) *rebecae* were morphometrically identical with those previously described by Andrade-Salas et al. (1994) and redescribed by Moravec et al. (1995a) from cichlids in the Mexican States of Campeche and Tabasco, and Yucatan, respectively.

Hosts: *Mayaheros urophthalmus* (Günther), Mexican mojarra, TBL 8–15 cm; *Thorichthys helleri* (Steindachner), Yellow cichlid, TBL 7–15 cm; *T. meeki* Brind, Firemouth cichlid, TBL 8–9 cm; *Thorichthys* sp., TBL 10–13 cm; *Vieja melanurus* (Günther), Redhead cichlid, TBL 10–12 cm; and *Wajpamheros nourissati* (Allgayer), Bluemouth cichlid, TBL 8–11 cm (all Cichlidae).

Site of infection: Intestine, less often stomach or rectum.

Locality: Lacantún River including Laguna El Oaxaco (Usumacinta River basin), Chiapas State, southern Mexico (collected 16–20 November 2007).

Prevalence and intensity: *M. urophthalmus*: 2 fish infected/5 fish examined; 1 nematode per fish. *T. helleri*: 2/4; 1 and 4. *Thorichthys* sp.: 3/5; 1 and 2. *V. melanurus*: 2/3; 3 and 6. *W. nourissati*: 4/6; 1–2.

Deposition of voucher specimens: Not deposited.

Comments: *Procamallanus* (*S.*) *rebecae* seems to be a common and widespread intestinal parasite of many species of cichlids in southern Mexico (States of Campeche, Chiapas, Oaxaca, Quintana Roo, Tabasco, Veracruz and Yucatán) (Caspeta-Mandujano 2005). The species was already reported from the Lacantún River and its tributary Lacanjá River in Chiapas by Caspeta-Mandujano (2005) and Salgado-Maldonado et al. (2011b).

The life cycle of this parasite was experimentally studied by Moravec et al. (1995b) (see also Moravec 1998) in Yucatán, Mexico. As suitable experimental hosts were found copepods *Mesocyclops chaci* Fiers, Reid, Iliffe et Suárez-Morales (intermediate hosts), guppies *Poecilia reticulata* Peters (paratenic hosts) and cichlids *M. urophthalmus* (definitive hosts).

Family Daniconematidae Moravec et Køie, 1987

Mexiconema cichlasomae Moravec, Vidal et Salgado-Maldonado, 1992

The present material comprised only one immature female of this nematode.

Host: *Thorichthys helleri* (Steindachner) (Cichlidae), Yellow cichlid; TBL 15 cm.

Site of infection: Intestine.

Locality: Lacantún River (Usumacinta River basin), Chiapas State, southern Mexico (collected 19 November 2007).

Prevalence and intensity: 1 fish infected/4 fish examined; 1 nematode.

Deposition of voucher specimen: Not deposited.

Comments: This nematode species is a frequent parasite of the abdominal cavity and viscera (rarely of skin) of many species of cichlids in southern Mexico (States of Campeche, Quintana Roo, Tabasco, Veracruz and Yucatán), occasionally also recorded from *Xiphophorus hellerii* Heckel (Poeciliidae) (Moravec et al. 1992b, 1998, Caspeta-Mandujano 2005).

Infective larvae of *M. cichlasomae* were recorded from naturally infected *Argulus yucatanus* Poly (Branchiura) in Yucatán, where these blood-sucking ectoparasites of cichlids apparently serve as the nematode's intermediate hosts (Moravec et al. 1999, Moravec 2006).

Family Rhabdochonidae Travassos, Artigas et Pereira, 1928

***Rhabdochona kidderi kidderi* Pearse, 1936**

Syn.: *Rhabdochona ictaluri* Aguilar-Aguilar, Rosas-Valdéz et Pérez-Ponce de León, 2010

Results of detailed studies of this nematode species from fishes of the Lacantún River (part of the present material) have already been published in the paper by Moravec et al. (2012).

Comments: Moravec et al. (2012) reported four-stage larvae of *Rhabdochona kidderi* Pearse, 1936 from the intestine of *Eugerres mexicanus* in the Lacantún River. In the same host and locality, adults of a new congeneric species, *Rhabdochona juliacarabiasae* Caspeta-Mandujano, Salinas-Ocampo, Suárez-Rodríguez, Ramírez-Martínez et Matamoros, 2021, were later described by Caspeta-Mandujano et al. (2021). The authors speculated that the larvae reported by Moravec et al. (2012) probably belonged to *R. juliacarabiasae*. However, the shape of deirids of these larvae was characteristic of *R. kidderi*, as visible in a SEM micrograph (fig. 3e) of Moravec et al. (2012). In this case, *E. mexicanus* served as a paratenic or transport host for *R. kidderi* larvae.

