Description of *Piscicapillaria bursata* sp. n. (Capillariidae) and redescription of *Parascarophis sphyrnae* Campana-Rouget, 1955 (Cystidicolidae), two nematode parasites of hammerhead sharks (*Sphyrna* spp.) off Australia

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Abstract: Examinations of two species of hammerhead sharks, *Shyrna lewini* (Grifith et Smith) and S. *mokarran* (Rüppel) (Sphyrnidae, Carcharhiniformes), from off the northern

coast of Australia revealed the presence of two species of intestinal nematode parasites, *Piscicapillaria bursata* sp. n. (Capillariidae) and *Parascarophis sphyrnae* Campana-Rouget, 1955 (Cystidicolidae). The new capillariid species *P. bursata* sp. n. from *S. mokarran* (type host) and *S. lewini* differs from its congeners mainly in the spicule length (330 µm), body length of gravid females 12.80–21.26 mm and in possessing a subterminal female anus. Light and scanning electron microscopical examination of the specimens of *P. sphyrnae* (type species of *Parascarophis* Campana-Rouget, 1955), recorded from *S. lewini*, made it possible to redescribe the female and, for the first time, to describe the male. Amended diagnosis of *Parascarophis* is provided. *Parascarophis* is mainly characterized by the presence of lateral alae, a unique feature within the Cystidicolidae, and by the cephalic structures (presence of a cuticular hood and a pair of anterolateral plate-like structures in the mouth). Species of *Parascarophis* previously described from teleosts, *P. bharatii* Agrawal, 1965, *P. oteroi* Arya, 1992 and *P. mulloidi* Imam, Tawfik et Abdel Hady, 1982, are designated as *species inquirendae* and *incertae sedis*. The finding of *P. sphyrnae* in Australian waters represents a new geographical record of this parasite outside the Atlantic Ocean.

Key words: Parasitic nematode, Trichinelloidea, Habronematoidea, Sphyrnidae, Australian waters

During investigations into parasites of hammerhead sharks (Sphyrnidae, Carcharhiniformes) in Australian waters, carried out by the junior author (D. P. Barton) in 2015–2018, two species of adult nematodes were recorded from the spiral valve of the scalloped hammerhead *Sphyrna lewini* (Griffith et Smith) and the great hammerhead *Sphyrna*

mokarran (Rüppel). Their closer examination showed that they represented a new species of the genus *Piscicapillaria* Moravec, 1982 (Capillariidae) and the already known, but inadequately described, type species of the genus *Parascarophis* Campana-Rouget, 1955 (Cystidicolidae). Results of this study are presented below. Both species of hammerheads examined have a circumpolar distribution in coastal warm temperate and tropical seas (Froese and Pauly 2018).

MATERIALS AND METHODS

Sharks were collected from 10 localities off the Northern Territory, New South Wales and Queensland coast of Australia. Sharks were collected as part of various other projects and made available for parasite examination. The sharks collected from northern New South Wales (NSW) were caught in five bather-protection gill-nets deployed off Ballina and Evans Head during the austral summer of 2016/2017. Dead great hammerheads were removed from the gill-nets and frozen whole. Sharks were defrosted and the stomach and spiral valve were removed, placed in bags and refrozen. Sharks collected from Queensland (Qld) (Ayr and Cleveland Bay (NO) and Cairns (FNO)) and the Northern Territory (NT) were comprised of by-catches of regional commercial fishers and were frozen whole prior to dissection. The NT specimens were grouped by location: Gulf of Carpentaria (GoC), Arafura Sea (ARF), North NT (NNT) (offshore locations between the Tiwi islands and the Wessel Islands), Darwin (DRW), Joseph Bonaparte Gulf (JBG) and the Timor Sea (TS). Some specimens were defrosted and processed, with the digestive system bagged and refrozen. Other specimens were processed at the time of dissection.

Independent of the source of the sharks, processing of specimens remained the same. The digestive system was separated at the junction of the stomach and the spiral valve. The stomach was opened longitudinally on a tray and examined for dietary components and parasites. In stomachs with a large quantity of food or liquid, the stomach and its contents were placed into a jar and washed. The spiral valve was opened longitudinally, washed and examined for parasites. The washings for each section were searched using a dissecting microscope.

The nematodes obtained were washed in physiological saline and then fixed and preserved in 70% ethanol. For light microscopical examination, the nematodes were cleared using glycerine. Drawings were made with the aid of a Zeiss drawing attachment. Specimens used for scanning electron microscopy (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 in micrometres unless otherwise indicated. The fish nomenclature adopted follows FishBase (Froese and Pauly 2018).

RESULTS

Capillariidae Railliet, 1915

***Piscicapillaria bursata* sp. n.** Figs. 1–3

Description: Small, filiform nematodes with finely transversely striated cuticle (Figs. 2A, C–F, 3A, F). Two lateral bacillary bands extend along body (Fig. 3E, F). Oral aperture

terminal, roughly oval, oriented dorsoventrally, surrounded by 2 elevated lips almost connected at angles of mouth; outer margin of lips rounded (Figs. 1B, 2A, 3B). Stylet absent. Mouth surrounded by 12 cephalic papillae arranged in 2 circles, each consisting of 6 papillae, and pair of small lateral amphids (Figs. 1B, 2A, 3B, D). Muscular oesophagus long, narrow (Fig. 1A). Stichosome consisting of single row of approximately 50 elongate stichocytes. Stichocytes in anterior part of stichosome formed by elongate stichocytes with little visible nuclei; these stichocytes are all alike, their anterior margin being dome-shaped. In posterior part of stichosome, two long, more granular stichocytes with numerous (4–16) transverse annuli and well visible large nuclei alternating always with one very short stichocyte also with large nucleus (Fig. 1F, G). Two wing-like glandular cells present at level of oesophago-intestinal junction (Fig. 1F).

Male (1 specimen, holotype): Length of body 6.75 mm, maximum width 42. Width of lateral bacillary bands at level of posterior end of oesophagus 15. Length of entire oesophagus 3.74 mm, representing 55% of body length. Length of muscular oesophagus 330, of stichosome 3.41 mm; number of stichocytes probably 52. Nerve ring situated 87 from anterior extremity. Spicule canal well developed, 117 long (Fig. 1E). Spicule well sclerotised, 330 long and 6 wide, its proximal end nonexpanded, distal end rounded; surface of spicule smooth, without rough transverse grooves (Fig. 1E, H, I). Spicular sheath invaginated, with numerous small spines (Fig. 1D, E). Posterior end of body provided with fairly long, rounded membranous bursa supported by conical dorsal caudal projection and, on each side, by wide, posteriorly directed ray; large spherical papilla present at base of each of them (Figs. 1C, D, 2C–F).

