

Research Article

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Description of *Ophthalmonema diodontis* gen. et sp. n. (Nematoda: Cystidicolidae), a parasite of the eye and surrounding tissues of porcupinefishes (*Diodon* spp.), with a key to cystidicolid genera

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Abstract: A new nematode genus and species, *Ophthalmonema diodontis* gen. et sp. n. (Cystidicolidae), are established based on female specimens (males remain unknown) collected from both eyes of an aquarium-kept spot-fin porcupinefish, *Diodon hystrix* Linnaeus (Diodontidae, Tetraodontiformes), originally caught in coastal waters off Florida, USA. Examination by light (LM) and scanning electron microscopy (SEM) revealed that the mouth structure of this nematode, particularly the presence of two conspicuously large, rounded, opposing dorsoventral plates, each connected by a narrow bridge to the inner end of the pseudolabium, is unique among all cystidicolid genera. Inadequately described cystidicolid nematodes previously reported from the eye and surrounding tissues of *D. hystrix* and *Diodon nictemerus* Cuvier in the Caribbean Sea and in waters off southern Australia, respectively, as *Metabronema* sp. or Cystidicolidae gen. sp. are considered to belong to the new species *O. diodontis*. A key to cystidicolid genera is provided.

Keywords: Parasitic nematode, Spirurida, taxonomy, marine fish, North-West Atlantic, South-East Indian Ocean

Species of cystidicolid nematodes (Cystidicolidae) represent a large and important group of the order Spirurida parasitising fishes. This diverse and species-rich group has a world-wide distribution and many species are known to parasitise the digestive tract and, less frequently, the swim-bladder of freshwater, brackish-water and marine fishes (Anderson et al. 2009, Gibbons 2010). However, the taxonomy and classification of the Cystidicolidae, often based on details of cephalic structures visible only by SEM in these small nematodes, remain unsatisfactory (Moravec 2024). It will become evident whether these tiny features are of generic importance only as more cystidicolids are described using SEM and as comparative molecular data become available (Ferrer et al. 2005, Moravec 2007). Unfortunately, many cystidicolid species have not yet been studied by SEM. Nevertheless, there is increasing consensus in the literature that cystidicolid genera should be defined on the basis of cephalic morphology (Pereira et al. 2013).

To date, the following 27 cystidicolid genera can be considered valid (Moravec and Barton 2019): *Ascarophis* van Beneden, 1871, *Ascarophisnema* Moravec et Justine, 2010, *Caballeronema* Margolis, 1977, *Capillospirura* Skryabin, 1924, *Collarinema* Sey, 1970, *Comephoronema* Layman, 1933, *Crenatobronema* Solov'eva, 1987, *Crist-*

itectus Petter, 1970, *Ctenascarophis* Mamaev, 1968, *Cyclozone* Dogiel, 1932, *Cystidicola* Fischer, 1798, *Cystidicoloides* Skinker, 1931, *Johnstonmawsonoides* Machida, 1975, *Mastigospirura* Machida et Syahailatua, 1994, *Metabronema* Yorke et Maplestone, 1926, *Metabronemoides* Moravec et Justine, 2010, *Moravecnema* Justine, Cassone et Petter, 2002, *Neascarophis* Machida, 1976, *Parascarophis* Campana-Rouget, 1955, *Placonema* Brugni, Viozzi, Fernández et Vega, 2009, *Prospinitectus* Petter, 1979, *Pseudascarophis* Ko, Margolis et Machida, 1985, *Pseudoproleptus* Khera, 1955, *Salmonema* Moravec, Santos et Brasil-Sato, 2008, *Salvelinema* Trofimenko, 1962, *Spinitectoides* Petter, 1969 and *Spinitectus* Fourment, 1884.

Hodda (2022) also listed *Dogielophis* Doweld, 2016 (a new name for the preoccupied *Dogielina* Sobolev, 1949) and *Neospinitectus* Kalyankar, 1971 as valid cystidicolid genera. However, since the type species of the former genus was poorly described, *Dogielina* should be considered a *genus inquirendum* and *incertae sedis*. *Neospinitectus* was not considered a valid genus by Chabaud (1975) because of “a peculiar cervical ornamentation” and its too poorly known type species, but it was re-established by Sood (1989). According to Moravec and Yooyen (2011), “the three pairs of spines directed anteriorly”, a principle differentiating feature

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from *Spinitectus*, were apparent artifacts (see also Ali 1980) and, therefore, they considered *Neospinitectus* a junior synonym of *Spinitectus*. The genus *Johnstonmawsonoides*, originally placed in the Rhabdochonidae, has recently been transferred by Moravec (2026) to the Cystidicolidae based on the general morphology of its type species.

In contrast to all hitherto known species of cystidicolids, which are gastrointestinal or swimbladder parasites of fishes, Soto et al. (2013) were the first to report adult cystidicolid nematodes from the eye and retrobulbar tissues of the spot-fin porcupinefish *Diodon hystrix* Linnaeus (Diodontidae, Tetraodontiformes) caught in Caribbean coastal waters off the island of Saint Kitts. Based mainly on histological sections and molecular data, they identified the specimens as *Metabronema* sp. (Cystidicolidae); however, they did not provide a relevant description of their morphology. Most likely, only female nematodes were available to them and they provided only a single microphotograph showing the filamented eggs of the nematode.

Four years later, Sasaki et al. (2017) published a paper reporting adult cystidicolids (again, only females), designated as Cystidicolidae gen. sp., found in the subcutaneous tissue surrounding the eye of the slender-spined porcupinefish *Diodon nitchmerus* Cuvier imported from South Australia and kept at Osaka Aquarium Kaiyukan in Osaka, Japan. Based solely on LM, the authors presented a very brief and incomplete description of these nematodes, accompanied by only a few microphotographs and line drawings.

In early March 2025, two adult cystidicolid nematodes (both females) were recorded inside the eye-ball of *D. hystrix* kept in a quarantine facility of a public aquarium in Arizona, USA (Fig. 1); the infected fish had originally been caught in the Florida Keys, between Fiesta Key to the south and Lower Matecumbe Key to the north, off the Florida coast. Subsequent LM and SEM examinations of these specimens made it possible to study in detail taxonomically important morphological features, particularly the mouth structures. Considering the unique structure of the cephalic end among all known cystidicolids, as well as the unusual site of infection in the fish definitive host, a new genus and species are proposed for these nematodes, despite the fact that conspecific males remain unknown. Taking into account morphological similarity, congeneric hosts and their distribution, as well as the location within the host, the nematodes previously reported by Soto et al. (2013) and Sasaki et al. (2017) are considered to belong to this new species.

The authors are aware that the above-mentioned new genus and species are described solely on the basis of females (males are unknown), a practice that cannot generally be recommended. However, in the present case, the new genus and species appear to be well established and, therefore, it is considered more reasonable and useful to assign the parasite a generic and specific name rather than to report it as Cystidicolidae gen. sp. and wait years until conspecific males become available.