Moravec et al. (2012) synonymised *Rhabdochona ictaluri* Aguilar-Aguilar, Rosas-Valdéz et Pérez-Ponce de León, 2010 from *Ictalurus* spp. in Mexico with *R. kidderi*. However, based on new comparative morphological and molecular studies of *R. ictaluri* and *R. kidderi*, the validity of the former species was resurrected by Lagunas-Calvo et al. (2019), reporting the allegedly presence/absence of six basal teeth in the prostom (but no such structures are apparent in their SEM micrographs figs. 1a and 1b) and the number of eggs in the uterus to be the main interspecific morphological differences. However, such features are doubtful and not used in rhabdochonid taxonomy. Therefore, since the molecular differences pointed out by Lagunas-Calvo et al. (2019) are not supported by morphological or ecological differences, we still consider both forms as synonymous for now.

Family Cystidicolidae Skryabin, 1946

***Spinitectus osorioi* Choudhury et Pérez-Ponce de León, 2001**

Results of detailed studies of this nematode species from fishes of the Lacantún River (part of the present material) have already been dealt with in the paper by Moravec et al. (2009).

***Spinitectus tabascoensis* Moravec, García-Magaña et Salgado-Maldonado, 2002**

Syn.: *Spinitectus macrospinosus* Choudhury et Perryman, 2003

Results of detailed studies of *S. tabascoensis* from fishes of the Lacantún River (part of the present material) have already been published by Moravec et al. (2009).

Larval nematodes

Family Kathlaniidae Lane, 1914

***Falcaustra* sp. third-stage larvae**

These larvae were already described by Moravec et al. (1995c) from fishes in Texas, USA, and by Moravec et al. (1995d) and Caspeta-Mandujano (2005) from fish hosts in the States of Yucatán, Quintana Roo, Campeche, Tabasco and Chiapas, Mexico.

Host: *Rhamdia guatemalensis* (Günther) (Heptapteridae), Pale catfish, TBL 25 cm.

Site of infection: Swimbladder.

Locality: Lacantún River (Usumacinta River basin), Chiapas State, southern Mexico (collected 11 November 2007).

Prevalence and intensity: 1 fish infected/2 fish examined; 15 nematodes.

Deposition of specimens: Not deposited.

Comments: According to Moravec et al. (1995c), these larvae probably belong to one or more species of *Falcaustra* parasitic in freshwater turtles, where fishes play a role of paratenic hosts. Moravec and Vargas-Vázquez (1998) recorded adults of *Falcaustra affinis* (Leidy, 1856) from the turtle *Trachemys scripta* (Schoepf) in a small lake in central Yucatán.

In Yucatán, larvae of *Falcaustra* Lane, 1915 were recorded from many fish species (including *R. guatemalensis*) of different families, being found free or encapsulated in the host's abdominal cavity (mainly on the surface of intestine), liver, gall-bladder, mesentery or brain (Moravec et al. 1995d, Caspeta-Mandujano 2005).

Family Anisakidae Railliet et Henry, 1912

***Contracaecum* sp. larvae Type 1 of Moravec et al. (1993b)**

Descriptions of these larvae were already provided by Moravec et al. (1993b, 1995d) and Caspeta-Mandujano (2005).

Host: *Brycon guatemalensis* Regan (Bryconidae), Machaca, TBL 29 cm; and *Chuco intermedium* (Günther) (Cichlidae), Northern checkmark cichlid, TBL 13 cm.

Site of infection: Surface of intestine.

Locality: Lacantún River (Usumacinta River basin), Chiapas State, southern Mexico (collected 16 and 17 November 2007).

Prevalence and intensity: *B. guatemalensis*: 1 fish infected/4 fish examined; 9 nematodes. *C. intermedium*: 1/6, 1.

Deposition of specimens: Not deposited.

Comments: These larvae are characterised by the presence of a markedly long ventricular appendix the length of which usually slightly exceeds that of the intestinal caecum. They were reported from many fish species in Brazil, Venezuela and Mexico (Moravec et al. 1993b, 1995d, Moravec 1998, Caspeta-Mandujano 2005). The adult forms of these larvae are apparently parasitic in fish-eating birds; fishes serve either as the second intermediate hosts or as paratenic hosts.

***Contracaecum* sp. larvae Type 2 of Moravec et al. (1993b)**

Descriptions of these larvae were already provided by Moravec et al. (1993b, 1995d), Moravec (1998) and Caspeta-Mandujano (2005).