Female (1 complete ovigerous specimen, allotype, and 1 incomplete paratype specimen, both from *S. mokarran*; measurements of latter in parentheses. Measurements of 2 ovigerous, 1 complete and 1 incomplete, paratype specimens from *S. lewini* in brackets):

Length of body 21.26 (-) [12.80] mm, maximum width 81 (105) [69–75]. Width of lateral bacillary bands at level of posterior end of oesophagus 24 (30) [18]. Length of entire oesophagus 5.77 (6.94) [5.30–5.56] mm, representing 27% (-) [43%] of body length. Length of muscular oesophagus 366 (333) [318–339], of stichosome 5.40 (6.61) [5.30–5.56] mm; number of stichocytes approximately 48 (45) [50]. Nerve ring situated 93 (72) [96] from anterior extremity. Vulva located 5.77 (6.95) [5.30–5.57] mm from anterior end of body, at 27% (-) [43%] of body length, 0 (15) [0–3] posterior to level of oesophago-intestinal junction. Vulval lips not elevated (Fig. 1F). Vagina short, muscular. Eggs in anterior part of uterus arranged in single file. Eggs oval, without protruding polar plugs, usually somewhat narrowed equatorially (Figs. 1K, 3C). Egg wall three-layered; inner layer hyaline; outer layer with fine superficial dotted sculpturing. Eggs 60–66 × 24–27 (60–66 × 24–27) [57–66 × 27]; thickness of egg wall 3 (3) [3]; polar plugs 6 (6) [6] long and 6 (6) [6] wide. Content of fully developed eggs uncleaved. Caudal end rounded; anus subterminal; tail 12 (-) [6] long (Fig. 1J). Rectum formed by hyaline tube 81 (-) [51] long (Fig. 1J).

Type host: Great hammerhead *Sphyrna mokarran* (Rüppel) (Sphyrnidae, Carcharhiniformes).

Other host: Scalloped hammerhead *Sphyrna lewini* (Griffith et Smith) (Sphyrnidae).

Site of infection: Spiral valve.

Type locality: Off Northern Territory (DWN), Australia (collected 9 March 2017).

Other localities: *S. mokarran*: Off Northern Territory (JBG [collected 5 October 2017] and NNT [collected 5 March 2017], off Queensland (NQ [collected 30 October 2017]); *S. lewini*: Off Northern Territory (TS [collected 24 October 2016] and GoC [collected 8 December 2017]), Australia.

Total prevalence and intensity: *S. mokarran*: 12.3% (7 fish infected/57 fish examined); intensity 1–2 (mean 1.3) nematodes per fish. *S. lewini*: 1% (2/209); 1–3 (2) (Table 1).

Deposition of type specimens: Holotype, allotype and one paratype, all mounted on SEM stub, in the Helminthological Collection of the Institute of Parasitology, Biology Centre of the Czech Academy of Sciences, České Budějovice, Czech republic (Cat. No. N–……). Six paratypes in South Australian Museum (SAM), Adelaide, Australia (Cat. Nos. ……).

Etymology: The species name *bursata* is a Latin adjective and relates to the fact that the male of this species has a well developed caudal bursa.

Remarks

In having the stichosome consisting of a single row of stichocytes and males possessing a well-developed membranous bursa supported by a dorsal caudal projection and two lateral rays, the spiny spicular sheath and the absence of lateral caudal alae, the present specimens from *S. mokarran* belong to the capillariid genus *Piscicapillaria* (see Moravec 1982, 1987, 2001a). One species, *P. tuberculata* (Linstow, 1914), listed in the subgenus *Lomakinela* Moravec, 1987, is a parasite of European sturgeons (Acipenseridae), whereas five other congeneric species, all representatives of the nominotypical subgenus *Piscicapillaria* Moravec, 1982, are parasites of elasmobranchs (sharks and rays): *P. baylisi* Moravec, 1987 from *Scyliorhinus stellaris* (Linnaeus) (Scyliorhinidae, Carcharhiniformes) off the Atlantic coast of Europe; *P. freemani* (Moravec, Margolis et McDonald, 1981) from *Raja rhina* Jordan et Gilbert, *R. stellulata* Jordan et Gilbert (both Rajidae, Rajiformes) and *Bathyraja interrupta* (Gill et Townsend) (Arhynchobatidae, Rajiformes) in the Pacific Ocean along the western coast of Canada; *P. hathawayi* (Read, 1948) from *Squalus acanthias* Linnaeus (Squalidae, Squaliformes) off the Atlantic coast of the USA (Gulf of Mexico); *P. orectolobi* (Johnston et Mawson, 1951) from *Orectolobus ornatus* (De Vis) (Orectolobidae, Orectolobiformes) in the Indian Ocean off South Australia; and *P. rhinobati* (Johnston et Mawson, 1945) from

Aptychotrema rostrata (Shaw) (Rhinobatidae, Rhinopristiformes) in the Indian Ocean off South Australia (Linstow 1914; Johnston and Mawson 1945, 1951; Read 1948; Moravec et al. 1981; Moravec 1987, 2001). The present nematodes are representatives of the subgenus *Piscicapillaria*.

Of the above-mentioned congeneric species, *P. bursata* sp. n. can be easily distinguished by the length of spicule (330 µm) from *P. freemani* (653–984 µm), *P. orectolobi* (approximately 1 mm), *P. rhinobati* (1.60 mm) and *P. tuberculata* (657–786 µm). Whereas the spicule surface is smooth in the new species, the spicule of *P. freemani*, *P. orectolobi* and *P. rhinobati* is with numerous superficial transverse rough grooves. Moreover, females of *P. bursata* sp. n. have a subterminal anus, but the anus in *P. freemani* and *P. rhinobati* is terminal; *P. rhinobati* possesses a long vulval appendage, but no vulval appendage is present in the new species.

Piscicapillaria baylisi and *P. hathawayi*, both parasites of sharks, are known solely by females, so that their comparison with the new species is more difficult. Nevertheless, *P. hathawayi* differs in having a terminal (*vs* subterminal) anus and much longer gravid females (25–32 mm *vs* 13–21 mm); *P. baylisi* has a subterminal anus as in the new species, but its gravid females are much longer (30–36 mm *vs* 13–21 mm) and eggs distinctly larger (78–87 × 30–36 µm *vs* 60–66 × 24–27 µm). In addition, *P. bursata* sp. n. differs in the host family (Sphyrnidae *vs* Scyliorhinidae and Squalidae) and the geographical region (Pacific Ocean *vs* Atlantic Ocean).

Only capillariid females and no male were found in *S. lewini* in this study. Nevertheless, because their morphology is identical with that of females of *P. bursata* sp. n. from the congeneric host species, and considering the fact that fish capillariids usually exhibit their specificity at the level of host families (Moravec 2001; Moravec and Beveridge 2017; Moravec and Barton 2018), these are also identified as *P. bursata* sp. n.

The new species is the third representative of *Piscicapillaria* recorded from sharks and rays in Australian waters and the 13th nominal species of capillariids reported from fishes and elasmobranchs in Australia.

Cystidicolidae Skryabin, 1946

***Parascarophis* Campana-Rouget, 1955**

Amended diagnosis: Body filiform, cuticle with transverse striations. Anterior end of body with cephalic cuticular hood. Narrow lateral alae present. Four single cephalic papillae, located dorso- and ventrolaterally, and 2 lateral amphids. Oral aperture oval, dorsoventrally elongate, with smooth margin. Submedian labia separate from pseudolabia. Submedian sublabia well developed, elongate, each extending along inner side of respective labium and forming 2 anteriorly directed teeth. Two opposing bi-dentate plate-like structures arise from anterolateral wall of buccal cavity. Lateral pseudolabia small; in apical view, flat inner parts of pseudolabia distinctly dorsoventrally expanded, forming 2 (1 dorsolateral and 1 ventrolateral) extensions on each. Stoma (vestibule) long, with funnel-shaped prostom in lateral view. Oesophagus divided into short anterior muscular and long posterior glandular portions. Nerve ring encircles anterior part of muscular oesophagus. Excretory pore posterior to nerve ring. Deirids small, stick-like. Male with ventral, precloacal area rugosa formed by longitudinal ridges. Spicules unequal and dissimilar; right spicule shorter. Male posterior end with subventral caudal alae. Four pairs of preanal and 6 pairs of postanal papillae. Uterus of female amphidelphic. Vagina directed anteriorly from vulva. Fully-developed eggs thick-

walled, oval, containing larvae; egg filaments absent. Intestinal parasites of sharks. Type species: *P. sphyrnae* Campana-Rouget, 1955.