MATERIALS AND METHODS

The nematodes were dissected out from the eye-ball of the infected *Diodon hystrix*. Altogether a few body fragments (in-

cluding the anterior part of body) of one larger female specimen (Fig. 1C, D) and one almost complete (mouth region missing) smaller female specimen were obtained. After washing in physiological solution, these were fixed in cold 70% ethanol. The specimens were preliminarily inspected by LM and then the anterior portion of a single female nematode was submitted in 70% ethanol to the Interdisciplinary Center for Biotechnology Research (ICBR)-Electron Microscopy Core at the University of Florida, USA. The sample was dehydrated in a graded ethanol series 75% through 100% with 5% increments, followed by anhydrous 100% ethanol. The nematode was then treated with hexamethyldisilazane (HMDS) 50% once and 100% twice for 10 min each and air dried in the hood overnight. Once dried, the nematode was mounted on a 12 mm carbon adhesive tab and aluminium stub, sputter coated with gold/palladium under argon gas, using a Denton Desk V sputter coater. The nematode was imaged using a Hitachi SU-5000 FE-SEM and EM Wizard software.

Subsequently, the same nematode specimen mounted on a SEM stub and the smaller specimen preserved in 70% ethanol were transported to the Institute of Parasitology, Biology Centre of the Czech Academy of Sciences in České Budějovice, Czech Republic (IPCAS). There, after being cleared with glycerine, the smaller specimen was examined by LM. Drawings were made with the aid of a Zeiss microscope drawing attachment. Then the same specimen was transferred to 4% formalin and used for SEM. It was postfixed in 1% osmium tetroxide (in phosphate buffer), dehydrated through a graded acetone series, critical-point-dried and sputter-coated with gold. This specimen and that which was previously studied in the USA (see above) were examined using an APREO scanning electron microscope (producer Thermo Fisher Scientific) at an accelerating voltage of 4 kV.

After examination, the type specimens were deposited in the Helminthological Collection of the Institute of Parasitology, BC CAS (IPCAS). A vial containing several body pieces of the new nematode species preserved in 96% ethanol, for subsequent molecular studies, was deposited in the same collection. All measurements given in the species description are in micrometres unless otherwise indicated. Fish nomenclature follows FishBase (Froese and Pauly 2026).

RESULTS

Family Cystidicolidae Skryabin, 1946

Ophthalmonema gen. n.

ZooBank number for genus:

[um:lsid:zoobank.org:act:15369B51-9328-43B0-8E51-C4D193DBE40C](https://www.zoobank.org/act:15369B51-9328-43B0-8E51-C4D193DBE40C)

Diagnosis. Cystidicolidae. Body filiform, with thick, transversely striated cuticle. Narrow lateral alae present. Cephalic end rounded, with 2 relatively broad, anteriorly protruding pseudolabia, each with rounded anterior protrusion at its base. Oral aperture large, almost circular, surrounded by 4 submedian cephalic papillae and pair of lateral amphids. Submedian labia and median wedge-shaped outgrowths of wall of buccal cavity absent. Sublabia well developed. Pseudolabia broad, each with 2 small dorsoventral extensions; inner parts of pseudolabia curved posteriorly towards

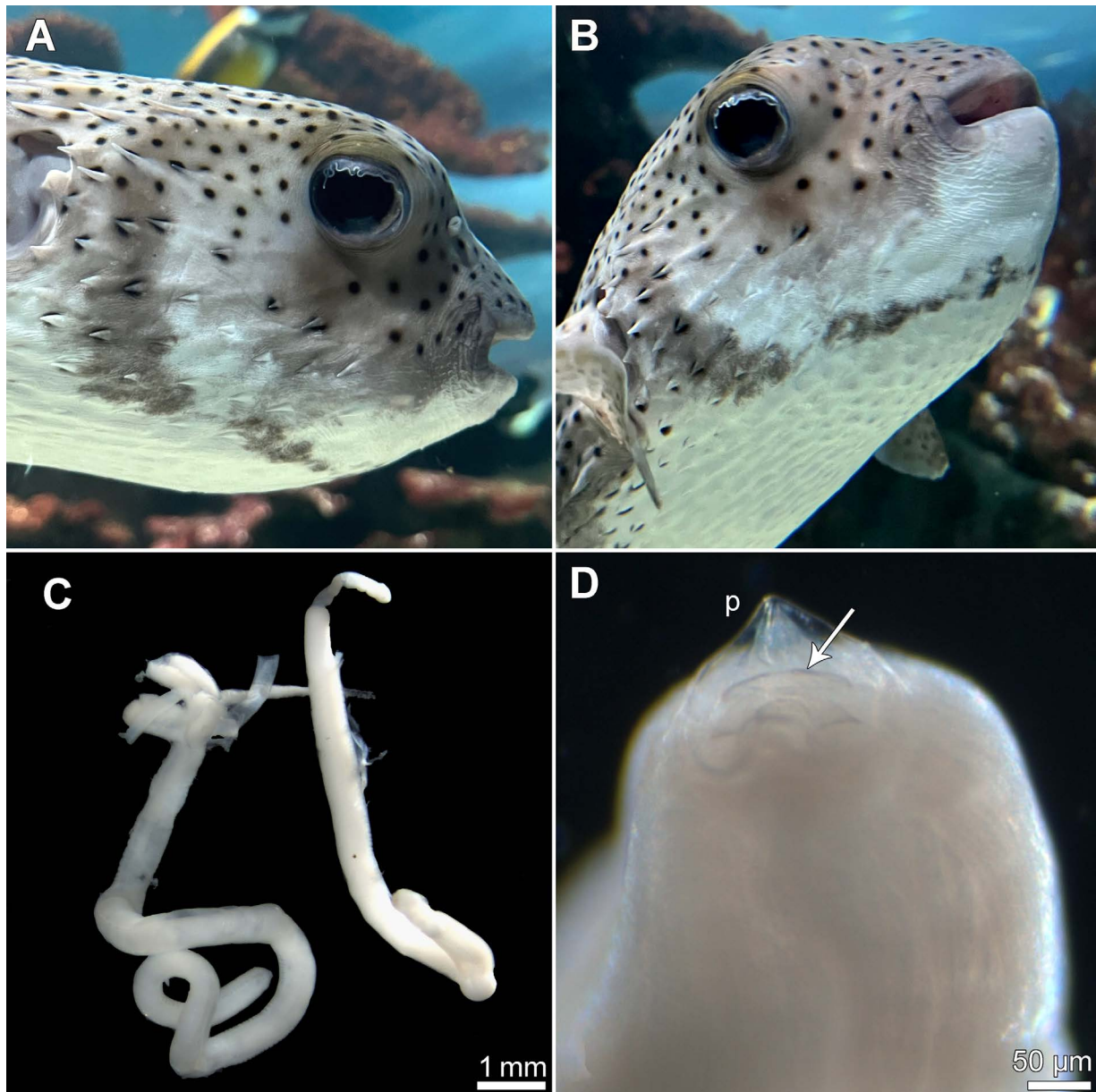


Fig. 1. A, B – two specimens of *Ophthalmonema diodontis* in eye of *Diodon hystrix* (different views); C – two body fragments of available larger female specimen of *O. diodontis* dissected out of infected fish eye; D – cephalic end of uncleared, ethanol-preserved specimen of *O. diodontis* (arrow indicates conspicuous dorsoventral plate-like structure with rounded anterior margin; p – pseudolabium).

middle of mouth. Two conspicuously large, parallel dorsoventral plate-like structures with rounded anterior margins present between both pseudolabia, each being connected to inner part of nearby pseudolabium by narrow basal bridge. Vestibule (stoma) divided into anterior broad, cup-shaped prostom and narrow, markedly short cylindrical posterior portion. Oesophagus consists of short anterior muscular and long posterior glandular portions. Deirids small, digitiform. Vulva near middle of body. Uterus amphidelphic. Mature eggs with polar filaments. Males not known. Parasites of eye and surrounding tissues of marine fishes.