Hosts: *Atractosteus tropicus* Gill (Lepisosteidae), Tropical gar; TBL 52–53 cm; *Dorosoma petenense* (Günther) (Dorosomatidae), Threadfin shad, TBL 11–17 cm; *Brycon guatemalensis* Regan (Bryconidae), Machaca, TBL 18 cm; *Ictalurus furcatus* (Valenciennes) (Ictaluridae), Blue catfish, TBL 39 cm; *Lacantunia enigmatica* Rodiles-Hernández, Hendrickson et Lundberg (Lacanthuniidae), Chiapas catfish, TBL 46 cm; *Rhamdia guatemalensis* (Günther) (Heptapteridae), Pale catfish, TBL 25 cm; *Chuco intermedium* (Günther) (Cichlidae), Northern checkmark cichlid, TBL 12 cm; *Mayaheros urophthalmus* (Günther) (Cichlidae), Mexican mojarra, TBL 19 cm; *Parachromis friedrichsthalii* (Heckel) (Cichlidae), Yellowjacket cichlid, TBL 14 cm; *Parachromis managuensis* (Günther) (Cichlidae), Jaguar guapote, TBL 24 cm; *Petenia splendida* Günther (Cichlidae), Bay snook, TBL 12–23 cm; *Thorichthys helleri* (Steindachner) (Cichlidae), Yellow cichlid, TBL 10 cm; *Thorichthys* sp. (Cichlidae), TBL 13 cm; and *Gobiomorus dormitor* Lacepède (Eleotridae), Bigmouth sleeper, TBL 38 cm.

Sites of infection: Abdominal cavity, surface of stomach and intestine, mesentery and liver.

Locality: Lacantún River (Usumacinta River basin), Chiapas State, southern Mexico (collected 12–20 November 2007).

Prevalence and intensity: *A. tropicus*: 2 fish infected/4 fish examined; 1–3 nematodes. *D. petenense*: 2/9; 1–2. *B. guatemalensis*: 1/9; 1. *I. furcatus*: 1/12; 3. *L. enigmatica*: 1/2; 4. *R. guatemalensis*: 1/2; 6. *Ch. intermedium*: 1/6; 1. *M. urophthalmus*: 1/6; 1. *P. friedrichsthalii*: 1/1; 2. *P. managuensis*: 2/2; 1. *P. splendida*: 3/4; 1–6. *T. helleri*: 1/4; 1. *Thorichthys* sp.: 1/5; 1. *G. dormitor*: 1/1; 1.

Deposition of specimens: Not deposited.

Comments: This type of larvae is mainly characterised by having the anterior intestinal caecum conspicuously longer than the ventricular appendix. Larvae of this type were reported from many fish species, e.g., in Brazil, Argentina, Venezuela, Cuba and southern Mexico (Moravec et al. 1993b, 1995d, Moravec 1998, Caspeta-Mandujano 2005). The adult forms of these larvae are mainly parasites of fish-eating birds; fishes serve either as the second intermediate hosts or as paratenic hosts.

Family Gnathostomatidae Railliet, 1895

***Gnathostoma binucleatum* Almeyda-Artigas, 1991 third-stage larva**

The morphology and measurements of the only available larva was in agreement with the description of *G. binucleatum* third-stage larvae provided by Moravec (1998).

Host: *Rhamdia guatemalensis* (Günther) (Heptapteridae), Pale catfish; TBL 25 cm.

Site of infection: Intestine.

Locality: Lacantún River (Usumacinta River basin), Chiapas State, southern Mexico (collected 11 November 2007).

Prevalence and intensity: 1 fish infected/2 fish examined; 1 nematode.

Deposition of specimen: Not deposited.

Comments: The definitive hosts of *G. binucleatum* are ocelots (*Leopardus pardalis* Linnaeus) and feral cats (*Felis catus* Linnaeus), in which adult nematodes occur in nodules in the stomach. This parasite develops with the participance of copepod intermediate hosts, whereas fishes serve as paratenic hosts. In Mexico, many freshwater and oligohaline fish species of different families were recorded to harbour *G. binucleatum* larvae in the musculature (Pérez-Ponce de León et al. 1996, Moravec 1998, Caspeta-Mandujano 2005). Most of the records of congeneric larvae unidentified to species from fishes in Mexico also relate to *G. binucleatum* larvae (Almeyda-Artigas 1991). The finding of this larva (as *Gnathostoma* sp.) in *R. guatemalensis* of the Lacantún River has already been reported by Salgado-Maldonado et al. (2011a,b). This nematode species is considered as the causative agent of human gnathostomosis, a common disease among inhabitants in the region of the lower Papaloapan River basin in Mexico (Moravec 1998).

***Spiroxys* sp. third-stage larvae**

Descriptions of *Spiroxys* larvae from fishes in Mexico were already provided by Moravec et al. (1995d) and Caspeta-Mandujano (2005).

Hosts: "*Cichlasoma*" sp., TBL 16 cm; *Mascaheros argenteus* (Allgayer), White cichlid, TBL20 cm; *Mayaheros urophthalmus* (Günther), Mexican mojarra, TBL 19–20 cm; *Thorichthys* sp., TBL 10 cm (all Cichlidae); and *Rhamdia guatemalensis* (Günther), Pale catfish (Heptapteridae), TBL 25 cm.

Sites of infection: Abdominal cavity (surface of stomach and intestine) and mesentery.

Locality: Lacantún River (Usumacinta River basin), Chiapas State, southern Mexico (collected 17–19 November 2007).

Prevalence and intensity: "*Cichlasoma*" sp.: 1 fish infected/1 fish examined; 1 nematodes. *Mas. argenteus*: 1/2; 26. *May. urophthalmus*: 2/6; 3 and 68. *Thorichthys* sp.: 1/5; 3. *R. guatemalensis*: 1/2; 6.

