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Monogeneans of the malabar grouper *Epinephelus malabaricus* (Perciformes, Serranidae) off New Caledonia, with a description of six new species of *Pseudorhabdosynochus* (Monogenea: Diplectanidae)

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Abstract

Eleven species were differentiated among more than 300 monogeneans collected on the gills of two wild malabar groupers, *Epinephelus malabaricus*, caught in the lagoon of New Caledonia, South Pacific. Diplectanids included seven species of *Pseudorhabdosynochus* Yamaguti, 1958, which were differentiated mainly on the basis of morphology of the sclerotised vagina. *P. manifestus* **n. sp.** was the most abundant species (65–80% of the diplectanids); all other species were rare. It is characterised by morphology of its vagina, in general shape of a question mark. *P. malabaricus* **n. sp.** and *P. maternus* **n. sp.** both have a vagina with two spherical chambers, and are differentiated on the basis of measurements of these chambers. *P. manipulus* **n. sp.** has an elongate vagina with a long primary chamber. *P. marcellus* **n. sp.** has a long vagina with two bends. *P. maaensis* **n. sp.** has a long vagina with a straight primary canal and the two chambers united in a common sclerotised part. Two specimens were provisorily attributed to *P.* cf. *shenzhenensis* Yang, Zeng & Gibson, 2005. *Diplectanum maa* **n. sp.** has a funnel-shaped male copulatory organ. Two species of *Haliotrema* (Ancyrocephalidae) and *Pseudomegalocotyla* sp. (Capsalidae) are mentioned but not described. The presence of 11 species of monogeneans in this fish, after a previous published record of 12 species in *E. maculatus*, provides additional argument for existence of a very rich fauna of monogeneans in groupers, and an impressive parasite biodiversity in coral reef fish in general. Lists are given for other parasites of the malabar grouper, including monogeneans, digeneans, cestodes and nematodes, including new records from New Caledonia; more than 40 parasite species have been recorded in the literature. The malabar grouper is a major fish for aquaculture in South East Asia and a precise description of its parasites is needed for identification of potential threats to farmed fish.

Key words: Monogenea, Diplectanidae, Serranidae, Parasite lists, New Caledonia, *Pseudorhabdosynochus manifestus* **n. sp.**, *Pseudorhabdosynochus malabaricus* **n. sp.**, *Pseudorhabdosynochus maternus* **n. sp.**, *Pseudorhabdosynochus manipulus* **n. sp.**, *Pseudorhabdosynochus marcellus* **n. sp.**, *Pseudorhabdosynochus maaensis* **n. sp.**, *Diplectanum maa* **n. sp.**, *Pseudorhabdosynochus* cf. *shenzhenensis*, Ancyrocephalidae, *Haliotrema* spp., Capsalidae, *Pseudomegalocotyla* sp.

Résumé
Onze espèces ont été identifiées parmi plus de 300 monogènes collectés sur les branchies de deux mères loches sauvages, *Epinephelus malabaricus*, pêchées dans le lagon de Nouvelle-Calédonie, Pacifique Sud. Les Diplectanidae incluent sept espèces de *Pseudorhabdosynochus* Yamaguti, 1958, qui ont été différenciées principalement par la morphologie du vagin sclérifié. *P. manifestus* **n. sp.** était l'espèce la plus abondante (65–80% des Diplectanidae), toutes les autres espèces étaient rares. Cette espèce est caractérisée par la morphologie du vagin, en forme de point d'interrogation. *P. malabaricus* **n. sp.** et *P. maternus* **n. sp.** ont tous deux des vagins avec deux chambres sphériques, et sont différenciés par les mesures de ces chambres. *P. manipulus* **n. sp.** a un vagin allongé avec une chambre primaire longue. *P. marcellus* **n. sp.** a un long vagin avec deux coudes. *P. maaensis* **n. sp.** a un long vagin avec un canal primaire droit et les deux chambres unies dans une partie sclérifiée commune. Deux spécimens ont été provisoirement attribués à *P.* cf. *shenzhenensis* Yang, Zeng & Gibson, 2005. *Diplectanum maa* **n. sp.** a un organe copulateur mâle en forme d'entonnoir. Deux espèces d'*Haliotrema* (Ancyrocephalidae) et *Pseudomegalocotyla* sp. (Capsalidae) sont mentionnés mais non décrits. La présence de onze espèces de monogènes chez ce poisson, après une publication précédente mentionnant douze espèces chez *E. maculatus*, fournit des arguments supplémentaires pour l'existence d'une riche faune de monogènes chez les mérous, et une biodiversité parasitaire impressionnante chez les poissons des récifs coralliens en général. Des listes des autres parasites de la mère loche sont fournies, incluant des monogènes, digènes, cestodes et nématodes, y compris des nouvelles mentions pour la Nouvelle-Calédonie, et plus de 40 espèces de parasites ont été signalées. La mère-loche est un poisson important pour l'aquaculture dans le Sud-est asiatique et une description précise de ses parasites est nécessaire pour identifier les dangers potentiels envers les poissons en élevage.

Introduction

Groupers harbour a rich fauna of parasites, especially a large number of monogeneans on the gills. Recently, Justine (2007a) mentioned 12 species of monogeneans on the highfin grouper, *Epinephelus maculatus* (Bloch) off New Caledonia, including 8 new species of the diplectanid *Pseudorhabdosynochus*. Description of these small monogeneans requires efforts but provides worthwhile information for estimating parasite biodiversity in the coral reef fishes. Justine (2007a) also mentioned comparative results on other groupers, with the total number of monogenean species ranging from 2 to 12.

Although a large number of bacterial and viral diseases have already been described in the malabar grouper (review in Bondad-Reantaso *et al*. 2002), the monogenean fauna is still very poorly known. In this paper, we present results based on examination of two fish only, which provided enough monogeneans (more than 300) for identification of 11 different species.

The malabar grouper, *Epinephelus malabaricus*, is a very big species. Heemstra & Randall (1993) and Randall (2005) state that the maximum size is uncertain because of confusion with other species of large groupers, and considered as confirmed a specimen of 97.4 cm standard length (115 cm total length). However, Froese & Pauly (2007) indicate a maximum size and weight of 234 cm and 150 kg. One of the specimens used for our parasitological study was 128 cm in fork length and thus ascertains that the monogenean fauna described here concerns a fully grown specimen. Confusions in the literature exist with two other species of large spotted groupers, *E. coioides* (Hamilton) and *E. tauvina* (Forsskål) (see Heemstra & Randall 1993). Recent molecular works demonstrated that these species are distinct, although very close (Govindaraju & Jayasankar 2004; Ding *et al*. 2006; Wang *et al*. 2007). Published

information (Bu *et al*. 1999; Yang *et al*. 2005) and our unpublished observations about *E. coioides* from New Caledonia show that the monogenean fauna of *E. malabaricus* and *E. coioides* are distinct, although some species of diplectanids are very closely related.