Type and the only species: *Ophthalmonema diodontis* sp. n.

Etymology: This generic name is composed of two parts, the Greek words *ophthalmos* (= eye) and *nema* (= nematode), relating to the unusual site of infection, and is neuter in gender.

***Ophthalmonema diodontis* sp. n.**

Figs. 1–4

Syns.: *Metabronema* sp. of Soto et al. (2013); Cystidicolidae gen. sp. of Sasaki et al. (2017).

ZooBank number for species:

[um:lsid:zoobank.org:act:AD9EE954-526C-4809-A777-8CEE50A1628F](https://www.zoobank.org/act:AD9EE954-526C-4809-A777-8CEE50A1628F)

Description of female (based on body fragments of 2 gravid specimens with immature eggs). Body robust, whitish, filiform, with thick cuticle bearing distinct transverse striations (Figs. 2A, 3A–F, 4C, D); in lateral view using LM, striations appear as small rounded outgrowths (bosses) on cuticle 3–9 high (Figs. 2E, F, H, K–M). Thick, narrow lateral alae, up to 41 wide, extend from oesophageal region nearly to anus. Overall length of available 2 body fragments of larger specimen about 36.20 mm, maximum width 639, and

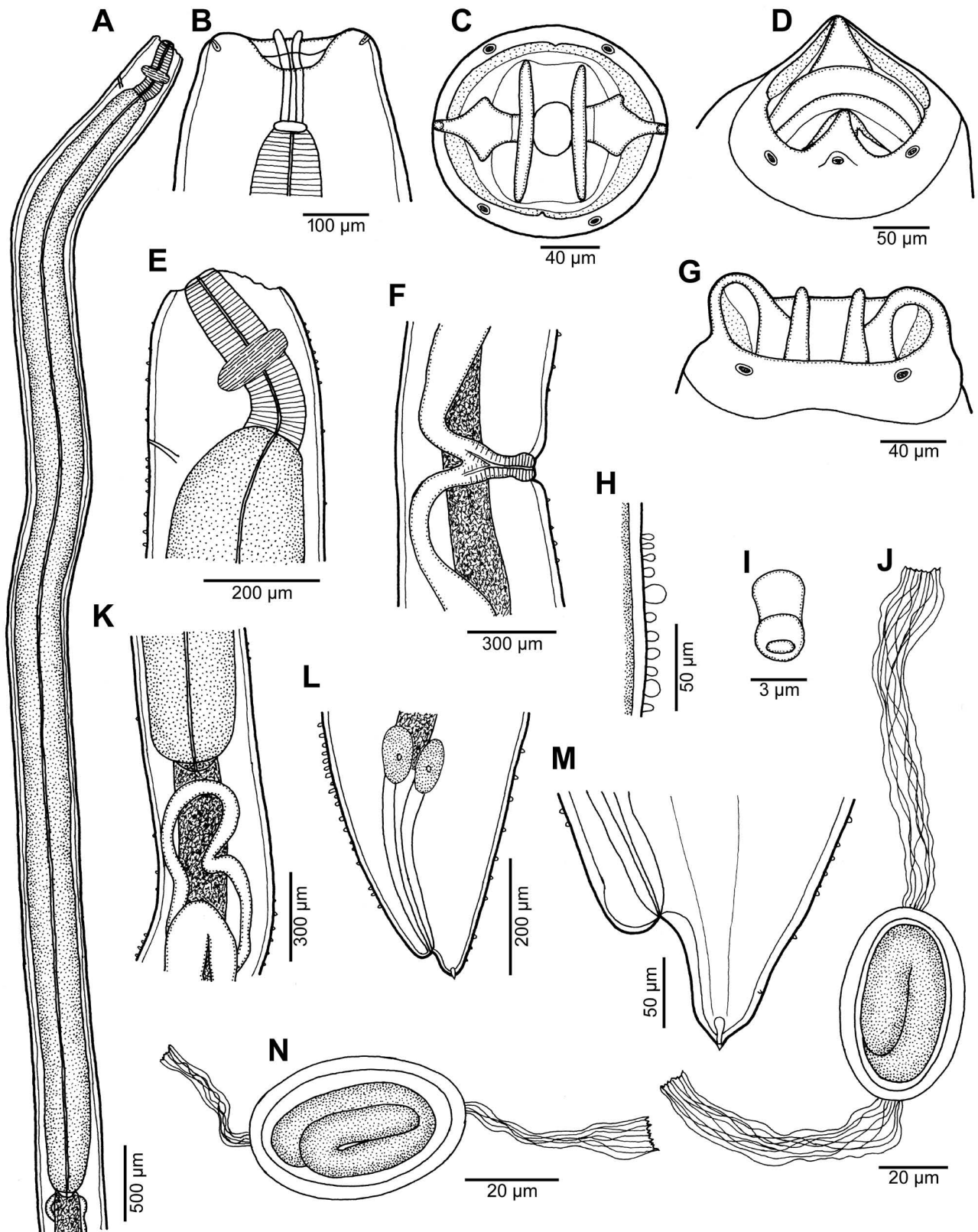


Fig. 2. *Ophthalmonema diodontis* gen. et sp. n., female. **A** – anterior end of young specimen with missing mouth region, lateral view; **B** – cephalic end, dorsoventral view (based on LM photograph); **C**, **D** – cephalic end, apical and sublateral views, respectively (based on SEM micrographs); **E**, **F** – anterior end of body (mouth and vestibular region absent) and region of vulva, respectively, of young specimen, lateral views; **G** – cephalic end, dorsoventral view (based on SEM micrograph); **H** – detail of enlarged cuticle at anterior part of body of young specimen with superficial bosses; **I** – deirid (based on SEM micrograph); **J**, **N** – eggs (based on LM photograph); **K**, **L** – region of oesophago-intestinal junction and posterior end of body, respectively, of young specimen, lateral views; **M** – tail of young specimen, lateral view. (**B** and **J** – redrawn from Sasaki et al. 2017; **N** – redrawn from Soto et al. 2013.)