Comments: These larvae belong to one or more species of *Spiroxys* Schneider, 1866, parasites mainly of freshwater turtles. In Mexico, Moravec and Vargas-Vázquez (1998) recorded adults of *Spiroxys contortus* (Rudolphi, 1819) infecting the turtle *Trachemys scripta* from a small lake in central Yucatán and this widely distributed parasite is also reported from congeneric turtles in Brazil (Mascarenhas and Müller 2015). Therefore, it is probable that most records of *Spiroxys* larvae from Mexican fishes relate to this species. In Mexico (States of Chiapas, Morelos, Nayarit, Veracruz and Yucatán), larvae of *Spiroxys* sp. were reported from many fish species belonging to different families (Caspeta-Mandujano 2005). *Spiroxys* larvae in fishes of the Lacantún River were previously reported by Salgado-Maldonado et al. (2011a,b).

The intermediate hosts of *Spiroxys* spp. larvae are various copepods (*Cyclops*, *Macrocyclops*, *Mesocyclops*), whereas fishes, amphibians and some invertebrates (freshwater snails, dragonfly nymphs) serve as paratenic hosts (Moravec et al. 1995d).

DISCUSSION

The Lacantún River is a river in the State of Chiapas, southern Mexico, the lower portion of which runs through the Lacandon Forest. It is an important tributary of the Usumacinta River (river in southeastern Mexico and northwestern Guatemala), which flows northwestward, receiving the Lacantún River, forming the border between Mexico and Guatemala at the Chiapas State border, and emptying into the Gulf of Mexico in Tabasco. The large and isolated Usumacinta River basin is well known to house a vast biodiversity (Britannica 2024).

As far as freshwater fish nematodes in the Lacantún River are concerned, to date 12 nominal species of adult nematodes, viz. *Cucullanus angeli*, *Cucullanus caballeroi*, *Mexiconema cichlasomae*, *Neocucullanus neocucullanus*, *Orientatractis chiapasensis*, *Procamallanus rebecae*, *Raillietnema kritscheri*, *Rhabdochona acuminata* (Molin, 1860), *Rhabdochona juliacarabiasae*, *Rhabdochona kidderi*, *Spinitectus osorioi* and *Spinitectus tabascoensis* were reported from this stream (Cabañas-Carranza and Caspeta-Mandujano 2007, Moravec et al. 2009, 2012, Salgado-Maldonado et al. 2011a,b, Caspeta-Mandujano et al. 2021), ten of which as a part of the material collected by us in November 2007. Three more nominal species of adult fish nematodes, *Atractis vidali*, *Cucullanus mexicanus* and *Cucullanus potamarii* sp. n., are reported from the Lacantún River in this paper for the first time. Most of the 15 above-mentioned species of adult fish nematodes recorded in the Lacantún River are probably widely distributed within the Usumacinta River basin in Chiapas and Tabasco (see Caspeta-Mandujano 2005, Caspeta-Mandujano et al. 2005, Salgado-Maldonado 2006, Salgado-Maldonado et al. 2011a,b), *C. potamarii* sp. n. and *R. juliacarabiasae* being probably endemic to this drainage system.

The great majority of nematode larvae (*Contracaecum* spp. types 1 and 2, *Falcaustra* sp., *Gnathostoma binucleatum*, *Spiroxys* sp.) reported now from fishes of the Lacantún River were previously recorded from other localities in the Usumacinta River basin (Salgado-Maldonado 2006, Salgado-Maldonado et al. 2011a,b).

The present study confirms a diverse, rich-in-species fauna of nematodes parasitising fishes of the Usumacinta River basin, which is evidently of a Neotropical character. Nevertheless, further studies are needed to recognise this fauna in detail, including studies on the life cycles and biology of individual species of these interesting parasites.

Acknowledgements. We thank Guillermina Cabañas-Carranza, Jessica Pérez-Sánchez, Jesús Montoya-Mendoza and Aliberth Mora-Bonilla, then students of the Institute of Biology, Universidad Autónoma de México (UNAM), Mexico City, and Ana Santana-Piñeros from Universidad de Mar (UMAR), for their help with collecting and examining fishes in Chiapas State. Thanks are also due to the staff of the Laboratory of Electron Microscopy, Institute of Parasitology, Biology Centre CAS, an institution supported by the MEYS CR (LM2015062 Czech-BioImaging) and ERDF (No. CZ.02.1.01/0.0/0.0/16_013/0001775), for support with obtaining the scientific data presented in this paper, and to Blanka Škoríková of the same Institute for help with the illustrations. This study was supported by the Mexican research projects PAPIIT IN217723 of the Universidad Nacional Autónoma de México (UNAM), Dirección General del Asuntos del Personal Académico, DGAPA, and CONAHCyT A-1S-19959; partly also by the grant 524/06/0170 from the Grant Agency of the Czech Republic and the Institute of Parasitology, BC CAS (RVO: 60077344).