***Parascarophis sphyrnae* Campana-Rouget, 1955** Figs. 4–6

Redescription (based on specimens from *S. lewini*): Small, elongate whitish nematodes. Maximum width of body near its middle. Cuticle with transverse striations (Figs. 5G, 6A), inflated at anterior end of body to form conspicuous cephalic hood, usually more developed dorsally (Fig. 4A–D, G, H, 6A). Narrow lateral alae extend approximately from level of nerve ring posteriorly far beyond level of posterior end of oesophagus (Figs. 4H, 5E). Cephalic end rounded, without distinct pseudolabial terminal protrusions (Figs. 5B, 6A, B, D, E, G). Oral aperture oval, laterally depressed, surrounded by four large submedian labia (2 dorsolateral and 2 ventrolateral). Sublabia well developed, elongate, each extending along inner side of respective labium and forming two anteriorly directed teeth (Figs. 4E, 5A, B, D–G, 6A, B). Two opposing bi-dentate plate-like structures arise from anterolateral wall of buccal cavity (Figs. 4E, 5F, G, 6A, B). Lateral pseudolabia rather small; in apical view, flat inner parts of pseudolabia somewhat dorsoventrally expanded, forming two (1dorsolateral and 1 ventrolateral) extensions on each; inner margins of both pseudolabia dorsoventrally straight, parallel to each other (Figs. 4E, 5B, 6A, B). Four oval submedian cephalic papillae and pair of lateral amphids present (Figs. 4E, 5B–F, 6A). Vestibule (stoma) weakly sclerotized, long, with well developed funnel-shaped anterior prostom visible in lateral view (Fig. 4A–D, G, H); prostom of large specimens sometimes transversely oval, with distinct basal teeth (Fig. 4B); posterior end of vestibule forming basal ring (Fig. 4A, G, H). Anterior muscular oesophagus narrow, long; glandular oesophagus wider and approximalely 2–8 times longer than muscular;

both parts of oesophagus indistinctly separated from each other. Nerve ring encircles muscular oesophagus near its anterior end; excretory pore located somewhat posterior to level of nerve ring; deirids small, stick-like, situated approximately at level of posterior end of vestibule (Figs. 4G, H, J, 5C).

Male (6 specimens): Length of body 7.82–11.86 mm, maximum width 45–69. Cephalic hood 42–51 long and 33–45 wide. Maximum width of lateral alae 6 (6). Vestibule including prostom 87–153 long; prostom 6–15 long and 6–15 wide. Length of muscular oesophagus 150–489, maximum width 12–15; length of glandular oesophagus 1.27–1.76 mm, maximum width 21–36; length ratio of muscular and glandular parts of oesophagus 1:3–8. Entire oesophagus 1.42–2.13 mm long. Length of entire oesophagus and vestibule represents 18–23% of total body length. Deirids, nerve ring and excretory pore 147–159, 114–171 and 135–249, respectively, from anterior extremity. Posterior end of body firmly spirally coiled, provided with broad caudal alae (Figs. 4F, K, 5F); maximum width of caudal alae 30–60 (54). Preanal papillae: 4 pairs of subventral pedunculate papillae present. Postanal papillae: 6 pairs present, including 5 pairs of pedunculate subventral papillae and 1 pair of minute ventral sessile papillae located posterior to level of last pair of subventrals (Figs. 4F, K, 5C, D, F). Ventral cuticular ridges (area rugosa) anterior to cloaca well developed (Figs. 4F, 5H). Large (left) spicule 675–825 (717) long, with sharply pointed distal tip; spicule shaft forming approximately 30% (30%) of overall length of spicule. Small (right) spicule narrow, 48–81 (81) long, with obtuse distal tip provided with small ventral reflexed barb (Fig. 4F, M, N). Length ratio of spicules 1:9–17 (1:9). Tail conical, 93–125 (93) long, with rounded tip (Figs. 4K, 5D).

Female (10 ovigerous specimens): Length of body 16.16–32.89 mm, maximum width 81–126. Cephalic hood 48–63 long and 36–54 wide. Maximum width of lateral alae 12–15 (12). Vestibule including prostom 141–180 long; prostom 6–15 long and 9–18 wide. Length of muscular oesophagus 444–645, maximum width 18–27; length of glandular oesophagus 1.09–2.37 mm, maximum width 33–51; length ratio of muscular and glandular parts of oesophagus 1:2–6. Entire oesophagus 1.54–2.97 mm long. Length of entire oesophagus and vestibule represents 9–12% of total body length. Deirids, nerve ring and excretory pore 153–165, 171–225 and 204–291, respectively, from anterior extremity. Tail conical, 96–123 long, with rounded tip without any terminal appendage; pair of small lateral phasmids present near tail tip (Figs. 4L, 5G). Vulva postequatorial, situated 8.21–18.71 mm from anterior end of body, at 51–67% of body length; vulval lips not elevated or anterior lip somewhat elevated. Vagina directed anteriorly from vulva. Amphidelphic. Anterior ovary and uterus not extending anteriorly to oesophageal part of body. Uterus filled with numerous eggs. Mature eggs (containing larvae) oval, thick-walled, size 27–30 × 15–18; thickness of egg wall 1–2 (1–2); surface of eggs smooth, without filaments (Fig. 4I).

Hosts: Scalloped hammerhead *Sphyrna lewini* (Grifith et Smith) and great hammerhead *Sphyrna mokarran* (Rüppel) (Sphyrnidae, Carcharhiniformes).

Site of infection: Spiral valve.

Localities: *S. lewini*: Off Queensland (NO) and Northern Territory (TS, DWN, NNT, GoC, JBG, AS), all Australia (collected various dates from July 2015 to May 2018); *S. mokarran*: Off Northern Territory (TS [collected 20 March 2017]).

Total prevalence and intensity: *S. lewini*: 43.1% (90 fish infected/209 fish examined); intensity 1–30 (mean 5.3) nematodes per fish. *S. mokarran*: 1.8% (1/57); 8 nematodes (Table 1).

Deposition of voucher specimens: South Australian Museum (SAM), Adelaide, Australia (Cat. No. ……..) and Helminthological Collection of the Institute of Parasitology, Biology Centre of the Czech Academy of Sciences, České Budějovice, Czech Republic (Cat. No. N–……).