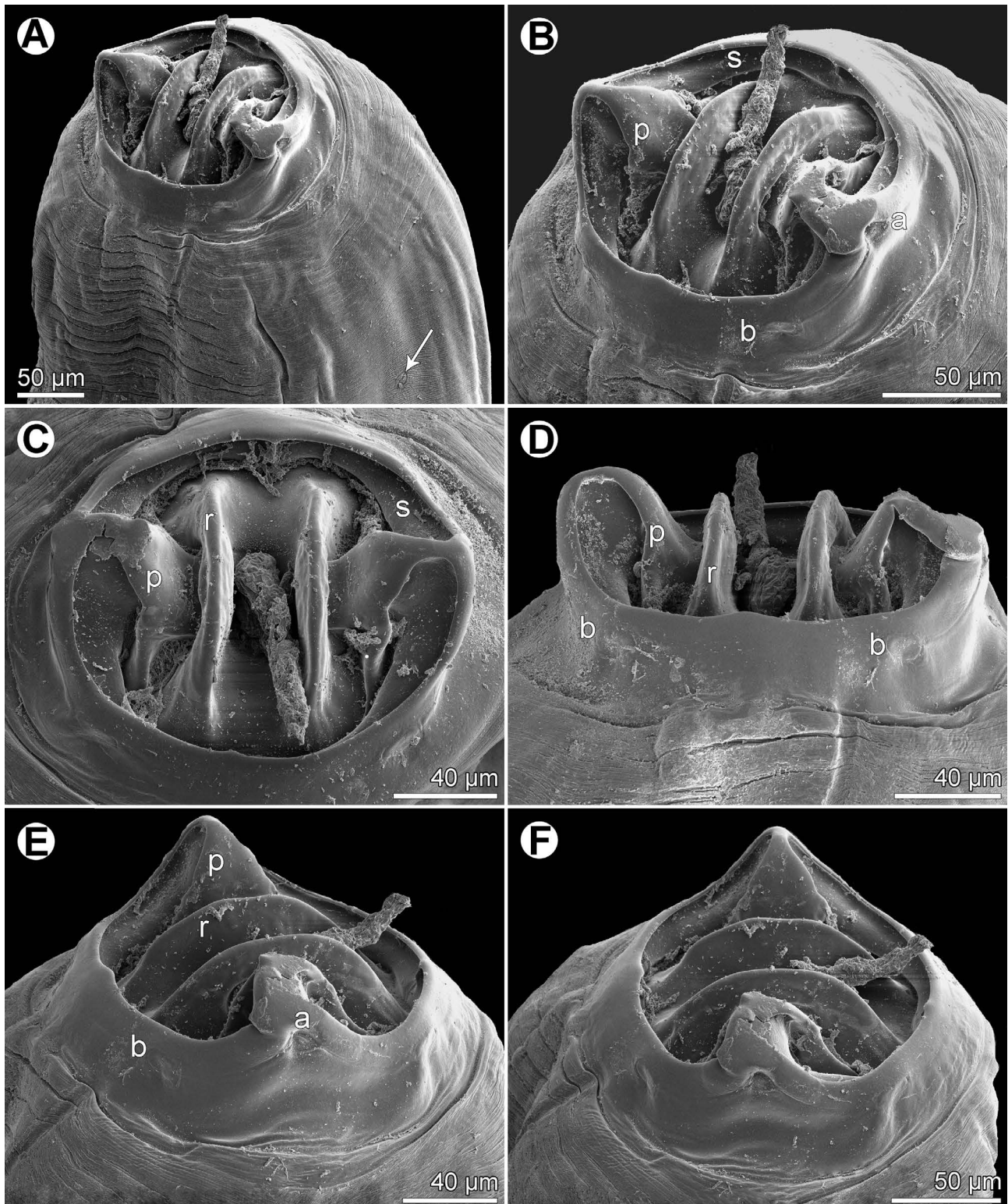


Fig. 3. *Ophthalmonema diodontis* gen. et sp. n., scanning electron micrographs of female. **A** – anterior end of body of gravid specimen, subapical view (arrow indicates deirid); **B** – cephalic end of gravid specimen, subapical view; **C, D** – same, apical and dorsoventral views, respectively; **E, F** – same, sublateral and lateral views, respectively. *Abbreviations:* a – amphid; b – cephalic papilla; p – pseudolabium; r – dorsoventral rounded plate; s – sublabium.

of 2 fragments of almost complete smaller specimen (region of vestibule and mouth lacking) 34.64 mm, maximum width 612. [Body lengths of specimens reported by Soto et al. (2013) from *Diodon hystrix* and Sasaki et al. (2017) from *Diodon nictemerus* were 15–45 mm and 80–109 mm, re-

spectively.] Cephalic end truncated, with 2 large, relatively broad, anteriorly protruding pseudolabia (Figs. 1D, 2D, G, 3A–F). Oral aperture large, almost circular, surrounded by ring of smooth cuticle bearing 4 submedian cephalic papillae and 2 lateral amphids located closely to outer edges of pse-