Author contribution. Guillermo Salgado-Maldonado initiated the study, organised the research expedition to Chiapas, carried out the identification of fishes and actively participated in fish examinations. František Moravec participated in examining fishes, carried out the identification and morphological analysis of nematodes and drafted the manuscript. David González-Solís participated in fish examinations and fixed and sorted the helminth material. All authors contributed substantially to the manuscript text, participated in its revision and appoved its final draft.

REFERENCES

Aguirre-Macedo M.L., Vidal-Martínez V.M., González-Solís D., Caballero P.I. 2007: Helminth communities of four commercially important fish species from Chetumal Bay, Mexico. J. Helminthol. 81: 19–31.

Almeyda-Artigas R.J. 1991: Hallazgo de *Gnathostoma binucleatum* n. sp. (Nematoda: Spirurida) en felinos silvestres y el papel de peces dulceacuícolas y oligohalinos como vectores de la gnathostomiasis humana en la cuenca baja del Río Papaloapan, Oaxaca – Veracruz, México. An. Inst. Cienc. Mar Limnol. Univ. Nal. Autón. México 18: 137–155.

Anderson R.C., Chabaud A.G., Willmott S. (Eds.) 2009: Keys to the Nematode Parasites of Vertebrates. Archival Volume. CABI, Wallingford, 463 pp.

Andrade-Salas O., Pineda-López R.F., García-Magaña L. 1994: *Spirocamallanus rebecae* sp. n. (Nematoda: Camallanidae) from freshwater fishes in south-eastern Mexico. Folia Parasitol. 41: 259–270.

Britannica 2024: Usumacinta River – Yucatán, Guatemala, Belize. https://britannica.com>place, version 08/2024.

Baker M.R. 1987: Synopsis of the Nematoda parasitic in amphibians and reptiles. Occasional Papers in Biology. Memorial University of Newfoundland, No. 11: 1–325.

Bharatha-Lakshmi B. 2000: A new parasite of the genus *Cucullanus* (Nematoda: Cucullanidae) from the fish *Arius thalassinus* (Ruppel). Bol. Chil. Parasitol. 55: 106–108.

Bilqees F.M., Fatima H. 1980: Marine fish nematodes of Pakistan. XII. *Cucullanus quadrii*, new species (Cucullanidae) from *Arius serratus* of Karachi coast. Pakistan J. Zool. 12: 27–31.

Cabañas-Carranza G., Caspeta-Mandujano J.M. 2007: A new cucullanid species (Nematoda) from the freshwater fish *Vieja intermedia* (Günther, 1862) (Cichlidae) in Mexico. J. Parasitol. 93: 646–649.

Caspeta-Mandujano J.M. 2005: Nematode Parasites of Freshwater Fish in Mexico: Key to Species, Descriptions and Distribution. Universidad Autónoma del Estado de Morelos, Cuernavaca, 175 pp.

Caspeta-Mandujano J.M., Cabañas-Carranza G., Salgado-Maldonado G. 2005: Nematode parasites of the characid freshwater fish *Brycon guatemalensis* in the Usumacinta River, Chiapas, Mexico. Helminthologia 42: 41–44.

Caspeta-Mandujano J.M., Moravec F., Aguilar-Aguilar R. 2000: *Cucullanus mexicanus* sp. n. from the intestine of *Rhamdia guatemalensis* (Pimelodidae) from freshwaters in Mexico. Helminthologia 37: 215–217.

Caspeta-Mandujano J.M., Salgado-Maldonado G., Martínez-Ramírez E. 2010: A new cucullanid species (Nematoda) from the freshwater fish *Thorichthys helleri* (Cichlidae) in Mexico. Helminthologia 47: 33–37.

Caspeta-Mandujano J.M., Salinas-Ocampo J.C., Suárez-Rodríguez R., Ramírez-Martínez C., Matamoros W.A. 2021: Morphological and molecular evidence for a new rhabdochonid species, *Rhabdochona* (Nematoda: Rhabdochonidae), parasitizing *Eugerres mexicanus* (Perciformes: Gerreidae), from the Lacantún River in the Biosphere Reserve of Montes Azules, Chiapas, Mexico. Rev. Mex. Biodiv. 92: e923266.

Cavalcante P.H.O., Silva M.T., Santos E.G.N., Chagas-Moutinho V.A., Santos C.P. 2017: *Orientatractis moraveci* n. sp. and *Rondonia rondoni* Travassos, 1920 (Nematoda: Atractidae), parasites of *Pimelodus blochii* (Osteichthyes, Pimelodidae) from the Acre and Xapuri Rivers, Western Amazon, Brazil. Parasitology 144: 226–236.

Froese R., Pauly D. (Eds.) 2024: FishBase. World Wide Web electronic publication. http://www.fishbase.org, version 06/2024.

González-Solís D., Mariaux J. 2017: *Orientatractis brycini* sp. nov. (Nematoda: Atractidae) from characiform freshwater fishes in Gabon, Africa. Rev. Suisse Zool. 124: 1–8.