Remarks

Based solely on the light microscopy (LM) of one complete female specimen and several body fragments collected from the scalloped hammerhead *Sphyrna lewini* (reported as *S. diplana*) from off the Atlantic coast of Senegal, Campana-Rouget (1955) erected a new genus *Parascarophis* Campana-Rouget, 1955 to accommodate the newly described species *P. sphyrnae* Campana-Rouget, 1955. The author distinguished this new genus from the related *Ascarophis* van Beneden, 1870 mainly by the presence of a cephalic hood, pseudolabia each armed allegedly with two teeth, the long vestibule dilated anteriorly into a dorsoventrally expanded cavity and the vulva situated in the anterior part of the body (see also Skryabin et al. 1967; Anderson et al. 2009). Later Campana-Rouget (1956) transferred to this genus *Filaria galeata* Linton, 1905, a nematode described from *Shyrna tiburo* (Linnaeus) (Sphyrnidae) and *Coryphaena equiselis* Linnaeus (Coryphaenidae) from off the Atlantic coast North Carolina, USA; however, only body fragments of *P. galeata* were found in the stomach of the latter host species, so that Linton (1905) mentions that "these worms have the appearance of having been introduced into the stomach of the dolphinfish along with some host in which they were adult". Since specimens from *C. equiselis* somewhat differed morphologically from those

obtained in *S. tiburo*, it cannot be excluded that they belonged to a different cystidicolid species and, consequently, that the only definitive host of *P. galeata* is *S. tiburo*.

Two species of *Parascarophis*, *P. bharatii* Agrawal, 1965 and *P. oteroi* Arya, 1992 [erroneously reported as *P. vagra* Arya, 1992 by Sood 2017] were inadequately described from freshwater fishes *Mastacembelus armatus* (Lacépède) (Mastacembelidae) and *Barilius vagra* (Hamilton) (Cyprinidae), respectively, in India (Agrawal 1965; Arya 1992). However, the presence of a very short vestibule and the absence of a cephalic hood in *P. bharatii* indicate that this nematode does not belong to *Parascarophis* and is likely a physalopterid (Sood 2017). The same concerns *P. oteroi*, as well as *Parascarophis* sp. reported from *Channa punctata* (Bloch) (Channidae) in India by Singha et al. (2014) (see also Sood 2017). In India, *Parascarophis* sp. has also been reported, but not described, from *Anabas testudineus* (Bloch) (Anabantidae), *Clarias batrachus* (Linnaeus) (Clariidae) and *Heteropneustes fossilis* (Bloch) (Heteropneustidae) (see Sangeeta et al. 2011; Ampili and Vishnu 2018), but the generic identification of these nematodes seems to be doubtful. *Parascarophis* sp. was also listed as a parasite of *Pseudotolithus elongatus* Bowdich (Sciaenidae) from the Niger River delta, Nigeria (Ogbeibu et al. 2014), but no morphological data were provided to support the generic identification of the nematodes recorded.

Another species of *Parascarophis*, *P. mulloidi* Imam, Tawfik et Abdel Hady, 1982, was poorly described from *Parupeneus forsskali* (Fourmanoir et Guézé) (Mullidae) (reported as *Mulloidicthys auriflamma*) in the Red Sea (off Egypt) (Imam et al. 1982). However, it is apparent from the drawings that the nematodes in question did not possess a long vestibule typical of *Parascarophis*, so that they could not belong to this genus. As indicated by the location of the muscular oesophagus at a short distance behind the cephalic extremity, it cannot be excluded that they belonged to the recently established physalopterid genus

Rasheedia Moravec et Justine, 2018, the representatives of which are parasites of *Parupeneus* spp. (see Moravec and Justine 2018).

It follows from the above discussion that only two nominal species, *P. sphyrnae* and *P. galeata*, both parasitizing hammerhead sharks, can be assigned to *Parascarophis*. All other nematodes reported as species of *Parascarophis* from teleosts belong to other genera; because of inadequate descriptions of *P. bharatii*, *P. oteroi* and *P. mulloidi*, all these three species should be designated as *species inquirendae* and *incertae sedis*.

The present specimens from *S. lewini* are morphologically very similar to *P. shyrnae*, described from the same host species as in the eastern Atlantic Ocean (see above), and the only important difference is their postequatorial position of the vulva (*vs* vulva allegedly in the anterior part of body). However, Campana-Rouget's information in this respect may not be reliable, because she had at her disposal only one complete, probably young specimen 12 mm long. Narrow lateral alae, found in the present specimens, have not been reported by Campana-Rouget (1955), but these could be easily overlooked.

According to Campana-Rouget (1955), there are two median teeth on the internal side of each pseudolabium in *Parascarophis*, in contrast to *Ascarophis*, where a single median tooth is present. However, her study of the mouth of *P. sphyrnae* was based solely on LM observations, whereas the cephalic structures of such small cystidicolid nematodes require to be studied with the use of SEM (Moravec 2007). In fact, as visible from fig. 1D in her paper, she did not distinguish between proper pseudolabia and labia and details of the mouth are not apparent from her illustrations; therefore, data concerning the cephalic structure in the original despription of this species are questionable. It is highly probable that the two reported teeth on each pseudolabium were in fact the teeth formed by anterolateral plate-like structures or by sublabia (see Figs. 5B, 6F, G). Despite these differences, we consider the present specimens to belong to *P. shyrnae*. The male of *P. shyrnae* is described for the first time in this study.

Within the present study, almost all specimens of *P. sphyrnae* were collected from *S. lewini*, whereas only eight body fragments of poorly preserved specimens from *S. mokarran* were available, including one male posterior end. Even though the left spicule was found to be slightly shorter (510 µm long) as compared with that of specimens from *S. lewini* and the right spicule was 84 µm long, we consider this difference to be within the intraspecific biometrical variability of *P. sphyrnae*.

A single female of this nematode species (*P. sphyrnae*) was also reported from the smooth hammerhead *Sphyrna zygaena* (Linnaeus) in the western Atlantic Ocean (off Brazil) (Knoff et al. 2001). Consequently, the present finding represents the third record of this nematode species and the first one in Australian waters. Records of this parasite in the eastern and western Atlantic and near Australia suggest that the distribution area of *P. sphyrnae* coincides with that of its type host, which has a circumglobal distribution in coastal warm temperate and tropical seas (Froese and Pauly 2018).

Comparison of the morphology of *P. sphyrnae* with that of the only other congeneric species *P. galeata* is difficult, because the latter nematode is poorly described. However, in contrast to the former species, the male of *P. galeata* is up to 35 mm (*vs* up to approximately 12 mm) long, with the oesophagus 4.2 mm (*vs* at most 2.13 mm) in the length. Moreover, *P. galeata* is from a different host species (*S. tiburo vs S. lewini*, *S. mokarran* and *S. zygaena*). Nevertheless, a redescription of *P. galeata* based on newly collected specimens from *S. tiburo* is needed.

Discussion

The present description of a new species of *Piscicapillaria* confirms that all representatives of this genus are specific parasites of elasmobranchs. Unfortunately, the

morphology of the majority of *Piscicapillaria* spp. remains insufficiently known and the males of two species (*P. baylisi* and *P. hathawayi*) have not been described to date (see above). *Piscicapillaria bursata* sp. n. is the first species of this genus studied with the use of SEM, so that the present data on the cephalic structure of this species represent the first information in this respect in a representative of this genus.

It is apparent from this study that the structure of the lips, the shape of the oral aperture and the number and arrangement of the cephalic papillae in *Piscicapillaria* are similar to those described in some species of *Capillaria* Zeder, 1800, *Capillaroides* Freitas et Lent, 1935, *Lobocapillaria* Moravec et Beveridge, 2017 and *Paracapillaria* Mendonça, 1963 (see Moravec 2001b; Moravec and Beveridge 2017; González-Solís et al. 2014; Moravec and Justine 2014; Moravec and Barton 2018). However, a stylet reported in some capillariids (e.g. Baruš et al. 1981; González-Solís et al. 2014) was not observed in *P. bursata* sp. n. Since no male of this new species with the extruded spicule sheath was available, the spination of the sheath could not be studied in detail by SEM.