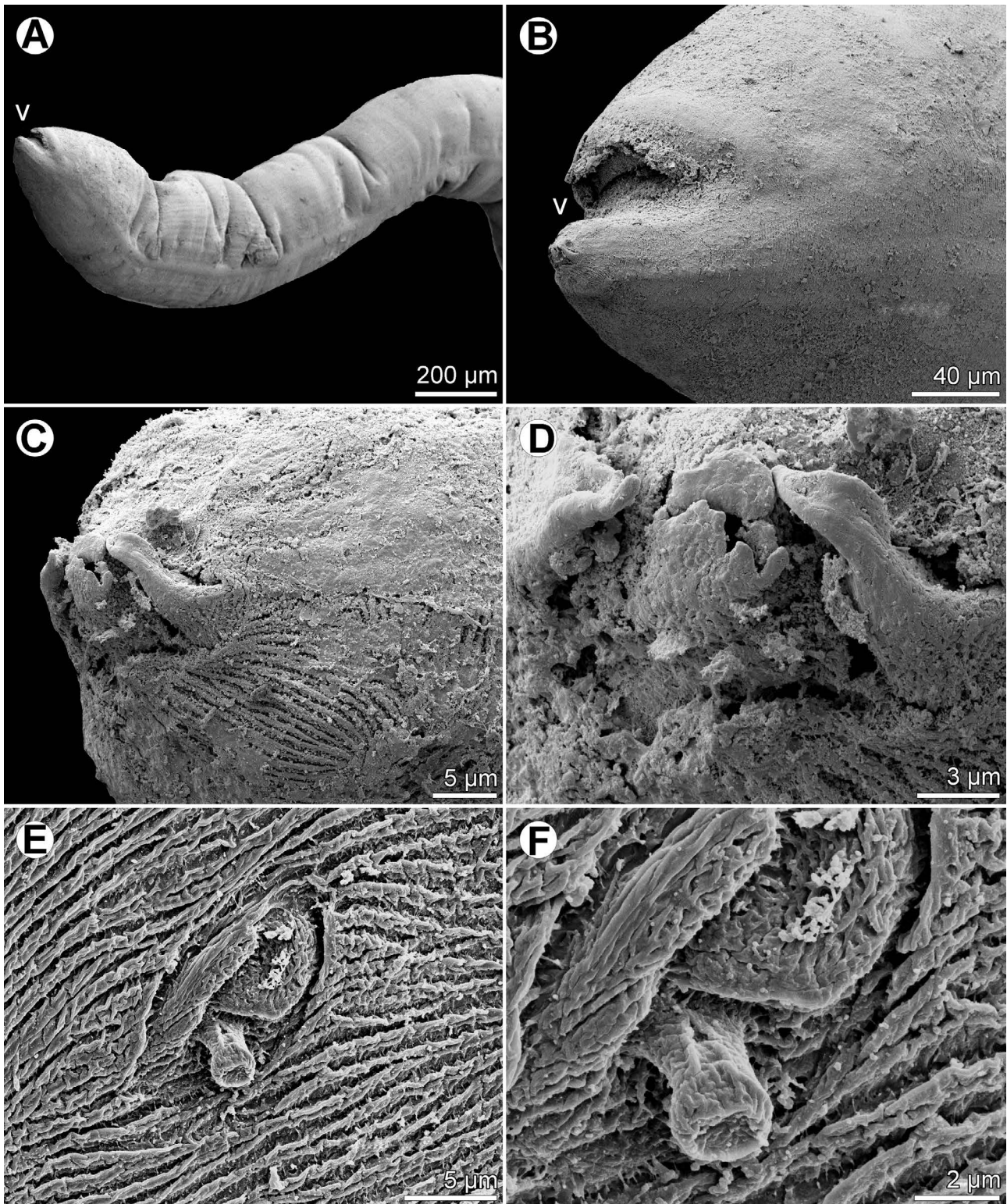


Fig. 4. *Ophthalmonema diodontis* gen. et sp. n., scanning electron micrographs of female. **A** – posterior end of body of young specimen, lateral view; **B** – tail of young specimen, lateral view; **C**, **D** – tail tip of young specimen, lateral and apical views, respectively; **E**, **F** – deirid of gravid specimen (different magnifications). *Abbreviation:* v – anus.

udolabia (Figs. 2C, D, G, 3A–F). Submedian labia and median wedge-shaped outgrowths of mouth wall absent. Pseudolabia arise from inner edge of circumoral ring of smooth cuticle, each forming distinct rounded anterior protrusion (protuberance) at its base. In apical view, starting from its anterior protrusion, each pseudolabium becomes gradually

broader and curved posteriorly towards middle of mouth; broad part of each pseudolabium with 2 (1 dorsolateral and 1 ventrolateral) extensions connected with wall of mouth. Conspicuously large, dorsoventral plate-like structure with rounded anterior margin arises from wall of buccal cavity proximally to each pseudolabium, being connected with

inner part of pseudolabium by narrow basal bridge (Figs. 2C, D, G, 3A–F). In apical view, both opposite dorsoventral plates are parallel to each other, extending almost across entire diameter of oral opening (Fig. 3C). Sublabia well developed, smooth, dorsally and ventrally undivided (Figs. 2C, D, G, 3A–C). Vestibule (stoma) divided into anterior broad, cup-shaped prostom and narrow markedly short cylindrical posterior portion (about 90 long as can be derived from LM photograph – fig. 2A of Sasaki et al. 2017), provided with basal ring (Fig. 2B). Oesophagus divided into short, narrow anterior portion and long, wider posterior portion (Fig. 2A, E). Length of muscular oesophagus of present smaller specimen 340, width 95, and that of glandular oesophagus 5.64 mm, maximum width 381. Intestine narrow, straight; length of rectum 367. Nerve ring encircles muscular oesophagus approximately at its middle, 190 from its anterior end. Excretory pore posterior to nerve ring level, approximately at level of muscular-glandular junction of oesophagus (Fig. 2A, E). Deirids very small, digitiform with somewhat inflated distal tip, located probably at level of anterior end of muscular oesophagus (Figs. 2I, 3A, 4E, F). In smaller specimen, vulva situated 13.97 mm from posterior end of body or 1.13 mm from posterior end of glandular oesophagus; vulval lips not elevated (Fig. 2F). Vagina short, 231 long, forming small rounded ovijector at its distal end. Uterus amphidelphic, containing numerous immature eggs 24–30 × 18–21 in size. Mature (larvated) eggs about 60 × 30 µm and 60–67 × 30–40 µm according to Soto et al. 2013 and Sasaki et al. 2017, respectively, provided with long polar filaments; length of filaments over 500 µm according to the latter authors (Fig. 2J, N). Ovaries reflected; anterior ovary extends anteriorly to posterior end of oesophagus (Fig. 2K). Posterior end of body tapered (Fig. 2L). Tail conical, 68–99 long, with tip bearing 2 lateral, posteriorly pointed structures 15 long (Figs. 2M, 4B–D).

Male. Not known.

Type host: Spot-fin porcupinefish, *Diodon hystrix* Linnaeus (Diodontidae, Tetraodontiformes).

Other host: Slender-spined porcupine fish, *Diodon niethermerus* Cuvier (Diodontidae, Tetraodontiformes).

Sites of infection: Eye (corneal tissue), retrobulbar tissues and subcutaneous tissue around the eye.

Type locality: Public aquarium in Arizona, USA (collected in early March 2025); wild fish caught off the coast of Florida (Florida Keys, between Fiesta Key to the south and Lower Matecumbe Key to the north), USA.

Other localities: Caribbean coastal waters off the island of Saint Kitts, Lesser Antilles (in *D. hystrix*) (Soto et al. 2013) and Osaka Aquarium Kaiyukan in Osaka, Japan (in *D. niethermerus* imported from Southern Australia) (Sasaki et al. 2017).

Deposition of type specimens: IPCAS N-1294 (holotype and paratype mounted on SEM stubs). In addition, pieces of the nematode body in 96% ethanol were also deposited for future molecular studies.

Etymology: The specific name *diodontis* is a noun, the genitive form of the generic name of the fish host.

Remarks. The new genus *Ophthalmonema* gen. n. differs from all other cystidicolid genera in having a large, almost circular oral aperture without surrounding submedian

labia or median wedge-shaped outgrowths, and, most notably, in the presence of conspicuously large, rounded opposing plates projecting from the anterolateral wall of the buccal cavity, a feature that is unique within the Cystidicolidae. Homologous plate-like structures in the mouth have also been described in species of *Caballeronema* and *Capillospirura*. However, in contrast to the new genus, these structures are small, somewhat wider than the pseudolabia, and each is bidentate or terminates in a two-pronged, horn-like projection (Margolis 1977, Appy and Anderson 1982).