The malabar grouper is widespread in the Indian and South Pacific Oceans, from the Red Sea and East Africa to Tonga, north to Japan, and south to Australia (Froese & Pauly 2007); the species is traded as live fish (Lee & Sadovy 1998) and is very important for aquaculture in South-East Asia (Tookwinas 1989; APEC/ NACA/ BOBP/ GOI 2002). Precise description of its monogeneans might reveal useful when identification of parasites will be needed for aquacultured fish. The specimens used in this study were wild and collected in the relatively well preserved lagoon of New Caledonia and thus provide a basis for comparison of infestation rates and relative abundance of parasite species in fish, wild or aquacultured, in other parts of the Pacific Ocean.

A list of parasites mentioned from the malabar grouper, including monogeneans and other groups, is also provided, as a tool for future research and as a mean to evaluate parasite biodiversity in this fish.

Materials and methods

Two specimens of *E. malabaricus* were used in this study. A large wounded specimen (designated as JNC1536) was noticed by divers off Nouméa, New Caledonia. The wound affected all the upper jaw and prevented the fish from eating; it was decided to kill the animal and use it for parasitological research. The fish was spear-fished (18.v.2005, 22°19’114S, 166°27’092E) and immediately brought back to the laboratory, photographed and measured (fork length 1280 mm, weight 45 kg). Other parasites collected in this fish have already been described (digeneans: Bray & Justine 2006; trypanorhynch cestodes: Beveridge *et al*. 2007). A second, much smaller (fork length 395 mm, weight 795 g) specimen (designated as JNC2130) was spear-fished in Baie Maa, New Caledonia (9.iii.2007, 22°12’780S, 166°19’933E). The parasitological material was then assigned a corresponding JNC linked to the respective fish host.

Gills were extracted and examined in seawater with a dissecting microscope. Live monogeneans were individually picked off the gills with fine needles and immediately prepared. Specimens were routinely processed for carmine staining, including initial flattening between a slide and a coverslip in ethanol (referred to as ‘carmine’ – see Justine 2005a), according to Justine (2005a), or with ammonium picrate-glycerine, according to Malmberg (1957), but slightly modified (referred to as ‘picrate’ – see Justine 2005a). ‘Picrate’ slides were made with a single or several worms; ‘carmine’ slides were made with a single worm per slide for the preparation of the different monogenean species.

Monogeneans were drawn using a BH2 microscope equipped with a camera lucida and differential interference contrast optics. Measurements were taken on the pencil drawings with the help of a custom-made transparent rule, previously calibrated with a stage micrometer. Drawings were scanned and redrawn on a computer with Adobe Illustrator. All drawings of bodies, and all drawings of other parts, are at the same scale for all species. Method of measurement of sclerotised parts (Figure 1) is as in Justine (2005a); measurements of the right-hand haptoral hard-parts and left-hand equivalents were pooled. All measurements are given in micrometres as: the holotype (h), and mean and standard deviation (when n>30, and not given for the number of rodlets) followed by the range and number of measurements in parentheses. Measurements of ammonium picrate preparations (p) and of specimens flattened in ethanol

stained with carmine (c) may vary significantly (Justine 2005a) and are separated when indicated; measurements of soft parts are given only for 'carmine' specimens.

Three species of monogeneans are only briefly mentioned but not described in this paper which concentrates on diplectanids. They are, however, important for an evaluation of parasite biodiversity in this fish species. Two species of *Haliotrema* Johnston & Tiegs (Ancyrocephalidae) were found. One was characterised by a long penis and is referred to as *Haliotrema* sp. 1; the other has a short penis and is referred to as *Haliotrema* sp. 2. These species are probably new. Capsalids were identified by Ian Whittington as *Pseudomegalocotyla* sp. Table 1 shows the numerical results for the collection of monogeneans from two fish.

Names of new species described here all begin by "ma–" to provide an easy way to identify these species from *E. malabaricus* among the numerous species of *Pseudorhabdosynochus* already described or to be described.

Comparative material examined: *P. shenzhenensis* Yang, Zeng & Gibson, 2005, voucher MNHN JNA5A1, and *P. serrani* (Yamaguti, 1953) Kritsky & Beverley-Burton, 1986, voucher MNHN JNA6A1, both from *E. coioides*, South China Sea (Yang *et al*. 2005).

Abbreviations: MNHN, Muséum national d'Histoire Naturelle, Paris; BMNH, Natural History Museum, London; USNPC, United States National Parasite Collection, Beltsville; SAMA AHC, South Australian Museum Adelaide, Australian Helminthological Collection; HCIP, Helminthological Collection, Institute of Parasitology, Biology Centre, Academy of Sciences of the Czech Republic, České Budějovice; SLZU, School of Life Sciences, Zhongshan University (Sun Yat-sen University), Guangzhou, China; h, holotype; c, carmine; p, picrate.

Results

Family Diplectanidae Bychowsky

Genus *Pseudorhabdosynochus* Yamaguti

Pseudorhabdosynochus manifestus n. sp.

(Figs 2–5)

Type-host: *Epinephelus malabaricus* Bloch & Schneider (Serranidae).

Type-locality: Lagoon off Nouméa, New Caledonia.

Site: Between secondary gill lamellae.

Type-specimens: Holotype, JNC1536A26, off Ouen Toro, Nouméa, New Caledonia (22°19'S, 166°27'E, 18.v.2005).

Material examined: 220 specimens: 129 'carmine' (c), 91 'picrate' (p).

Material deposited: Holotype (c) and 204 paratypes (113 c, 91 p), MNHN; for all other collections, 3 paratypes (c) including 1 from fish JNC1536 and 2 from fish JNC2130: BMNH 2007.6.1.1-3; USNPC 99867-8; SAMA AHC 29213-4; HCIP M-440; SLZU 20070613-1-1–3.

Prevalence: 100% (2/2). The only species which was found in the two fish examined.

Intensity: See Table 1. Maximum intensity for both gill sides evaluated to several hundreds. This species was the dominant species in both fish, and represented 65–80% of the diplectanids (65–66% of the monogeneans).

Etymology: From '*manifestus*' (Latin), clear, evident, refers to the fact that this was the most abundant species.

Description. Body elongate; length h 670, c 665±85 (450–870, n = 29), width h 290, c 306±50 (170–410, n = 30). Tegument scaly; posterior region with scales on ventral and dorsal

faces from squamodiscs to level of ovary and testis. Anterior region with 3 pairs of head organs and 2 pairs of eye-spots; distance between outer margins of anterior eye-spot pair h 43, c 46±11.6 (31–70, n = 30), of posterior eye-spot pair h 44, c 44±8.9 (28–65, n = 30).