González-Solís D., Moravec F. 2002: A new atractid nematode, *Atractis vidali* sp. n. (Nematoda: Atractidae), from cichlid fishes in southern Mexico. Folia Parasitol. 49: 227–230.

González-Solís D., Moravec F. 2004: Two new nematode species, *Orientatractis campechensis* n. sp. and *Orientatractis chiapasensis* n. sp. (Nematoda: Atractidae) from cichlid fishes in southern Mexico and Nicaragua. J. Parasitol. 90: 1443–1449.

Jesus R.F., Oliveira S.C.G., Ramos I.M.C., Melo F.T.V. 2023: A new species of *Orientatractis* (Nematoda: Cosmocercoidea: Atractidae) parasite of aellow-spotted Amazon river Turtle, *Podocnemis unifilis* Troschel, 1848 (Testudines: Podocnemididae) in Brazilian Amazon. Int. J. Parasitol. Parasites Wildl. 22: 108–112.

Koubková B., Baruš V., Hodová I., Šimková A. 2008: Morphometric and molecular characteristics of *Labeonema synodontisi* n. comb. (Nematoda: Atractidae) from the West African fishes. Parasitol. Res. 102: 1013–1020.

Lacerda A.C.F., Takemoto R.M., Marchiori N.C., Martins M.L., Pavanelli G.C. 2013: New species of *Cucullanus* (Nematoda: Cucullanidae), an intestinal parasite of the peacock bass *Cichla piquiti* (Perciformes: Cichlidae) from the Tocantins River, Brazil. J. Helminthol. 89: 1–4.

Lagunas-Calvo O., Santacruz A., Hernández-Mena D.I., Rivas G., Pérez-Ponce de León G., Aguilar-Aguilar R. 2019: Taxonomic status of *Rhabdochona ictaluri* (Nematoda: Rhabdochonidae) based on molecular and morphological evidence. Parasitol. Res. 118: 441–452.

López-Caballero J., Osorio-Sarabia D., García-Prieto L. 2009: *Cucullanus costaricensis* n. sp. (Nematoda: Cucullanidae), a parasite of *Bagre pinnimaculatus* (Siluriformes: Ariidae) from Río Tempisque, Costa Rica. J. Parasitol. 95: 413–423.

Luque J.L., Aguiar J.C., Viera F.M., Gibson D.I., Santos C.P. 2011: Checklist of Nematoda associated with the fishes of Brazil. Zootaxa 3082: 1–88.

Mascarenhas C.S., Müller G. 2015: *Spiroxys contortus* (Gnathostomatidae) and *Falcaustra affinis* (Kathlaniidae) from *Trachemis dorbigni* (Emydidae) in southern Brazil. Comp. Parasitol. 82: 129–136.

Moravec F. 1998: Nematodes of Freshwater Fishes of the Neotropical Region. Academia, Prague, 464 pp.

Moravec F. 2000a: Nematodes as parasites of inland fishes in Mexico. In: G. Salgado-Maldonado, A.N. García-Aldrete and V.M. Vidal-Martínez (Eds.), Metazoan Parasites in the Neotropics: A Systematic and Ecological Perspective. Commemorative Vol., Instituto de Biología, UNAM, Mexico City, pp. 155–165.

Moravec F. 2000b: Systematic status of *Laurotravassoxyuris bravoae* Osorio-Sarabia, 1984 (Nematoda: Pharyngodonidae) [= *Atractis bravoae* (Osorio-Sarabia, 1984) n. comb.: Cosmocercidae]. Syst. Parasitol. 46: 117–122.

Moravec F. 2006: Dracunculoid and Anguillicoloid Nematodes Parasitic in Vertebrates. Academia, Prague, 634 pp.

Moravec F. 2019: Parasitic Nematodes of Freshwater Fishes of Africa. Academia, Prague, 406 pp.

Moravec F., Huffman D.G., Swim D.J. 1995c: The first record of fish as paratenic hosts of *Falcaustra* spp. (Nematoda: Kathlaniidae). J. Parasitol. 81: 809–812.

Moravec F., Jiménez-García M.I., Salgado-Maldonado G. 1998: New observations on *Mexiconema cichlasomae* (Nematoda: Dracunculoidea) from fishes in Mexico. Parasite 5: 289–293.

Moravec F., Jirků M. 2017: Some nematodes of freshwater fishes in Central Africa. Folia Parasitol. 64: 033.

Moravec F., Justine J.-L. 2017: Two new species of nematode parasites, *Cucullanus epinepheli* sp. n. (Cucullanidae) and *Procamallanus* (*Spirocamallanus*) *sinespinis* sp. n. (Camallanidae), from marine serranid and haemulid fishes off New Caledonia. Folia Parasitol. 64: 011.

Moravec F., Justine J.-L. 2020: New records of cucullanid nematodes from marine fishes off New Caledonia, with descriptions of five new species of *Cucullanus* (Nematoda, Cucullanidae). Parasite 27: 37.