As mentioned above, Soto et al. (2013) considered the nematodes from the eye and retrobulbar tissues of *D. hystrix* (apparently identical with *O. diodontis* sp. n.) to be representatives of *Metabronema*. However, the only valid species of *Metabronema*, *M. magnum* (Taylor, 1925), from the swimbladder of carangid fishes, differs considerably from *Ophthalmonema* gen. n. in oral structure (different shape and structure of the pseudolabia, absence of large opposing submedian plates and median wedge-shaped outgrowths), in having a much longer vestibule and in possessing non-bifurcate deirids (see Moravec and Justine 2007).

The distinction of *Ophthalmonema* gen. n. from all other cystidicolid genera is evident from the key presented below. Although the new genus is based on morphological features, its erection is also supported by the fact that the type and the only species, *O. diodontis* sp. n., differs from all other cystidicolids in the site of infection (eye and surrounding tissues vs digestive tube or swimbladder).

DISCUSSION

The description of nematodes reported as *Metabronema* sp. (= *Ophthalmonema diodontis* sp. n.) by Soto et al. (2013) from the Caribbean porcupinefish *Diodon hystrix* is very brief and fragmentary. The authors mentioned only the nematode body length, a transversely striated cuticle, narrow lateral alae in the region of the glandular oesophagus, a sclerotised vestibule and the presence of eggs provided with at least two long, thread-like filaments at each pole. Despite the limited information available in terms of morphology and measurements, it is almost sure that these nematodes were conspecific with those of the present material, considering that both forms were collected from the same host species (*D. hystrix*) in neighbouring regions of the North Atlantic Ocean (the Caribbean Sea vs coastal waters of Florida), that their location in the host is very similar, and that the estimated body length of the present nematodes (about 35–40 mm) is comparable to the body length (up to 45 mm) reported by Soto et al. (2013). The only small difference is in the site of infection in the host: the present nematodes were inside the eye-ball, whereas those of Soto et al. (2013) were collected from the orbit (i.e. tissues behind the eye). However, e.g. *Philometroides oveni* Parukhin, 1975 (Philometridae) is found both in the orbit and inside the eye-ball of its fish host *Serranus hepatus* (Linnaeus) (see Moravec 2023).

Nevertheless, the situation is more complicated with specimens reported by Sasaki et al. (2017), whose nematodes are from a different congeneric host species in a distant geographical region. Moreover, the nematodes were found

in the subcutaneous tissue surrounding the eye and they were reported to be much longer than those from the Atlantic region and possessing elevated vulval lips. However, similarly as in a case of nematodes from the Caribbean Sea, the description of specimens reported as Cystidicolidae gen. sp. by Sasaki et al. (2017) is rather poor. The authors had at their disposal three gravid females obtained from a single slender-spined porcupinefish (*Diodon nictemerus*) caught off southern Australia (Indian Ocean) and subsequently imported to Japan. Although the oral structure of these nematodes was not described, it is apparent from the LM photographs provided (fig. 2A, B) that it was identical to that found in the present specimens from the USA. Moreover, fig. 2A also enables us to see the true shape and structure of the vestibule. However, compared with nematodes from *D. hystrix*, the specimens from *D. nictemerus* were almost 3 times longer (body length 80–109 mm), although the general morphology of both forms was practically identical.

It is well known in some cystidicolids that considerable differences in the body length of gravid females may occur. For example, the gravid female of *Spinitectus inermis* (Zeder, 1800), a stomach parasite of the European eel *Anguilla anguilla* (Linnaeus), may vary between 12 and 22 mm in length (Moravec 2013). However, in some other fish nematodes, in particular in species with a long body, the difference between the body length of the smallest and the largest conspecific gravid females is higher, for example approximately 3 times in *Philometra ocularis* Moravec, Ogawa, Suzuki, Miyazaki et Donai, 2002 and *Philometroides huronensis* Uhazy, 1976 (both Philometridae), 5 times in *Anguillicoloides crassus* (Kuwahara, Niimi et Itagaki, 1974) (Anguillicolidae) or even 10 times in *Philometra cyanopodi* Moravec et Justine, 2008 (see Moravec 2006, 2013, 2023). The body length of *Ophthalmonema* females might also be influenced by their different location in the host (eye-ball and orbit vs surrounding subcutaneous tissue) and a so-called space factor. Regarding the presence of elevated vulval lips reported by Sasaki et al. (2017); generally in nematodes this feature is apparent in larger (older) specimens but may be absent in smaller (younger) conspecific specimens, which is the case for the present material where the vulva was observed in a female containing only immature eggs.

Soto et al. (2013) reported that the eggs of their nematodes possessed at least two thread-like filaments at each pole (see above), whereas Sasaki et al. (2017) illustrated an egg with a tuft of thread-like filaments at either pole. However, photographs of the eggs in both papers (fig. 2E and fig. 2D, respectively) show rather the presence of a single ribbon-like filament of fibrous structure at each egg pole. Since there are no taxonomically important morphological differences between the nematodes from *D. nictemerus* and those from *D. hystrix*, both are considered to belong to *O. diodontis* sp. n. Of the five recognised species of *Diodon* (Linnaeus), three (*D. eydouxii* Brisout de Bameville, *D. holocanthus* Linnaeus and *D. hystrix*) have a circum-tropical or subtropical distribution and occur both in the Atlantic and the Indo-Pacific regions: *Diodon liturosus* Shaw occurs in tropical and subtropical waters of the In-

do-Pacific region from Africa to Japan, and *D. nictemerus* occurs in the Indian Ocean off southern Australia (Froese and Pauly 2026). The findings of *O. diodontis* sp. n. to date indicate that this parasite is most probably specific to *Diodon* spp. and that its area of distribution coincides with that of its hosts.

To date we know almost nothing about the intraspecific morphometrical variability of *O. diodontis* sp. n. Of course, it cannot be excluded that subsequent studies will show that the nematodes from *D. nictemerus* belong to another species of *Ophthalmonema* gen. n. However, at present, when neither morphological nor genetic data are available to show this, for the time being, we consider it more useful to consider these nematodes as *O. diodontis* sp. n. If the existence of a different species is confirmed, then this species can easily be separated from *O. diodontis*.

Adult cystidicolids occur mainly in the intestine of marine and freshwater fishes, but some are found in the stomach and pyloric caeca. Several species are adapted to the swimbladder of physostomous fishes (Anderson 2000). Whereas intermediate hosts of cystidicolid species parasitising freshwater fishes include both aquatic crustaceans and insects, the intermediate hosts of species parasitic in marine fishes are presumably limited to marine crustaceans (e.g., Amphipoda, Decapoda) (Anderson 2000, Moravec 2007, 2013), in which the infective third-stage larvae of the nematodes may attain a body length of up to 10 mm. Since crustaceans are an important component in the diet of *Diodon* (porcupinefish) (Froese and Pauly 2026), they probably also serve as intermediate hosts for *O. diodontis* sp. n. Fish definitive hosts acquire infection by ingesting intermediate hosts containing third-stage larvae. Infective larvae of swimbladder nematodes reach their final site by migrating up the duct (*ductus pneumaticus*) connecting the swimbladder with the intestine (Anderson 2000).