The taxonomy and classification system within the family Cystidicolidae is rather complicated. Some of the many genera have been based on details in the cephalic structures visible only with the use of SEM, whereas representatives of a number of other genera have been studied solely by LM. Moravec (2007) reported 23 cystidicolid genera usually considered by different authors to be valid, but *Mastigospirura* Machida et Sayhailatua, 1994 was omitted. Subsequently, Moravec et al. (2008) designated *Sterliadochona* Skryabin, 1948 as a *genus inquirendum*, Moravec and Sobecka (2012) resurrected *Collarinema* Sey, 1970 and the genus *Similascarophis* Muñoz, González et George-Nascimento, 2004 was considered a subgenus of *Ascarophis* by Moravec and Justine (2007). Moreover, an additional four cystidicolid genera, *Salmonema* Moravec, Santos et Brasil-Sato, 2008, *Placonema* Brugni, Viozzi, Fernández et Vega, 2009, *Ascarophisnema* Moravec et Justine, 2010 and

Metabronemoides Moravec et Justine, 2010, were established (Moravec et al. 2008; Bruni et al. 2009; Moravec and Justine 2010). Consequently, at present the family Cystidicolidae includes 27 valid genera.

It follows from the present study that *Parascarophis* differs from the great majority of other cystidicolid genera, including *Ascarophis*, in possessing a pair of anterolateral bi-dentate plate-like structures in the mouth. Presence of similar, bi-dentate plate-like structures was only used by Appy and Anderson (1982) to distinguish species of *Capillospirura* Skryabin, 1924, parasites of acipenserids, from *Ascarophis* spp.; *Capillospirura* was previously considered a synonym of *Ascarophis* by Polyanskiy (1952) and Chabaud (1975) and both genera have recently been found to show close phylogenetic relationships (Choudhury and Nadler 2018). Prongs formed by extensions of the lateral wall of the prostom and aligned with either side of pseudolabia in *Caballeronema* Margolis, 1977 (see Margolis 1977) are probably analogous to such plate-like structures.

A characteristic feature of *Parascarophis* spp. is the presence of the cuticular cephalic hood, but similar cephalic cuticular structures also occur in the cystidicolid genera *Collarinema*, *Cyclozone* Dogiel, 1932, *Cystidicoloides* Skinker, 1931 and *Pseudoproleptus* Khera, 1955. Somewhat inflated cuticle in the region of the anterior end of the body is also present in some species of *Ascarophis* (*A. cestus* Chitwood, 1934, *A. chalinurae* Johnston et Mawson 1945, *A. crassicollis* Dollfus et Campana-Rouget, 1956, *A. collaris* Petter, 1970 and A. *longiovata* Moravec et Klimpel, 2009) and *Neoascarophis* Machida, 1976 (*N. mariae* Pereira, Timi, Vieira et Luque, 2012). In contrast to species of *Ascarophis* and some other *Ascarophis*-like genera, deirids in *Pseudascarophis* are simple, stick-like (*vs* deirids bifurcate). However, as found in this paper, the type species of *Parascarophis* (*P. sphyrnae*) possesses well-developed lateral alae, a feature that is unique within the Cystidicolidae. Based

on the present study, *Pseudascarophis* is considered a valid genus and its amended diagnosis is provided.

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Conservation Act 1999, from the application of sections 18, 18A, 20, 20A, 23 and 24A of Part 3 and Parts 7 to 9 of Chapter 4 of the Act, by the Commonwealth Minister for the Environment and Energy.

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Fig. 1. *Piscicapillaria bursata* sp. n. A – anterior end of male, lateral view; B – cephalic end of female, apical view; C. D – caudal end of male, ventral and lateral views; E – posterior end of male, lateral view; F – region of vulva, lateral view; G – stichocyte in middle part of stichosome; H, I – proximal and distal end of spicule, respectively; J – caudal end of female, lateral view; K – egg.

Fig. 2. *Piscicapillaria bursata* sp. n., scanning electron micrographs of male. A, B – cephalic end, apical and dorsoventral views, respectively (arrows indicate cephalic papillae); C, D – caudal end, lateral and apical views respectively; E, F – caudal end, ventral and dorsal views, respectively. *Abbreviations*: a – caudal papilla; b – caudal bursa; c – cloaca; d – outlined median caudal projection.

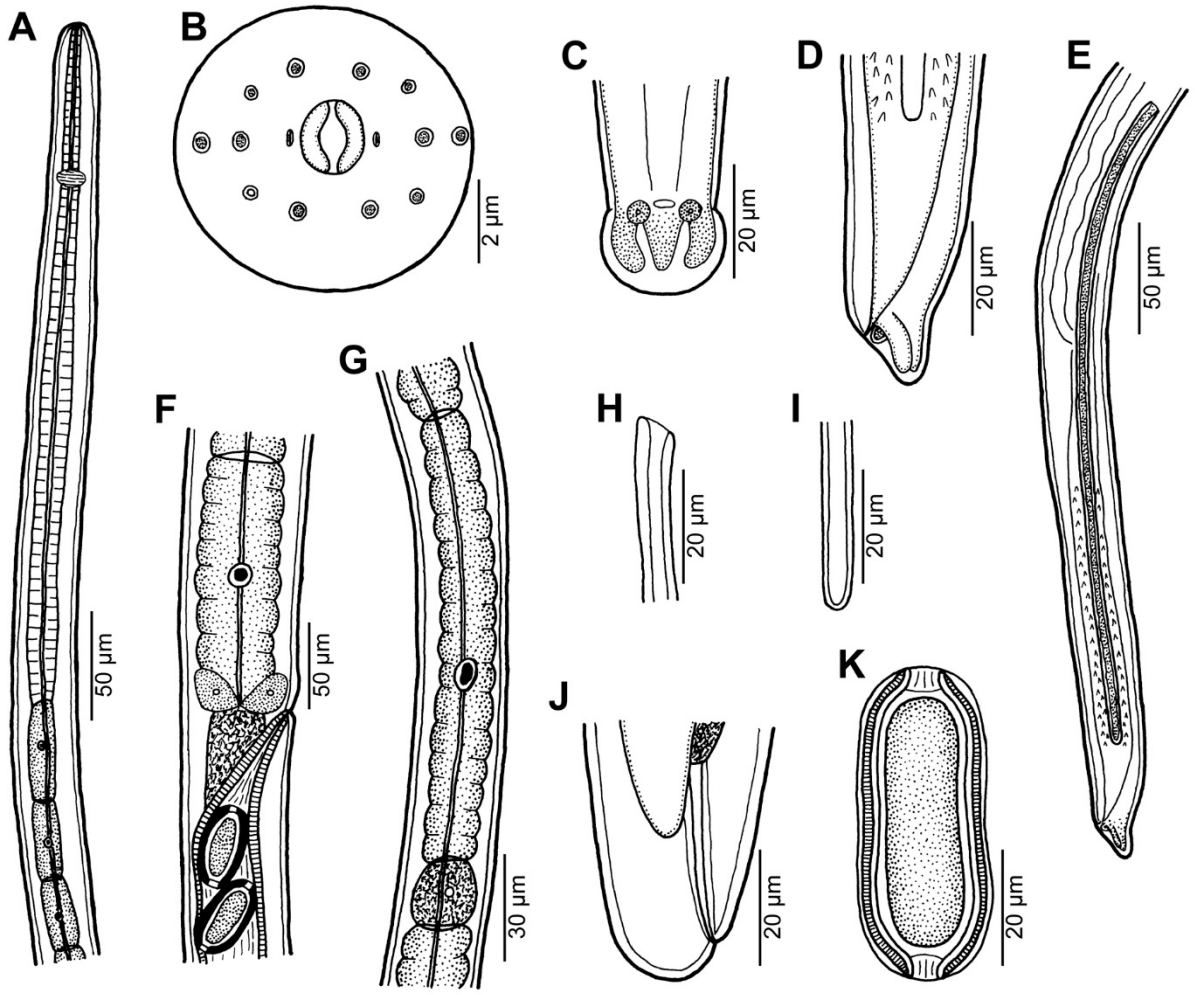
Fig. 3. *Piscicapillaria bursata* sp. n., scanning electron micrographs. A – anterior end of male, dorsoventral view; B – cephalic end of female, apical view (arrow indicates amphid); C – egg inside body; D – cephalic end of female, sublateral view (arrow indicates amphid); E – part of female body with cuticular papillae in lateral bacillary band; F – cuticular papillae of