Moravec F., Kamchoo K., Pachanawan A. 2015: New nematode species, *Orientatractis mekongensis* n. sp. (Atractidae) and *Neosynodontisia suratthaniensis* n. g., n. sp. (Pharyngodonidae) from freshwater fishes in Thailand. Syst. Parasitol. 92: 197–209.

Moravec F., Kohn A., Fernandes B.M.M. 1992a: Nematode parasites of fishes of the Paraná River, Brazil. Part 1. Trichuroidea, Oxyuroidea and Cosmocercoidea. Folia Parasitol. 39: 327–353.

Moravec F., Kohn A., Fernandes B.M.M. 1993b: Nematode parasites of fishes of the Paraná River, Brazil. Part 2. Seuratoidea, Ascaridoidea, Habronematoidea and Acuarioidea. Folia Parasitol. 40: 115–134.

Moravec F., Kohn A., Fernandes B.M.M. 1997: New observations on seuratoid nematodes parasitic in fishes of the Paraná River, Brazil. Folia Parasitol. 44: 209–223.

Moravec F., Mendoza-Franco E., Vargas-Vázquez J., Vivas-Rodríguez C. 1995b: Studies on the development of *Procamallanus* (*Spirocamallanus*) *rebecae* (Nematoda: Camallanidae), a parasite of cichlid fishes in Mexico. Folia Parasitol. 42: 281–292.

Moravec F., Řehulka J. 1987: First record of the cosmocercoid nematode *Raillietnema synodontisi* Vassiliadès, 1973 from the aquarium-reared upside-down catfish *Synodontis eupterus* Boulenger. Folia Parasitol. 34: 163–164 + 2 plts.

Moravec F., Salgado-Maldonado G., Caspeta-Mandujano J.M., González-Solís D. 2009: Redescription of *Spinitectus tabascoensis* (Nematoda: Cystidicolidae) from fishes of the Lacandon rain forest in Chiapas, southern Mexico, with remarks on *Spinitectus macrospinosus* and *S. osorii*. Folia Parasitol. 56: 305–312.

Moravec F., Salgado-Maldonado G., González-Solís D., Caspeta-Mandujano J.M. 2012: Host-parasite relationships of *Rhabdochona kidderi* Pearse, 1936 (Nematoda: Rhabdochonidae) in fishes of the Lacantún River in the Lacandon rain forest of Chiapas State, southern Mexico, with a key to Mexican species of *Rhabdochona* Railliet, 1916. Syst. Parasitol. 82: 1–12.

Moravec F., Salgado-Maldonado G., Pineda-López R. 1993a: *Raillietnama kritscheri* sp. n. (Nematoda: Cosmocercidae) from *Cichlasoma* spp. (Pisces) from Mexico. Ann. Naturhist. Mus. Wien 94/95 B: 35–40.

Moravec F., Thatcher V.E. 1997: New data on the morphology and systematic status of *Klossinemella iheringi* (Nematoda: Atractidae) from an Amazonian serrasalmid fish. Folia Parasitol. 44: 48–54.

Moravec F., Van As J.G. 2004: Nematode from the squeaker fishes *Synodontis nigromaculatus* and *S. vanderwaali* from the Okavango River, Botswana, including three new species. Syst. Parasitol. 59: 169–187.

Moravec F., Vargas-Vázquez J. 1998: Some endohelminths from the freshwater turtle *Trachemys scripta* from Yucatan, Mexico. J. Nat. Hist. 32: 455–468.

Moravec F., Vidal V., Salgado-Maldonado G. 1992b: *Mexiconema cichlasomae* gen. et sp. n. (Nematoda: Daniconematidae) from *Cichlasoma* spp. (Pisces) from Mexico. Folia Parasitol. 39: 33–40.

Moravec F., Vidal-Martínez V.M., Aguirre-Macedo M.L. 1999: Branchiurids (*Argulus*) as intermediate hosts of the daniconematid nematode *Mexiconema cichlasomae*. Folia Parasitol. 46: 79.

Moravec F., Vivas-Rodríguez C., Scholz T., Vargas-Vázquez J., Mendoza-Franco E., González-Solís D. 1995a: Nematodes parasitic in fishes of cenotes (= sinkholes) of the Peninsula of Yucatan, Mexico. Part 1. Adults. Folia Parasitol. 42: 115–129.

Moravec F., Vivas-Rodríguez C., Scholz T., Vargas-Vázquez J., Mendoza-Franco E., Schmitter-Soto J.J., González-Solís D. 1995d: Nematodes parasitic in fishes of cenotes (= sinkholes) of the Peninsula of Yucatan, Mexico. Part 2. Larvae. Folia Parasitol. 42: 199–210.

Osorio-Sarabia D. 1984: Descripción de una especie nueva del género *Laurotravassoxyuris* Vigueras, 1938 (Nematoda: Syphaciidae) en peces de agua dulce de México. An. Inst. Biol. Univ. Nac. Autón. México, Ser. Zool., 54: 23–33.