Haptor differentiated from rest of body, less wide than body, width 220, c 247±26 (190–300, n = 28), provided with 2 similar squamodiscs, 2 pairs of lateral hamuli, 3 bars and 14 marginal hooklets. Squamodiscs round in shape, made up of rows of rodlets; central rows forming almost closed ovals; rodlets progressively thinner from centre to periphery; rodlets adjacent in all rows except last row; last row with very thin, separated rodlets; ventral and dorsal squamodiscs similar, but ventral slightly larger; ventral squamodisc length h 63, c 60 (53–67, n = 18), width h 65, c 61 (54–70, n = 18), with 10–11 (n = 18) rows of rodlets and 0–2 closed ovals; total number of rodlets h 87; dorsal squamodisc, length h 54, c 54 (48–62, n = 19), width h 57, c 56 (50–62, n = 20), with 10–12 (n = 20) rows of rodlets and 0–2 closed ovals; total number of rodlets h 86. Ventral hamulus with thick handle and distinct guard, outer length h 57, c 57±2.5 (53–62, n = 59), p 59±1.9 (55–62, n = 64), inner length h 48, c 49±2.1 (44–53, n = 59), p 47±1.2 (44–51, n = 64). Dorsal hamulus with indistinct guard, outer length h 50, c 48±1.6 (44–52, n = 64), p 48±1.3, (45–52, n = 64), inner length h 31, c 30±1.0 (27–33, n = 64), p 30±1.1 (28–34, n = 64). Dorsal (lateral) bars straight, with flattened medial extremity and thick cylindrical lateral extremity, length h 83, c 84±3.7 (74–90, n = 64), p 87±4.5 (79–99, n = 64), maximum width h 27, c 26±2.2 (20–31, n = 62), p 27±2.4 (21–33, n = 64). Ventral bar flat, massive, with slightly constricted median portion and blunt extremities, length h 114, c 117±4.1 (108–126, n = 31), p 118±5.2 (108–128, n = 32), maximum width h 23, c 23±2.3 (16–27, n = 30), p 24±2.6 (20–34, n = 32); groove visible on its ventral side.

Pharynx subspherical, length h 50, c 56±7.8 (35–70, n = 32), width h 44, c 46±5.1 (35–58, n = 32). Oesophagus apparently absent, such that intestinal bifurcation immediately follows pharynx. Caeca simple, terminate blindly at level of posterior margin of vitelline field.

Testis subspherical, intercaecal, length h 70, c 58 (35–75, n = 22), width h 50, c 66 (35–126, n = 22). Vas deferens emerges from antero-sinistral part of testis, enlarges into seminal vesicle; seminal vesicle in middle region of body, transforms into duct; duct forms bends then connects with quadriloculate organ; terminal portion of duct enlarged. Prostatic reservoir small, connects with quadriloculate organ. Quadriloculate organ with fourth (posterior) chamber slightly more sclerotised than 3 anterior chambers; fourth chamber ends in elongate sclerotised cone, prolonged by sclerotised tube; end of tube prolonged by thin unsclerotised filament of variable length. Inner length of quadriloculate organ h 51, c 57±2.6 (50–60, n = 31), p 70±6.3 (58–83, n = 33); cone length h 20, c 19±1.6 (17–23, n = 31), p 20±3.0 (15–32, n = 33); tube length h 23, c 22±1.6 (18–25, n = 29), p 21±2.3 (18–28, n = 30); tube diameter h 3, c 3.0±0.5 (3–4, n = 31), p 3.0±0.6 (3–4, n = 30); filament length h 47, c 0–48 (n = 28), p 0–45 (n = 30).

Ovary subequatorial, intercaecal, pre-testicular, encircles right caecum. Ovary width h 80, c 89 (65–115, n = 24). Oviduct passes medially to form oötype, surrounded by Mehlis' gland; oötype short, opens into uterus. Uterus dextral. Unsclerotised vagina often inconspicuous, elongate (Figure 3U,V). Duct from sclerotised vagina to oötype inconspicuous. Vitelline fields extend posteriorly from posterior to pharyngeal level in 2 lateral bands, confluent in post-testicular region and terminate anterior to peduncle. Bilateral connections from vitelline fields to oötype inconspicuous. Egg *in utero* oval, 103 (90–115) × 41 (28–54) (n = 4), with long filament.

Sclerotised vagina (nomenclature of parts according to Justine 2007a; see Figure 20). Sinistral, a complex sclerotised structure; aspect changes according to specimen and orientation (Figure 3). General shape resembling a "?" in dorsal view (Figure 3A–C). Sclerotised vagina comprises anterior trumpet, followed by primary canal, primary chamber and secondary chamber; trumpet in continuity with unsclerotised vagina; primary canal cone-shaped, coiled in its anterior part and straight in its posterior part; wall of anterior part thin, wall of posterior part thicker with distinct ring often visible at mid-length; canal continues into primary chamber;

primary chamber roughly spherical, aligned and in continuity with primary canal, more sclerotised and larger than it; thin longitudinal median wall in primary chamber, inserted posteriorly, visible in certain specimens (Figure 3A, B, I, M, Q, V, X); secondary canal inserted laterally on primary chamber; secondary chamber sclerotised, elongate, lateral to primary chamber; accessory structure, weakly sclerotised, inserted on secondary chamber and directed anteriorly. Duct from sclerotised vagina to oötype connects to secondary chamber (Figure 3 J,V). Total length of sclerotised vagina (measured from extremity of trumpet to extremity of primary chamber, i.e. not taking in account curved length along bend and coil of canal) h 35, c 34±1.6 (31–38, n = 32), p 33±3.2 (25–38, n = 33). Orientation of sclerotised vagina: trumpet always anterior.

Differential diagnosis. Three species, *Pseudorhabdosynochus huitoe* Justine, 2007 from *E. maculatus* off New Caledonia, and *P. shenzhenensis* Yang, Zeng & Gibson, 2005, *P. serrani* (Yamaguti, 1953) Kritsky & Beverley-Burton, 1986 (in its redescription by Yang *et al*. 2005), both from *E. coioides* off China share with *P. manifestus* the following characteristics of the sclerotised vagina: a conical primary canal (wider at the anterior part), with a single coil in its anterior part and a straight posterior part, and small primary and secondary chambers. (Table 2).

P. huitoe shares additional characteristics of the vagina with *P. manifestus*: a spherical primary chamber with thin longitudinal internal wall, and an elongate secondary chamber with distinct secondary canal. *P. manifestus* can be differentiated from this species by the posterior part of the primary canal, thick with distinct ring vs thin without ring, and longer vagina, 34 vs 25. Similarities also include ventral bar length, dorsal bar length, and a quadriloculate organ with long cone and long tube; however, measurements of the quadriloculate organ, ventral hamuli and dorsal hamuli are distinctly greater in *P. manifestus*. Clearly, these two species are very similar but can be distinguished on the basis of vagina structure and various measurements.