lateral bacillary band near posterior end of male. *Abbreviations*: a – cephalic papilla; e – polar plug; o – oral aperture.

Fig. 4. *Parascarophis sphyrnae* Campana-Rouget, 1955. A – anterior end of male, lateral view; B – cephalic end of gravid female, lateral view; C – cephalic end of gravid female, lateral view (specimen with symmetrical cephalic hood); D – cephalic end of gravid female, dorsoventral view; E – cephalic end of female, apical view; F – posterior end of male, lateral view; G, H – anterior end of female, lateral and dorsoventral views; I – egg; J – deirid; K – caudal end of male, ventral view; L – tail of female, lateral view; M – distal end of left spicule, lateral view; N – right spicule, lateral view.

Fig. 5. *Parascarophis sphyrnae* Campana-Rouget, 1955 scanning electron micrographs. A – anterior end of body, sublateral view; B – cephalic end of male, apical view (arrow indicates amphid); C – deirid; D, E – cephalic end, sublateral and subdorsoventral views, respectively; F, G – region of mouth, apical and subdorsoventral views, respectively. *Abbreviations*: a – cephalic papilla; h – cephalic hood; l – labium; p – pseudolabium; r – anterolateral bi-dentate plate-like structure; s – sublabium.

Fig. 6. *Parascarophis sphyrnae* Campana-Rouget, 1955. A, B – cephalic end of female, apical and sublateral views, respectively (arrow indicates bi-dentate anterolateral plate-like structure); C – region of cloaca, ventral view; D – tip of male tail, ventral view; E – anterior end of body, dorsoventral view (upper arrow indicates situation of deirid, two