Paredes-Trujillo A., Martínez-Aquino A., Rodiles-Hernández R., González-Solís D. 2020: Metazoan parasite communities of three endemic cichlid fish species from the upper Grijalva River, Chiapas, Mexico. Helminthologia 57: 344–352.

Pereira F.B., Luque J.L. 2016: Morphological and molecular characterization of cucullanid nematodes including *Cucullanus opisthoporus* n. sp. in freshwater fish from the Brazilian Amazon. J. Helminthol. 91: 739–751.

Pereira F.B., Vieira F.M., Luque J.L. 2015a: New morphological data and first description of gravid female of *Cucullanus bagre* Petter, 1974 (Seuratoidea: Cucullanidae) from *Bagre bagre* (Linnaeus, 1766) (Siluriformes: Ariidae) off Brazil. Acta Parasitol. 60: 138–145.

Pereira F.B., Tavares L.E.R., Paiva F., Scholz T., Luque J.L. 2015b: A morphological and molecular study of *Spectatus spectatus* (Kathlaniidae), including redescription of the species and amendment of genus diagnosis. J. Parasitol. 101: 468–475.

Pérez-Ponce de León G., García-Prieto L., Osorio-Sarabia D., León-Regagnon V. 1996: Listados Faunísticos de México. VI. Helmintos Parásitos de Peces de Aguas Continentales de México. Universidad Nacional Autónoma de México, Instituto de Biología, México, 100 pp.

Petter A.J. 1966: Équilibre des espèces dans les populations de nématodes parasites du colon des tortues terrestres. Mem. Mus. Natl. Hist. Nat. Zool. 39: 1–245.

Petter A.J. 1974a: Essai de classification de la famille des Cucullanidae. Bull. Mus. Nat. Hist. Nat., 3 série No. 255, Zool., 177: 1469–1490.

Petter A.J. 1974b: Deux nouvelles espèces de Cucullanidae parasites de poissons en Guyane. Bull. Mus. Nat. Hist. Nat., 3 série No. 255, Zool., 177: 1459–1467.

Petter A.J. 1989: Nématodes de poissons du Paraguay. V. Cucullanidae. Description de deux espèces nouvelles et redéfinition de genre *Neocucullanus* Travassos et al. Rev. Suisse Zool. 96: 591–603.

Petter A.J., Le Bel J. 1992: Two new species in the genus *Cucullanus* (Nematoda: Cucullanidae) from the Australian region. Mem. Inst. Oswaldo Cruz 87: 201–206.

Ramallo G. 2012: A new species of the genus *Neocucullanus* (Nematoda: Cucullanidae) in *Salminus brasiliensis* (Pisces: Characidae) from Argentina. Munis Entomol. Zool. 7: 543–549.

Salgado-Maldonado G. 2006: Checklist of helminth parasites of freshwater fishes from Mexico. Zootaxa 1324: 1–357.

Salgado-Maldonado G., Caspeta-Mandujano J., Moravec F., Soto-Galera E., Cabañas-Carruza G., Rodiles-Hernández R. 2011a: Helmintos parásitos de peces de agua dulce de Chiapas. In: F. Álvarez (Ed.), Chiapas: Estudios Sobre su Diversidad Biológica. UNAM, Mexico City, pp. 185–207.

Salgado-Maldonado G., Caspeta-Mandujano J., Moravec F., Soto-Galera E., Rodiles-Hernández R., Cabañas-Carruza G., Montoya-Mendoza J. 2011b: Helminth parasites of freshwater fish in Chiapas, Mexico. Parasitol. Res. 108: 31–59.

Saraiva A., da Silva F.A., Silva-Souza Â.T. 2006: *Neocucullanus neocucullanus* Travassos, Artigas et Pereira, 1928 (Nematoda: Cucullanidae) from the Characidae fish, *Brycon hilarii* Valenciennes, 1850, from Brazil. Mem. Inst. Oswaldo Cruz 101: 669–672.

Travassos L., Artigas P., Pereira C. 1928: Fauna helminthológica dos peixes de água doce do Brasil. Arch. Inst. Biol. S. Paulo 1: 5–68 + 14 Plts.

Vassiliadès G. 1973: Un nouveau *Raillietnema* (Nematoda; Cosmocercoidea) parasite de poisson, au Sénégal. Bull. Inst. Fondam. Afr. Noire, Ser. A, 35: 815–821.

Yamaguti S. 1954: Parasitic worms mainly from Celebes Part 9. Nematodes of fishes. Acta Med. Okayama 9: 122–133 + 2 Plts.

Received 31 January 2025 Accepted 10 April 2024 Published online 4 July 2025

Cite this article as: Moravec F., Salgado-Maldonado G., González-Solís D. 2025: Some nematodes from fishes of the Lacantún River in the Lacandon rain forest of Chiapas State, southern Mexico, including *Cucullanus potamarii* sp. n. (Cucullanidae) from the endemic catfish *Potamarius usumacintae* (Ariidae). Folia Parasitol. 72: 020.