P. shenzhenensis and *P. serrani* also have a vagina with a primary canal coiled in its anterior part and a grossly similar shape of the chambers. In *P. serrani*, the measurements of dorsal and ventral bars are very similar to *P. manifestus*, but the species can be differentiated by measurements of ventral hamuli, dorsal hamuli, and quadriloculate organ which are distinctly greater in *P. manifestus*. *P. shenzhenensis* is easily differentiated from the three other species by its shorter ventral bar. Examination of specimens shows that the posterior part of the primary canal, in *P. shenzhenensis* and *P. serrani* do not show the distinctive ring of *P. manifestus*, and the shape of chambers are different. The tegumental scales might be an additional useful distinctive character.

Remarks on a juvenile specimen (Figure 5). Among the large number of specimens collected, several juvenile specimens were observed. We report observation on a specimen in which the sclerotised vagina was already fully formed, thus allowing identification of the species. Proportions of the body were very different from the adult, with a comparatively wider haptor (Figure 5A). Measurements were: body length 410 (61% of adult mean), width 100 (33%), haptor width 190 (77%). Sclerotised organs all showed measurements ranging 75–84% of their adult equivalents: ventral hamuli outer length 48, inner length 40, dorsal hamuli outer length 40, inner length 24, lateral bar length 64, ventral bar length 101, ventral squamodisc width 47, dorsal squamodisc width 43. Although growth of the male quadriloculate organ (inner length 57, 79% of adult mean) and sclerotised vagina (length 28, 82%) were similar in proportions, the development of these two organs was different. The sclerotised vagina was perfectly similar to an adult organ. The quadriloculate organ was very different, with more elongate general shape, thinner external walls, and the cone and tube were indistinguishable. The ovary was visible, but not the testis. These observations show that development of female organs precedes that of male organs in this species, and probably in other species of *Pseudorhabdosynochus*.

***Pseudorhabdosynochus malabaricus* n. sp.**
(Figs 6–8)

Type-host: *Epinephelus malabaricus* Bloch & Schneider (Serranidae).

Type-locality: Lagoon off Nouméa, New Caledonia.

Site: Between secondary gill lamellae.

Type-specimens: Holotype, JNC1536A107, off Ouen Toro, Nouméa, New Caledonia (22°19'S, 166°27'E, 18.v.2005).

Material examined: 9 specimens: 8 ‘carmine’ (c), 1 ‘picrate’ (p), all from JNC1536.

Material deposited: Holotype (c) and 6 paratypes (5 c, 1 p), MNHN; 1 paratype (c), BMNH 2007.6.1.4; 1 paratype (c), USNPC 99869;

Prevalence: 50% (1/2).

Intensity: See Table 1. A rare species (5% of the diplectanids).

Etymology: From the host name.

Description. Body very wide; length h 630, c 543 (450–650, n = 7), width h 390, c 317 (240–410, n = 7). Tegument scaly; posterior region with scales on ventral and dorsal faces from squamodiscs to level of ovary and testis. Anterior region with 3 pairs of head organs and 2 pairs of eye-spots; distance between outer margins of anterior eye-spot pair h 51, c 43 (37–51, n = 8), of posterior eye-spot pair h 44, c 40 (29–50, n = 8).

Haptor differentiated from rest of body, wider than body, width h 390, c 331 (270–420, n = 7), provided with 2 similar squamodiscs, 2 pairs of lateral hamuli, 3 bars and 14 marginal hooklets. Squamodiscs round in shape, made up of rows of rodlets; central row often dislocated; central rows forming almost closed ovals; rodlets adjacent and of similar width in all rows except last row with very thin, separated rodlets; ventral and dorsal squamodiscs similar, but ventral slightly larger; ventral squamodisc length c 63 (54–69, n = 6), width c 77 (74–79, n = 6), with 11–12 (n = 6) rows of rodlets and 1–2 closed ovals, total number of rodlets h 147; dorsal squamodisc, length h 65, c 64 (59–68, n = 6), width 79, c 71 (68–79, n = 6), with 10–12 (n = 6) rows of rodlets and 0–1 closed oval, total number of rodlets h 133. Ventral hamulus with thick handle and distinct guard, outer length h 62, c 58 (53–63, n = 13), p 61 (n = 2), inner length h 42, c 42 (39–45, n = 14), p 42 (n = 2). Dorsal hamulus with indistinct guard, outer length h 48, c 48 (45–50, n = 16), p 49 (n = 2), inner length h 31, c 30 (27–32, n = 16), p 29 (n = 2). Dorsal (lateral) bars straight, with flattened medial extremity and thick cylindrical lateral extremity, length h 118, c 113 (103–124, n = 15), p 128 (n = 2), maximum width h 23, c 24 (19–31, n = 15), p 26 (n = 2). Ventral bar flat, with slightly constricted median portion and pointed extremities, length h 140, c 132 (92–156, n = 7), p 150, maximum width h 17, c 17 (14–19, n = 7), p 20; groove visible on its ventral side.

Pharynx subspherical, length h 53, c 52 (43–75, n = 8), width h 54, c 49 (42–60, n = 8). Oesophagus apparently absent, such that intestinal bifurcation immediately follows pharynx. Caeca simple, terminate blindly at level of posterior margin of vitelline field.

Testis subspherical, intercaecal, length h 110, c 101 (83–110, n = 3), width h 110, c 90 (80–110, n = 3). Vas deferens emerges from antero-sinistral part of testis, enlarges into seminal vesicle; seminal vesicle in middle region of body, coiled, transforms into duct; duct forms bends then connects with quadriloculate organ; terminal portion of duct enlarged. Prostatic reservoir connects with quadriloculate organ. Quadriloculate organ with fourth (posterior) chamber slightly more sclerotised than 3 anterior chambers; first chamber with very thin anterior wall; fourth chamber ends in short sclerotised cone, prolonged by sclerotised tube; end of tube prolonged by thin unsclerotised filament of variable length. Inner length of quadriloculate organ h 57, c 52 (45–57, n = 7), p 75; cone length h 11, c 11 (10–11, n = 8), p 11; tube length h 15, c

16 (15–18, n = 8), p 16; tube diameter h 3, c 3 (n = 8), p 3; filament length h 4, c 0–19 (n = 8), p 5.

Ovary subequatorial, intercaecal, pre-testicular, encircles right caecum. Ovary width h 100, c 92 (74–114, n = 4). Oviduct passes medially to form oötype, surrounded by Mehlis' gland; oötype short, opens into uterus. Uterus dextral. Unsclerotised vagina inconspicuous. Duct from sclerotised vagina to oötype inconspicuous. Vitelline fields extend posteriorly from posterior to pharyngeal level in 2 lateral bands, confluent in post-testicular region and terminate anterior to peduncle. Bilateral connections from vitelline fields to oötype inconspicuous. Egg *in utero* oval, 115–124 × 56–65 (n = 2), with wall thicker at one extremity suggesting presence of filament in mature egg.