However, in the case of *O. diodontis* sp. n., the question arises as to how the relatively large infective larvae of this parasite can migrate from the digestive tract to the eye and surrounding tissues of the fish. Some adult philometrids (Philometridae) of the genera *Philometra* Costa, 1845 (*P. ocularis* and *P. salgadoi* Vidal-Martínez, Aguirre-Macedo et Moravec, 1995) and *Philometroides* Yamaguti, 1935 (*P. oveni*) also occur within the eye and retrobulbar tissues of their fish hosts. However, in contrast to cystidicolids, their infective third-stage larvae from copepod intermediate hosts are generally much smaller and, moreover, as in other dracunculoids, are adapted for migration through host tissues (third-stage larvae are more slender and sometimes smaller than conspecific second-stage larvae) (Moravec 2006, 2023).

Until more information becomes available, it can only be speculated that the infective larvae of *O. diodontis* sp. n. penetrate the wall of the porcupinefish's alimentary tract (most probably through the wide and highly elastic oesophagus or the large, sac-like and very distensible stomach) and subsequently migrate through other tissues to the region behind the fish eye, from where they may occasionally penetrate into the eye-ball (most probably via the aperture for the optic nerve) or the subcutaneous tissues surrounding it.

Apparently, *O. diodontis* sp. n. may be highly pathogenic to porcupinefishes, especially when numerous specimens parasitise a single host. As reported by Soto et al. (2013), these nematodes (reported as *Metabronema* sp.) were found to cause exophthalmia in the examined Caribbean porcupinefish *D. hystrix* when large numbers (“dozens”) of nematode specimens were observed in the retrobulbar area surrounded by extensive oedematous tissue. Moreover, the corneal stroma and anterior chambers of both eyes were cloudy, and the fish was observed to swim abnormally. According to Sasaki et al. (2017), this parasite may also pose a risk to phylogenetically and ecologically closely related farmed or pet pufferfishes (Tetraodontiformes).

Key to genera of the Cystidicolidae:

- 1 Cephalic zone with 8 deep longitudinal furrows giving it lobulate appearance in apical view. Pseudolabia large, each with single conical protuberance. Oral aperture dorsoventrally elongate, surrounded by 8 submedian cephalic papillae arranged in 2 circles. Gastrointestinal parasites of marine anguilliform fishes *Cristitectus*
 - Cephalic zone without longitudinal furrows. Oral aperture dorsoventrally elongate to almost circular, surrounded by 4 submedian cephalic papillae in circle. Pseudolabia may be small or poorly developed 2
- 2 Anterior regions of body with rows of cuticular ornamentations such as spines, festoons, combs or elevated transverse rings of cuticle with sharp posterior margins giving appearance of serrated sides of body3
 - Body without such cuticular ornamentations 7
- 3 Body in cervical region (between base of vestibule and nerve ring) with raised posterior margins of enlarged transverse rings of cuticle, giving appearance of serrated sides of body. Pseudolabia large, triangular. Vestibule short. Parasites of digestive tract of marine fishes *Crenatobronema*
 - Cuticular ornamentation otherwise 4
- 4 Body surface with 4 sublateral longitudinal rows of raised transverse combs armed with posteriorly directed spines. Combs with spines begin anteriorly just posterior to level of muscular and glandular oesophageal junction. Lateral alae present. Vestibule long. Gastric parasites of marine fishes *Ctenascarophis*
 - Cuticular ornamentation in form of transverse rings of spines or festoons. Lateral alae usually absent. Vestibule long, short or absent 5
- 5 Cuticular ornamentation in form of transverse rings with flat festoons with rounded posterior margins. Mouth with ring of small denticles. Vestibule short. Parasites of alimentary tract of marine fishes *Spinitectoides*
 - Cuticular ornamentation in form of transverse rings of spines. Mouth without ring of denticles. Vestibule long, short or absent 6
- 6 Vestibule absent. Pseudolabia reduced to 2 lateral lobes, each bearing single apical tooth. Parasites of alimentary tract of marine fishes *Prospinitectus*
 - Vestibule present. Pseudolabia of different shape and size, without teeth. Parasites of alimentary tract of freshwater and marine fishes *Spinitectus*
- 7 Cephalic end with markedly inflated cuticle forming cephalic hood or helmet-like cuticular structure 8
 - Cephalic end without markedly inflated cuticle 11
- 8 Anterior end of body with cuticular cephalic hood. Narrow lateral alae present. Parasites of digestive tract of sharks *Parascarophis*
 - Anterior end of body provided with helmet-like cuticular structure bearing thickened free posterior margin and capable of being turned forward to surround anterior extremity resembling inverted umbrella. Lateral alae usually absent. Gastrointestinal parasites of freshwater and marine teleosts 9
- 9 Pseudolabia large, each with small terminal protrusion. Both dorsolateral and ventrolateral sublabia fused dorsally and ventrally to form, in apical view, 2 dorsal and 2 ventral horn-like structures extending slightly beyond dorsal and ventral corners of pseudolabia. Deirids bifurcate. Gastrointestinal parasites of freshwater fishes *Pseudoproleptus*
 - Pseudolabia small, each with terminal protrusion. Dorsolateral and ventrolateral sublabia separated dorsally and ventrally, not exceeding labia externally. Deirids simple 10
- 10 Sublabia narrow, demarcating internally margin of oral aperture. Parasitic in stomach of marine *Collarinema*
 - Sublabia broad, forming 2 dorsolateral and 2 ventrolateral flat plates covering most of oral opening. Parasitic in stomach of freshwater fishes *Placonema*
- 11 Vestibule markedly short (sometimes shorter than wide) 12
 - Vestibule not markedly short (much longer than wide) 13
- 12 Cuticle of cervical region inflated to form single or several rings. Pseudolabia small, each bearing truncate apical tooth. Vestibule only slightly sclerotised. Four pairs of preanal papillae in male. Parasites of digestive tract of sturgeons *Cyclozone*
 - Cuticle of cervical region not inflated. Pseudolabia large; their inner parts connected by narrow basal bridge with conspicuously large, forwardly protruding rounded dorsoventral plates. Vestibule markedly short, well sclerotised. Parasites of eye and surrounding tissues of porcupinefishes *Ophthalmonema* gen. n.
- 13 Vestibule markedly short, but distinctly longer than wide. Pseudolabia rather large, each with conspicuous conical terminal protrusion; in apical view, flat inner parts of pseudolabia partly cover mouth and are somewhat dorsoventrally expanded, forming 2 extensions on each. Deirids bifurcate. Four pairs of preanal papillae in male. Parasites of stomach of marine fishes (especially macrourids) *Neosascarophis*
 - Vestibule long 14
- 14 Three pairs of preanal papillae in male. Oral aperture oval, dorsoventrally elongate; submedian labia and sublabia absent. Pseudolabia well developed, T-shaped in apical view, with inner dorsal and ventral laterally