lower arrows indicate lateral alae); F – posterior end of young male, lateral view; G – tail of female, lateral view (arrow indicates anus); inset: tail tip with phasmid; H – precloacal cuticular ridges. *Abbreviations*: c – cloacal aperture; p – pseudolabium; s – sublabium.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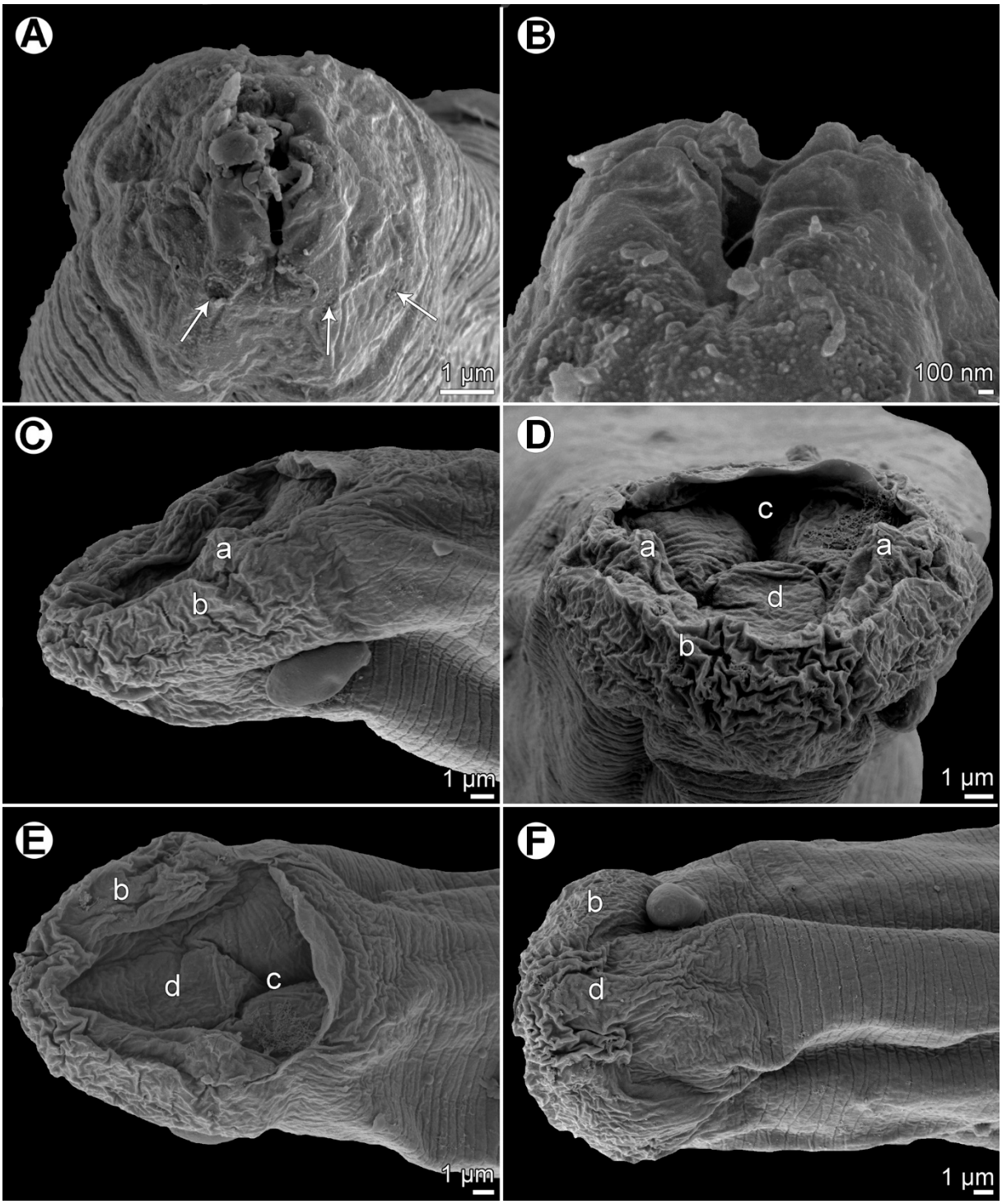
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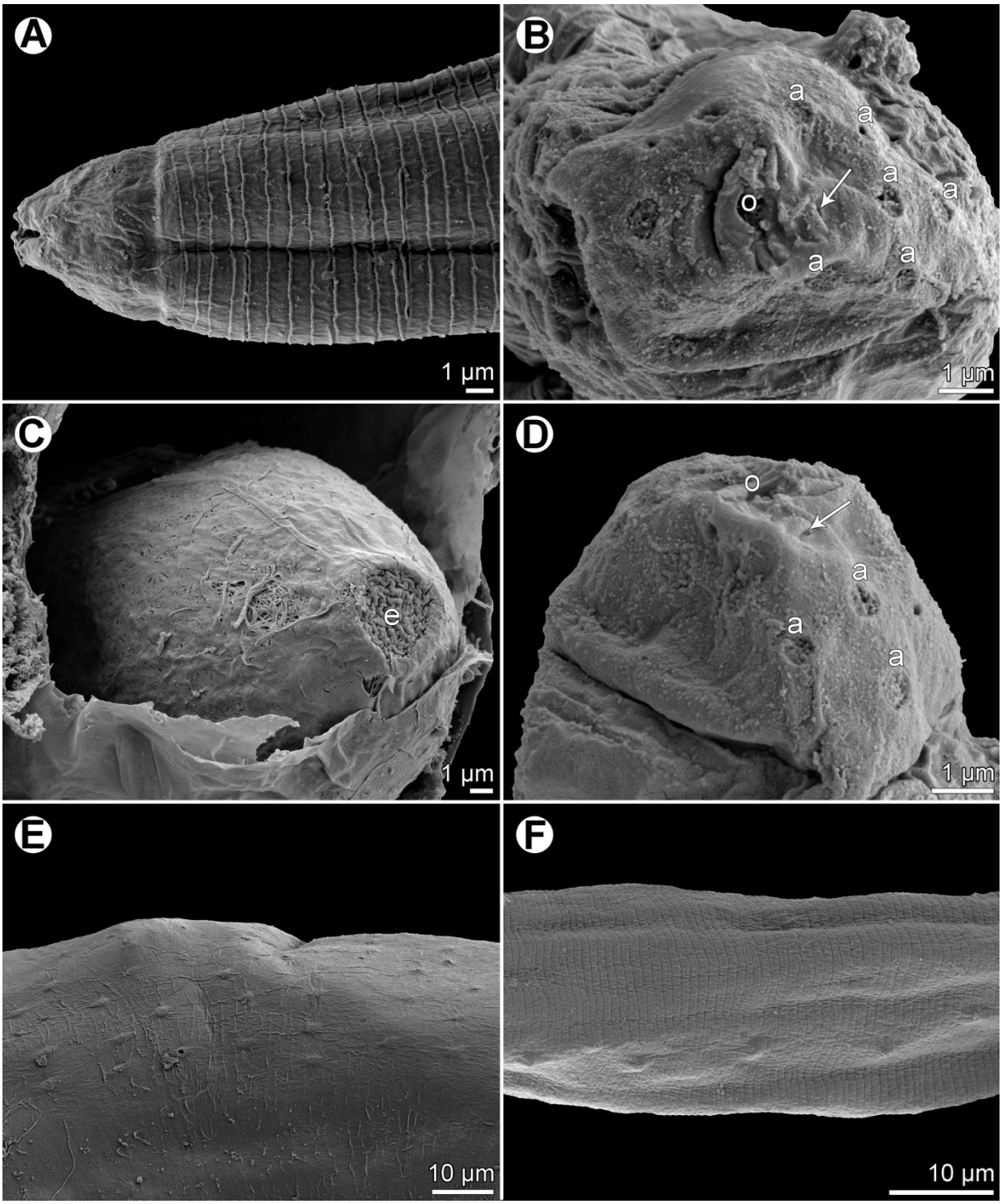
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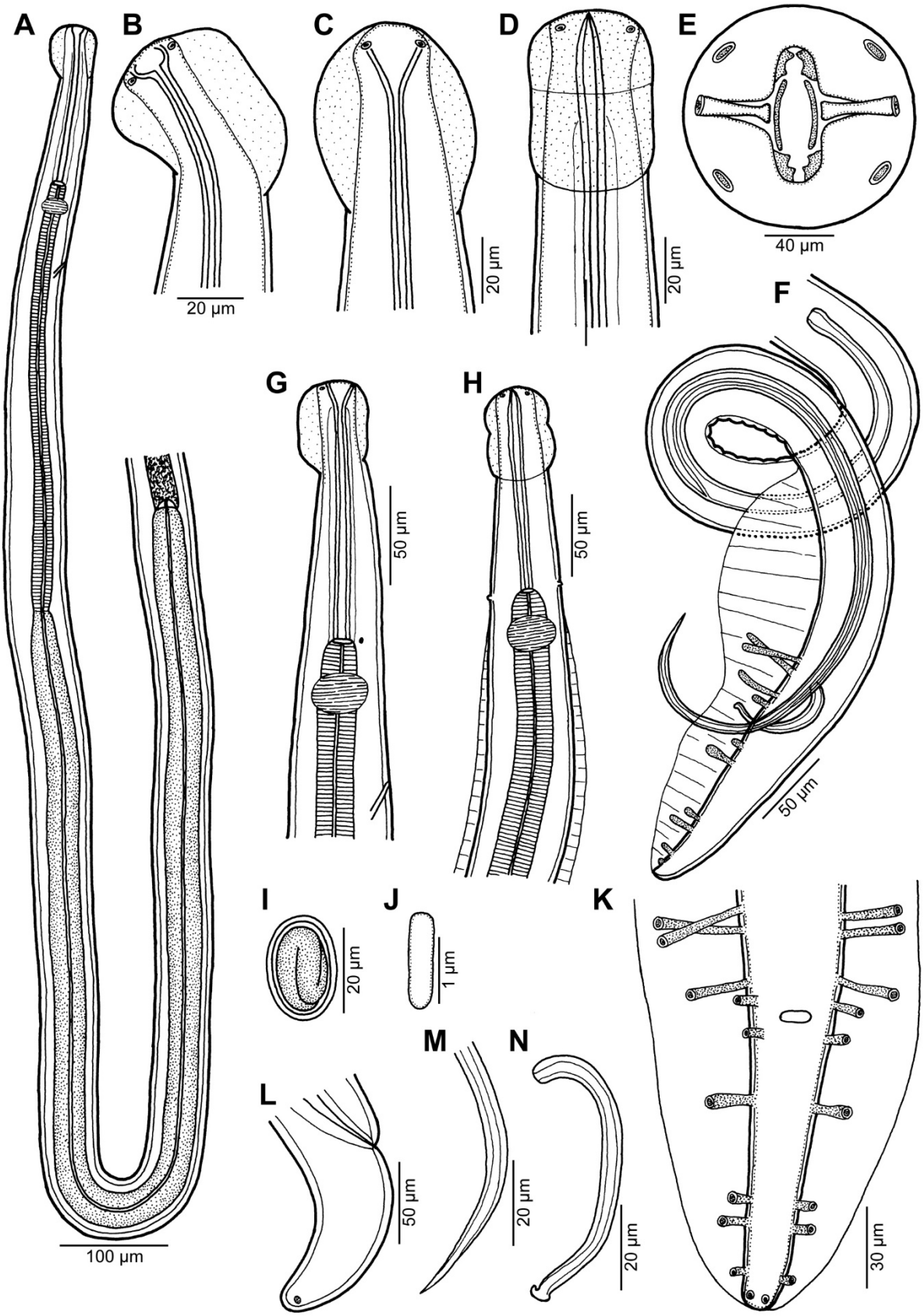
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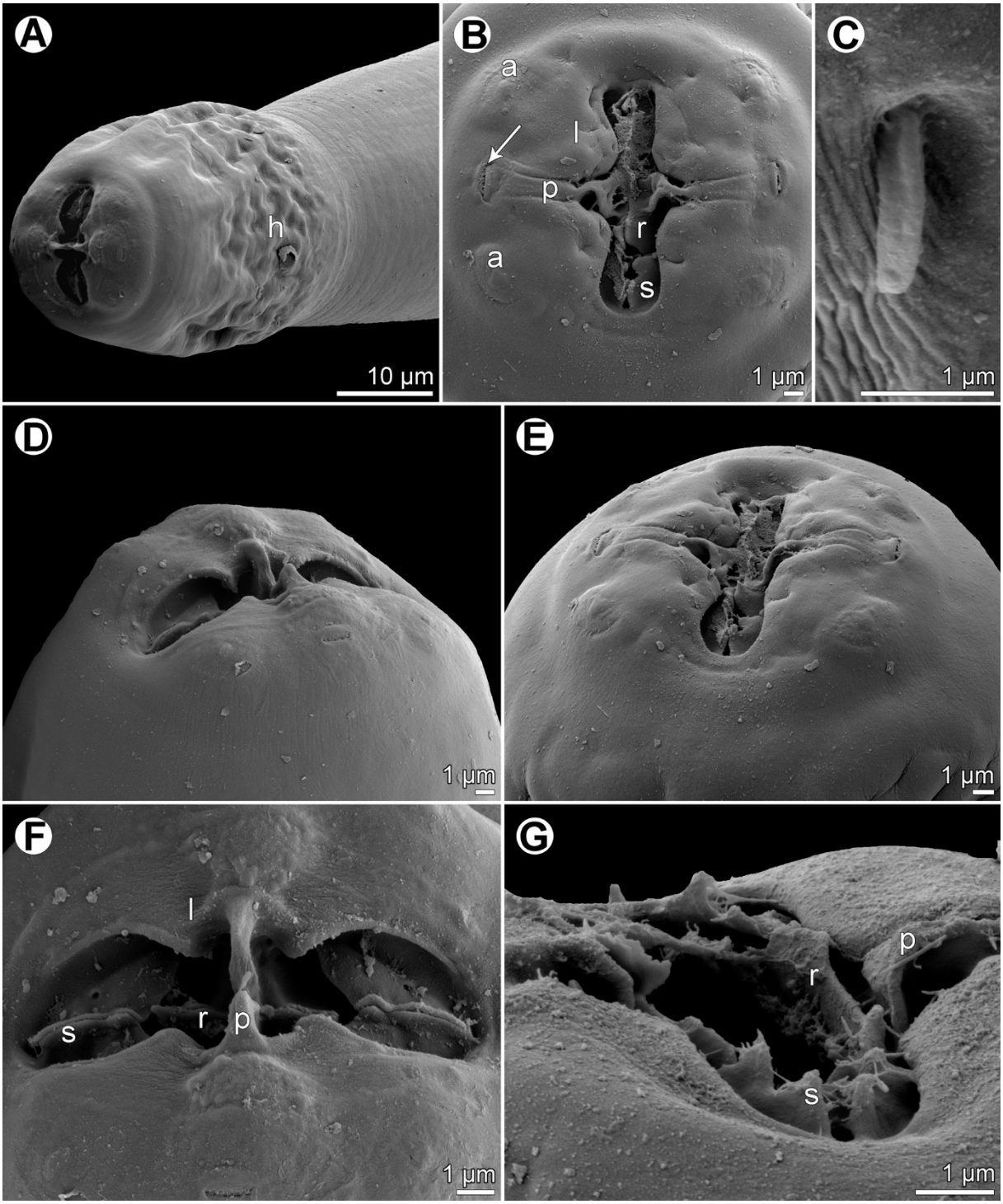
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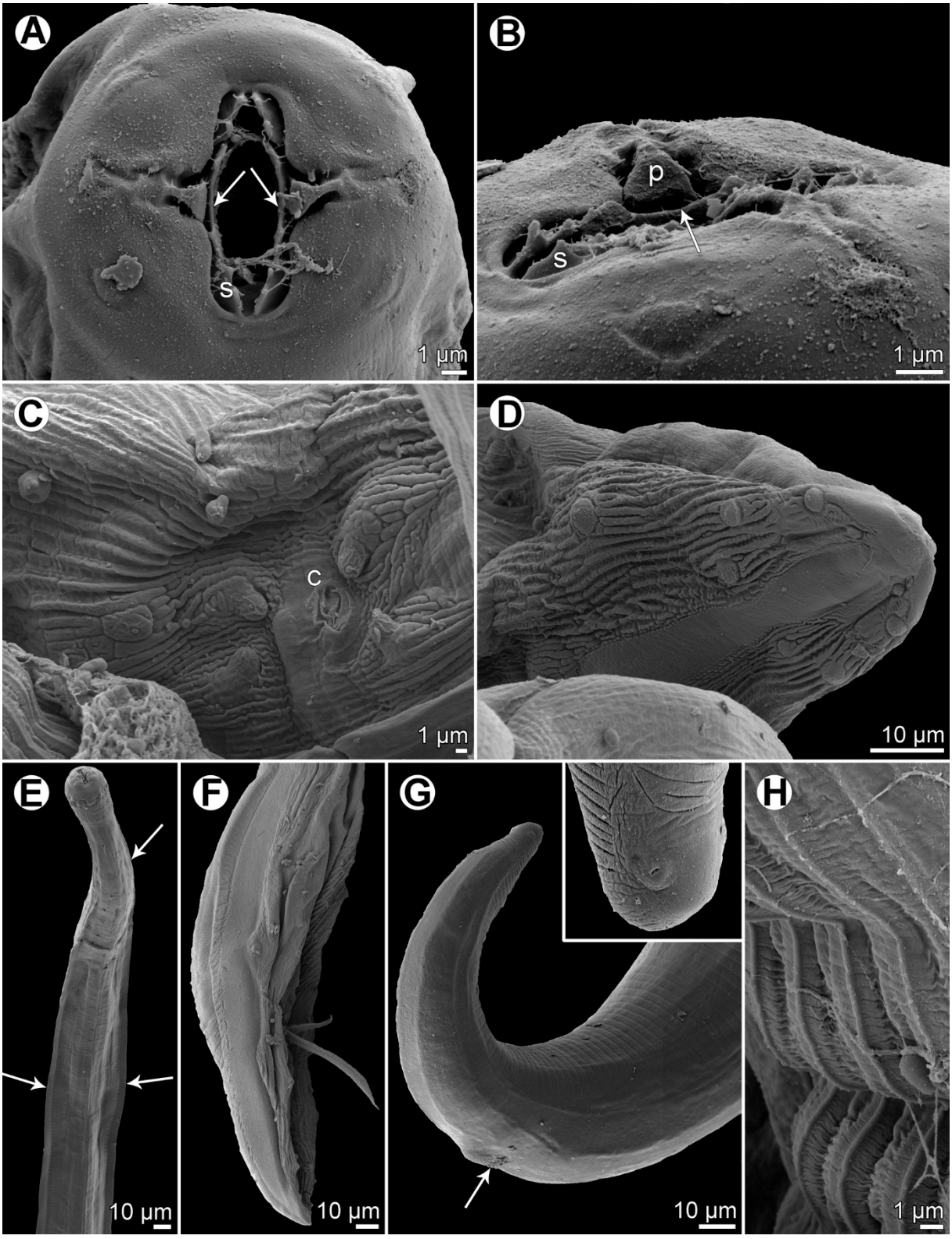
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