Sclerotised vagina (nomenclature of parts according to Justine 2007a; see Figure 20). Sinistral, a complex sclerotised structure; aspect changes according to specimen and orientation (Figure 7). Sclerotised vagina comprises anterior trumpet, followed by primary canal, big spherical primary chamber and small spherical secondary chamber; primary canal tubular, with posterior region slightly thinner than anterior region; primary canal with one coil (or bend) at midlength; primary canal connects to primary chamber on its ventral side; connection is oblique within wall (Figure 7E); primary chamber spherical with heavily sclerotised wall; internal wall, inserted laterally, visible in certain specimens (Figure 7C,F); secondary chamber ventral and adjacent to primary chamber, resulting in very short secondary canal; secondary chamber spherical, with wall less sclerotised than primary chamber; accessory structure, weakly sclerotised, ventral, connected to secondary chamber and directed anteriorly; total length of sclerotised vagina (measured from extremity of trumpet to posterior extremity, i.e. not taking in account curved length along bend and coil of canal) h 38, c 38 (34–44, n = 8), p 38; primary chamber external width h 13, c 13 (12–14, n = 8), p 16; primary chamber internal width h 9, c 9 (8–10, n = 8), p 12; secondary chamber external width h 8, c 8 (7–8, n = 8), p 9; primary chamber internal width h 5, c 5 (5–6, n = 8), p 6. Orientation of sclerotised vagina: trumpet always anterior.

Differential diagnosis. See after *P. maternus* **n. sp.**

***Pseudorhabdosynochus maternus* n. sp.**
(Figs 9–11)

Type-host: *Epinephelus malabaricus* Bloch & Schneider (Serranidae).

Type-locality: Lagoon off Nouméa, New Caledonia.

Site: Between secondary gill lamellae.

Type-specimens: Holotype, JNC1536A111, off Ouen Toro, Nouméa, New Caledonia (22°19'S, 166°27'E, 18.v.2005).

Material examined: 11 specimens: 10 'carmine' (c), 1 'picrate' (p), all from JNC1536.

Material deposited: Holotype (c) and 8 paratypes (7 c, 1 p), MNHN; 1 paratype (c), BMNH 2007.6.1.5; 1 paratype (c), USNPC 99870.

Prevalence: 50% (1/2).

Intensity: See Table 1. A rare species (7% of the diplectanids).

Etymology: refers to the local name of the host, 'mère loche' (Laboute & Grandperrin 2000) or 'mother grouper'.

Description. Body wide; length h 570, c 564 (450–690, n = 8), width h 320, c 320 (290–380, n = 8). Tegument scaly; posterior region with scales on ventral and dorsal faces from squamodiscs to level of ovary and testis. Anterior region with 3 pairs of head organs and 2 pairs of eye-spots; distance between outer margins of anterior eye-spot pair h 49, c 45 (33–61, n = 10), of posterior eye-spot pair h 45, c 38 (28–60, n = 10).

Haptor differentiated from rest of body, as wide as body, width h 300, c 290 (260–300, n = 6), provided with 2 similar squamodiscs, 2 pairs of lateral hamuli, 3 bars and 14 marginal hooklets. Squamodiscs round in shape, made up of rows of rodlets; central row often dislocated; central rows forming almost closed ovals; rodlets adjacent and of similar width in all rows except last row with very thin, separated rodlets; ventral and dorsal squamodiscs similar, but ventral slightly larger; ventral squamodisc length h 56, c 61 (56–66, n = 5), width h 69, c 68 (64–70, n = 5), with 11–12 (n = 6) rows of rodlets and 0–1 closed oval, total number of rodlets h 153; dorsal squamodisc, length h 52, c 58 (52–65, n = 8), width h 64, c 65 (60–72, n = 8), with 10–12 (n = 8) rows of rodlets and 0–1 closed oval, total number of rodlets h 147. Ventral hamulus with thick handle and distinct guard, outer length h 58, c 58 (50–63, n = 17), p 63 (n = 2), inner length h 44, c 44 (41–45, n = 16), p 42 (n = 2). Dorsal hamulus with indistinct guard, outer length h 50, c 47 (44–51, n = 17), p 48 (n = 2), inner length h 30, c 29 (28–32, n = 17), p 28 (n = 2). Dorsal (lateral) bars straight, with flattened medial extremity and thick cylindrical lateral extremity, length h 107, c 106 (101–110, n = 16), p 125 (n = 2), maximum width h 26, c 26 (21–28, n = 15), p 27 (n = 2). Ventral bar flat, with slightly constricted median portion and pointed extremities, length h 135, c 135 (127–141, n = 8), p 156, maximum width h 21, c 20 (14–24, n = 8), p 22; groove visible on its ventral side.

Pharynx subspherical, length h 53, c 51 (40–60, n = 10), width h 48, c 43 (36–55, n = 10). Oesophagus apparently absent, such that intestinal bifurcation immediately follows pharynx. Caeca simple, terminate blindly at level of posterior margin of vitelline field.

Testis subspherical, intercaecal, length h 85, c 74 (60–85, n = 4), width 56, c 72 (56–84, n = 4). Vas deferens emerges from antero-sinistral part of testis, enlarges into seminal vesicle; seminal vesicle in middle region of body, coiled, transforms into duct; duct forms bends, enlarges into small pyriform organ, then connects with quadriloculate organ. Prostatic reservoir inconspicuous, connects with quadriloculate organ. Quadriloculate organ with fourth (posterior) chamber slightly more sclerotised than 3 anterior chambers; first chamber with very thin anterior wall; fourth chamber ends in short sclerotised cone, prolonged by sclerotised tube; end of tube prolonged by thin unsclerotised filament of variable length. Inner length of quadriloculate organ h 44, c 45 (42–49, n = 9), p 61; cone length h 9, c 10 (9–12, n = 9), p 11; tube length h 18, c 18 (17–18, n = 9); tube diameter h 3, c 3 (n = 9), p 3; filament length h 5, c 0–16 (n = 9), p 0.

Ovary subequatorial, intercaecal, pre-testicular, encircles right caecum. Ovary width h 85, c 92 (75–128, n = 5). Oviduct passes medially to form oötype, surrounded by conspicuous Mehlis' gland; oötype short, opens into uterus. Uterus dextral. Unsclerotised vagina inconspicuous. Duct from sclerotised vagina to oötype inconspicuous. Vitelline fields extend posteriorly from posterior to pharyngeal level in 2 lateral bands, confluent in post-testicular region and terminate anterior to peduncle. Bilateral connections from vitelline fields to oötype inconspicuous. Egg *in utero* oval, 112–124 × 38–52 (n = 4), with wall thicker at one extremity suggesting presence of filament in mature egg.