- curved extensions. Four submedian anteriorly directed tooth-like digitiform processes present. Narrow lateral alae present or absent. Parasitic in stomach of marine fishes (especially kyphosids) *Pseudascarophis*
- Preanal papillae in male more numerous 15
 - 15 Preanal papillae 4 pairs, usually arranged in 2 couples ..16
 - Preanal papillae more numerous 25
 - 16 Oral aperture dorsoventrally elongate, hexagonal in shape. Pseudolabia rudimentary, with free rounded margins scarcely protruding into oral opening. Four submedian buccal processes on margin of oral aperture. Intestinal parasites of deep-sea fish *Moravecnema*
 - Oral aperture oval to slit-like. Mouth of different structure 17
 - 17 Oral aperture slit-like, laterally depressed, with 2 narrow lateral and 4 narrow submedian (2 dorsolateral and 2 ventrolateral) extensions in apical view. Four large submedian labia covering major part of mouth present. Lateral pseudolabia small, without inner extensions, each with single small rounded terminal protrusion. Sublabia absent. Deirids bifurcate. Parasitic in stomach of marine fishes *Metabronemoides*
 - Oral aperture of different shape, with or without dorsolateral and ventrolateral extensions. Submedian labia present or absent. Sublabia usually present 18
 - 18 Oral aperture large, almost circular, with 4 narrow dorsolateral and ventrolateral extensions. Submedian labia and sublabia absent. Pseudolabia strengthened internally by heavily sclerotised Y-shaped structure visible in lateral view, both arms of which are attached to wall of prostom. Each pseudolabium provided with distinct rounded anterior protrusion (protuberance) at its base. In apical view, flat inner parts of pseudolabia partly cover mouth and are somewhat dorsoventrally expanded, forming 2 (1 dorsolateral and 1 ventrolateral) extensions. Deirids with bifurcated tip. Parasitic in swimbladder of marine fishes *Metabronema*
 - Structure of mouth different. Oral aperture oval or slit-like. Deirids simple, bifurcated or trident-shaped. Parasites of digestive tract of fishes 19
 - 19 Mouth simple, without pseudolabia. Oral aperture oval, dorsoventrally elongate. Cephalic cuticle slightly swollen. Eggs with tufts of fine polar filaments. Intestinal parasites of marine fishes *Johnstonmawsonoides*
 - Pseudolabia present 20
 - 20 Oral aperture oval, dorsoventrally elongate. Submedian labia absent. Sublabia well developed, fused together dorsally and ventrally, forming thus 2 continuous dorsal and ventral U-shaped inner margins of oral aperture. Pseudolabia narrow, each provided with conspicuous conical terminal protrusion; in apical view, inner parts of pseudolabia only moderately cover mouth and are extended dorsoventrally forming 2 (1 dorsolateral and 1 ventrolateral) conspicuous elongate laterally curved extensions, each with distally rounded ends; in sublateral view, both extensions on each pseudolabium appear as tooth-like formations protruding anteriorly from common base of pseudolabium. Deirids trident-shaped. Parasites of stomach of marine fishes *Ascarophisnema*
 - Mouth of different structure. Submedian labia present or absent. Deirids usually bifurcate, less often simple ... 21
 - 21 Oral aperture oval, dorsoventrally elongate, somewhat narrowed equatorially. Pseudolabia rather large, each provided with conspicuous conical terminal protrusion; in apical view, inner parts of pseudolabia partly cover mouth. Submedian cephalic elevations (labia) 4, each in form of elongate mound, plus 2 small conical elevations, 1 dorsal and 1 ventral. Submedian sublabia 4, each modified to form single conical sclerotised spike and narrow plate situated nearer to pseudolabium. Walls of posterior part of prostom lined by 2 (dorsal and ventral) narrow longitudinal somewhat indistinct, tooth-like elevations visible in lateral view. Deirids simple, claw-shaped. Parasites of stomach of Neotropical freshwater fishes *Cystidicoloides*
 - Mouth of different structure 22
 - 22 Oral aperture oval, broad, somewhat dorsoventrally elongate, demarcated by 4 narrow, unlobed submedian sublabia. Pseudolabia broad, flat, each with small protuberance (pseudolabial terminal protrusion); inner part of each pseudolabium with 2 distinct dorsoventral extensions in apical view. Deirids small, simple. Parasites of digestive tract of freshwater fishes (especially salmonids) *Salmonema*
 - Pseudolabia rather small, narrow or substantially reduced. Parasites of marine or migratory fishes 23
 - 23 Bidentate plate-like structure arising from anterolateral wall of buccal cavity present. Anterior margin of pseudolabia narrow bridge. Parasites of digestive tract of sturgeons *Capillospirura*
 - Bidentate plate-like structure arising from anterolateral wall of buccal cavity absent 24
 - 24 Oral aperture dorsoventrally elongate, surrounded by 4 submedian labia and 2 narrow lateral pseudolabia; bilobed sublabium, with thickened free margin, attached by its base to inner surface of each labium. Pseudolabia continuous on inner margin with lateral anterior extensions of buccal cavity wall; these extensions terminate in 2-pronged horn-like projections; prongs of each projection lie on either side of corresponding pseudolabium. Intestinal parasites of marine fishes *Caballeronema*
 - Horn-like projections on either side of each pseudolabium absent; anterior surface of each pseudolabium with elevated structure appearing to be conical in lateral view. Lateral pseudolabia small, sometimes considerably reduced. Deirids usually bifurcate, less often simple *Ascarophis*
 - 25 Oral aperture dorsoventrally elongate, almost slit-like, without lateral notches, surrounded by 2 lateral pseudolabia attached medially to lateral edge of oral aperture. Submedian labia and sublabia absent. Vestibule markedly short. Preanal papillae 14 pairs. Intestinal parasites of marine fishes *Mastigospirura*
 - Oral aperture dorsoventrally elongate, rather narrow or very broad, sometimes with 2 medial extensions. Submedian labia and sublabia present or absent 26

- 26 Anterior margin of vestibule armed with at least 16 large subdorsal, subventral and lateral denticles, usually 4 in each quadrant. Oral aperture narrow; submedian labia absent. Pseudolabia very small, with marked pseudolabial terminal protuberances. Preanal papillae numerous (12–18 pairs), arranged in couples. Parasites of swimbladder of freshwater fishes (especially salmonids) *Cystidicola*
- Anterior margin of vestibule without denticles 27
- 27 Oral aperture large, almost circular. Cuticle surrounding mouth thickened dorsally and ventrally to form 2 semicircular bands extending from one pseudolabium to other. Submedian labia absent. Prostom broad, cup-shaped in lateral view, but actually being constricted centrally into 2 main chambers, dorsal and ventral, with its posterior region twisted laterally. Preanal papillae 18–26 pairs arranged in couples. Parasites of swimbladder of salmonids in North Pacific region
..... *Salvelinema*
- Oral aperture oval, dorsoventrally elongate, with 2 medianlateral extensions. Submedian labia and sublabia present. Prostom simple, funnel-shaped. Preanal papillae 6–18 pairs arranged in couples. Parasites of digestive tract of freshwater and marine fishes *Comephoronema*

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