Sclerotised vagina (nomenclature of parts according to Justine 2007a; see Figure 20). Sinistral, a complex sclerotised structure; aspect changes according to specimen and orientation (Figure 10). Sclerotised vagina comprises anterior trumpet, followed by primary canal, big spherical primary chamber and small spherical secondary chamber; anterior edge of trumpet ornamented with longitudinal (or radial) ribs; primary canal tubular, with posterior region slightly thinner than anterior region; primary canal with one coil (or bend) at midlength; canal connects to primary chamber; primary chamber spherical with heavily sclerotised wall; transverse internal wall visible in most specimens (Figure 9C,D, 10); secondary chamber ventral and adjacent to primary chamber, resulting in very short secondary canal; secondary chamber roughly spherical, with wall less sclerotised than primary chamber; accessory structure weakly sclerotised, ventral, curved, connected to secondary chamber, directed anteriorly; total length of sclerotised vagina (measured from extremity of trumpet to posterior extremity, i.e. not taking in

account curved length along bend and coil of canal) h 29, c 28 (19–35, n = 10), p 31; primary chamber external width h 9, c 9 (8–10, n = 10), p 10; primary chamber internal width h 6, c 6 (6–7, n = 10), p 8; secondary chamber external width h 5, c 5 (4–6, n = 10), p 6; primary chamber internal width h 3, c 3 (2–4, n = 10), p 3. Orientation of sclerotised vagina: trumpet always anterior.

Differential diagnosis (in common with *P. malabaricus*). *P. malabaricus* and *P. maternus* share the following characteristics of the sclerotised vagina: an anterior trumpet, a primary canal with a bend, a conspicuous heavily sclerotised primary chamber, and a smaller secondary chamber. Comparisons are here restricted to species with a distinct primary canal and large, heavily sclerotised chambers.

P. auitoe Justine, 2007 and *P. duitoe* Justine, 2007, both from *E. maculatus* off New Caledonia, have a straight primary canal, vs coiled.

P. fuitoe Justine, 2007, from *E. maculatus* off New Caledonia, has a long, heavily sclerotised, secondary canal, vs very short.

P. venus Hinsinger & Justine, 2006 from *E. howlandi* off New Caledonia, has a pear-shaped primary chamber (vs round) and the vagina is very large (total length 55) (Hinsinger & Justine 2006a).

P. vagampullum (Young, 1969) Kritsky & Beverley-Burton, 1986 from *E. quoyanus* off South China, in its redescription by Zeng & Yang (2007), has a wide straight primary canal (vs thin and coiled) and a very small secondary chamber (secondary chamber not seen in the original description nor in the redescription by Beverley-Burton & Suriano (1981) and Justine (2005a).

A species of *Pseudorhabdosynochus* from *Cephalopholis sonnerati* off New Caledonia has a vagina with coiled primary canal and round primary and secondary chambers connected by a very short secondary canal; however, the chambers are smaller, and the species is characterised by very small body size (Justine 2007b).

Differentiation of *P. malabaricus* and *P. maternus* from all these species is thus easy, based on the characters mentioned above; in addition, none of these species has the proportion and shapes of the chambers of these two species.

The two new species *P. malabaricus* and *P. maternus* are similar for many measurements, ventral and dorsal hamulus length, ventral bar length, and only slightly different for lateral bar length (113 vs 106); for the quadriloculate organ, proportions and measurements of cone and tube are similar, but inner length is slightly greater in *P. malabaricus* (52 vs 45). The general structure of the vagina is very similar in both species. Distinction can be done on the following characters: trumpet ornamented with ribs in *P. maternus* (vs unornamented in *P. malabaricus*); size of chambers, greater in *P. malabaricus* (primary chamber 13 vs 9, secondary chamber 8 vs 5); vagina length, greater in *P. malabaricus* (38 vs 28), with minimal overlap. These two species are probably closely related.

***Pseudorhabdosynochus manipulus* n. sp.**
(Figs 12–14)

Type-host: *Epinephelus malabaricus* Bloch & Schneider (Serranidae).

Type-locality: Lagoon off Nouméa, New Caledonia.

Site: Between secondary gill lamellae.

Type-specimens: Holotype, JNC1536A101, off Ouen Toro, Nouméa, New Caledonia (22°19'S, 166°27'E, 18.v.2005).

Material examined: 9 specimens: 2 ‘carmine’ (c), 7 ‘picrate’ (p).

Material deposited: Holotype (c) and 8 paratypes (1 c, 7 p), MNHN.

Prevalence: 50% (1/2).

Intensity: See Table 1. A rare species (5% of the diplectanids).

Etymology: From '*manipulus*' (Latin), handful, refers to the small number of specimens found.

Description. [Given as holotype, other carmine specimen, picrate specimens]. Body wide; length h 600, c 610, width h 400, c 400. Tegument scaly; posterior region with scales on ventral and dorsal faces from squamodiscs to level of ovary and testis; scales relatively large. Anterior region with 3 pairs of head organs and 2 pairs of eye-spots; distance between outer margins of anterior eye-spot pair h 40, c 39, of posterior eye-spot pair h 41, c 39.

Haptor differentiated from rest of body, less wide than body, width h 290, c 270, provided with 2 similar squamodiscs, 2 pairs of lateral hamuli, 3 bars and 14 marginal hooklets. Squamodiscs round in shape, made up of rows of rodlets; central rows forming almost closed ovals; rodlets of central rows with external face crenate; rodlets progressively thinner from centre to periphery; rodlets adjacent in all rows except last; last row with very thin, separated rodlets; ventral and dorsal squamodiscs similar, but ventral slightly larger; ventral squamodisc length h 69, c 61, width h 68, c 70, with 10–11 (n = 2) rows of rodlets and 0–1 closed oval, total number of rodlets h 105; dorsal squamodisc, length h 67, c 62, width h 64, c 63, with 12 (n = 2) rows of rodlets and 0 closed oval, total number of rodlets h 109. Ventral hamulus with thick handle and distinct guard, outer length h 59, c 62, p 63 (60–66, n = 14), inner length h 49, c 51, p 50 (48–54, n = 14). Dorsal hamulus with indistinct guard, outer length h 50, c 51, p 50 (48–52, n = 14), inner length h 29, c 30, p 32 (30–33, n = 14). Dorsal (lateral) bars straight, with flattened medial extremity and thick cylindrical lateral extremity, length h 93, c 94, p 99 (93–108, n = 14), maximum width h 25, c 26, p 26 (24–30, n = 12). Ventral bar flat, with slightly constricted median portion and pointed extremities, length h 132, c 131, p 133 (124–138, n = 7), maximum width h 21, c 25, p 24 (23–26, n = 7); groove visible on its ventral side.

Pharynx subspherical, length h 63, c 62, width h 47, c 46. Oesophagus apparently absent, such that intestinal bifurcation immediately follows pharynx. Caeca simple, terminate blindly at level of posterior margin of vitelline field.

Testis subspherical, intercaecal, length c 53, width c 75. Vas deferens emerges from antero-sinistral part of testis, enlarges into seminal vesicle; seminal vesicle in middle dextral region of body, transforms into duct; duct forms bends then connects with quadriloculate organ. Prostatic reservoir small, connects with quadriloculate organ. Quadriloculate organ with fourth (posterior) chamber slightly more sclerotised than 3 anterior chambers; fourth chamber ends in short sclerotised cone, prolonged by sclerotised tube; end of tube prolonged by thin unsclerotised filament of variable length. Inner length of quadriloculate organ h 60, c 60, p 70 (64–77, n = 6); cone length h 17, c 17, p 20 (18–21, n = 7); tube length h 18, c 19, p 18 (15–19, n = 6); tube diameter h 4, c 4, p 4 (3–4, n = 6); filament length h 0, c 30, p 3–38 (n = 6).

Ovary subequatorial, intercaecal, pre-testicular, encircles right caecum. Ovary width c 122. Oviduct passes medially to form oötype, surrounded by Mehlis' gland; oötype short, opens into uterus. Uterus dextral. Unsclerotised vagina often inconspicuous, elongate (Figure 13F). Duct from sclerotised vagina to oötype inconspicuous. Vitelline fields extend posteriorly from posterior to pharyngeal level in 2 lateral bands, confluent in post-testicular region and terminate anterior to peduncle. Bilateral connections from vitelline fields to oötype inconspicuous. Egg *in utero* oval, 127 × 53 (n = 1), with wall thicker at one extremity suggesting presence of filament in mature egg.

Sclerotised vagina (nomenclature of parts according to Justine 2007a; see Figure 20). Sinistral, a complex sclerotised structure; aspect changes according to specimen and orientation (Figure 13). Sclerotised vagina comprises anterior trumpet, followed by primary canal, primary chamber and secondary chamber; trumpet in continuity with unsclerotised vagina; primary canal cylindrical, coiled or bent once in its anterior part and straight in its posterior part; wall of anterior part thin, wall of posterior part slightly thicker; canal in continuity and aligned with

primary chamber; primary chamber elongate, with wall no more sclerotised than primary canal; thin longitudinal median wall in primary chamber, inserted at mid-length, visible in certain specimens (Figure 13 B,G); secondary canal curved, inserted laterally on anterior extremity of primary chamber; secondary chamber elongate, S-shaped, more sclerotised than primary chamber and primary canal, inserted grossly perpendicularly to axis of primary canal and primary chamber; accessory structure inserted on extremity of secondary chamber. Duct from sclerotised vagina to oötype connects to secondary chamber (Figure 13D,E). Total length of sclerotised vagina (measured from extremity of trumpet to extremity of primary chamber, i.e. not taking in account curved length along bend and coil of canal) h 39, c 35, p 38 (33–43, n = 7). Orientation of sclerotised vagina: trumpet always anterior.

Differential diagnosis. Several species of *Pseudorhabdosynochus* have a sclerotised vagina similar to that of *P. manipulus* **n. sp.** in general structure, with an anterior trumpet, a primary canal with a bend in its anterior part, a primary chamber aligned and in continuity with the primary canal, and a secondary chamber inserted laterally.

P. melanesiensis (Laird, 1958) from *E. merra* Bloch, *P. cupatus* (Young, 1969) from *Epinephelus fasciatus* (Forsskål), *P. calathus* Hinsinger & Justine 2006 from *E. rivulatus* (Valenciennes) and *P. cyathus* Hinsinger & Justine, 2006 from *E. howlandi* (Valenciennes), all from off New Caledonia and other localities, have a grossly similar vagina but their secondary chamber is more complex than *P. manipulus*; in addition, these species have a special ‘telescopic” arrangement of their squamodisc (‘lamellosquamodisc’) in the three later species, and their haptoral parts are smaller (Justine 2005a; Hinsinger & Justine 2006b).

P. hirundineus Justine, 2005 from *Variola louti* (Forsskål) off New Caledonia (Justine, 2005b) and *P. epinepheli* (Yamaguti, 1938) from *E. akaara* (Temminck & Schlegel) off Japan and in South China Sea have a vagina similar to *P. manipulus*, with a lateral insertion of the secondary chamber, but the primary chamber is oriented anteriorly by a second bend of the primary canal (Kritsky & Beverley-Burton 1986).

P. euitoe Justine, 2007 from *E. maculatus* has a vagina similar to *P. manipulus* by the general arrangement of primary canal, distal primary chamber and laterally inserted secondary chamber; however, the primary chamber is more sclerotised, the secondary chamber is round vs elongate, and there is a heavy sclerotised ring on the trumpet.

P. manifestus, *P. huitoe*, *P. serrani* and *P. shenzhenensis* have a general structure of the vagina similar to that of *P. manipulus*. However, the shape of the primary chamber is round vs elongate, and the insertion of the secondary chamber is more distal.

P. manipulus can be differentiated from all these species by the structure of its sclerotised vagina.

***Pseudorhabdosynochus marcellus* n. sp.**
(Figs 15–16)

Type-host: *Epinephelus malabaricus* Bloch & Schneider (Serranidae).

Type-locality: Lagoon off Nouméa, New Caledonia.

Site: Between secondary gill lamellae.

Type-specimens: Holotype, JNC1536A104, off Ouen Toro, Nouméa, New Caledonia (22°19'S, 166°27'E, 18.v.2005).

Material examined: 2 specimens in carmine.

Material deposited: Holotype (c) and 1 paratype, MNHN.

Prevalence: 50% (1/2).

Intensity: See Table 1. A very rare species (1 % of the diplectanids).

Etymology: refers to a character of a well-known Caledonian cartoon, Tonton Marcel.

Description. [Measurements given for holotype (h) and paratype (c)]. Body elongate; length h 590, c 580, width h 230, c 280. Tegument scaly; posterior region with scales on ventral and dorsal faces from squamodiscs to level of ovary and testis. Anterior region with 3 pairs of head organs and 2 pairs of eye-spots; distance between outer margins of anterior eye-spot pair h 36, c 37, of posterior eye-spot pair h 33, c 40.

Haptor differentiated from rest of body, as wide as body, width h 250, c 290, provided with 2 similar squamodiscs, 2 pairs of lateral hamuli, 3 bars and 14 marginal hooklets. Squamodiscs observed only in holotype; round in shape, made up of rows of rodlets; central rows forming almost closed ovals; rodlets progressively thinner from centre to periphery; rodlets adjacent in central rows, separated in peripheral rows; last row with very thin, separated rodlets; ventral and dorsal squamodiscs similar, but ventral slightly larger; ventral squamodisc length h 44, width h 50, with 9 rows of rodlets and 1 closed oval, total number of rodlets h 59; dorsal squamodisc, length h 44, width 36, with 10 rows of rodlets and 1 closed oval, total number of rodlets h 46. Ventral hamulus with distinct handle and guard, outer length h 54, c 54, inner length h 46, c 46. Dorsal hamulus with indistinct guard, outer length h 47, c 47, inner length h 28, c 29. Dorsal (lateral) bars straight, with flattened medial extremity and thick cylindrical lateral extremity, length h 86, c 90, maximum width h 25, c 24. Ventral bar flat, with slightly constricted median portion and blunt extremities, length h 106, c 111, maximum width h 20, c 22; groove visible on its ventral side.

Pharynx subspherical, length h 50, c 47, width h 43, c 40. Oesophagus apparently absent, such that intestinal bifurcation immediately follows pharynx. Caeca simple, terminate blindly at level of posterior margin of vitelline field.

Testis subspherical, intercaecal, length h 70, c 55, width h 55, c 45. Vas deferens inconspicuous; seminal vesicle in middle region of body, transforms into duct. Very small prostatic reservoir and inconspicuous prostatic duct both connect with quadriloculate organ. Quadriloculate organ with fourth (posterior) chamber as sclerotised as 3 anterior chambers; fourth chamber ends in very elongate sclerotised cone, prolonged by sclerotised tube; end of tube prolonged by thin unsclerotised filament of variable length. Inner length of quadriloculate organ h 42, c 42; cone length h 25, c 25; tube length h 21, c 20; tube diameter h 3, c 3; filament length h 49, c 3.

Ovary subequatorial, intercaecal, pre-testicular, encircles right caecum. Ovary width h 75, c 80. Oviduct passes medially to form oötype, surrounded by Mehlis' gland; oötype short, opens into uterus. Uterus dextral. Unsclerotised vagina inconspicuous. Duct from sclerotised vagina to oötype inconspicuous. Vitelline fields extend posteriorly from posterior to pharyngeal level in 2 lateral bands, confluent in post-testicular region and terminate anterior to peduncle. Bilateral connections from vitelline fields to oötype inconspicuous. Egg unknown.

Sclerotised vagina (nomenclature of parts according to Justine 2007a; see Figure 20). Sinistral, a complex sclerotised structure. Sclerotised vagina comprises anterior trumpet, followed by primary canal, primary chamber and secondary chamber; primary canal cylindrical, bent once in its anterior part and once in its posterior part; anterior part (before first bend) cylindrical, with very thin wall; median part (between bends), cylindrical with sclerotised wall; posterior part (forming posterior bend) with small diameter and thin wall; primary chamber in continuity with primary canal; primary and secondary chamber embedded in same distal heavily sclerotised part, thus secondary canal absent; accessory structure connects to distal sclerotised part. Total length of sclerotised vagina (measured from anterior extremity of first bend of primary canal to posterior extremity of second bend of primary canal, i.e. not taking in account curved length along bend and coil of canal) h 32, c 35. Orientation of sclerotised vagina: first bend of primary canal anterior.

Differential diagnosis. Several species have a sclerotised vagina with a long primary canal with a bend in the anterior part and a second bend in the posterior part, and the chambers small and apparently united in a common sclerotised part.

A species of *Pseudorhabdosynochus* from *Cephalopholis argus* off New Caledonia and Australia (Justine 2007b) has a vagina with structure and measurements similar to *P. marcellus*, but can be distinguished by more numerous squamodisc rodlets (80–90 vs 46–59), and a massive and shorter ventral bar (73 vs 109).

P. lantauensis (Beverley-Burton & Suriano, 1981) from *E. bruneus* Bloch and *E. longispinis* (Kner) has a vagina (see redescription in Justine, 2005a) which shares with *P. marcellus* a similar structure, a quadriloculate organ with a very long cone and squamodiscs with small numbers of rows (9–10) and rodlets (60); however, the anterior bend of its primary canal is double, not simple. Clearly, these species are closely related but can be differentiated on the basis of vaginal structure.

P. marcellus can be differentiated from all other species of *Pseudorhabdosynochus* by its vaginal structure.

***Pseudorhabdosynochus maaensis* n. sp.**
(Figs 17–18)

Type-host: *Epinephelus malabaricus* Bloch & Schneider (Serranidae).

Type-locality: Lagoon of New Caledonia.

Site: Between secondary gill lamellae.

Type-specimens: Holotype, JNC2130A85, Baie Maa, New Caledonia (22°12’780S, 166°19’933E, 9.iii.2007).

Material examined: 10 specimens: 9 ‘carmine’ (c), 1 ‘picrate’ (p).

Material deposited: Holotype (c) and 7 paratypes (6 c, 1 p), MNHN; 1 paratype (c), BMNH 2007.x.x.x.x; 1 paratype (c), USNPC xxxxx.

Prevalence: 50% (1/2).

Intensity: See Table 1. A rare species (7% of the diplectanids).

Etymology: refers to the locality.

Description. [Given as holotype, mean of carmine specimens, picrate specimen]. Body elongate, length h 450, c 498 (435–570, n = 8), width h 125, c 154 (115–200, n = 9). Tegument scaly; posterior region with scales on ventral and dorsal faces from squamodiscs to level of ovary and testis. Anterior region with 3 pairs of head organs and 2 pairs of eye-spots; distance between outer margins of anterior eye-spot pair h 24, c 26 (20–34, n = 9), of posterior eye-spot pair h 21, c 24 (18–28, n = 9).

Haptor differentiated from rest of body, wider than body, width h 160, c 181 (160–210, n = 7), provided with 2 similar squamodiscs, 2 pairs of lateral hamuli, 3 bars and 14 marginal hooklets. Squamodiscs round in shape, made up of rows of rodlets; central rows forming almost closed ovals; rodlets progressively thinner from centre to periphery; rodlets adjacent in all rows except last; last row with very thin, separated rodlets; ventral and dorsal squamodiscs similar, but ventral slightly larger; ventral squamodisc length h 44, c 44 (38–51, n = 7), width h 48, c 45 (40–50, n = 7), with 10 (n = 7) rows of rodlets and 0–2 closed ovals, total number of rodlets h 72; dorsal squamodisc, length c 40 (39–40, n = 2), width c 37 (35–39, n = 2), with 10–13 (n = 6) rows of rodlets and 0–2 closed ovals, total number of rodlets h 76. Ventral hamulus with distinct handle and guard, outer length h 42, c 42 (40–44, n = 18), p 45 (n = 2), inner length h 34, c 35 (33–37, n = 18), p 35 (n = 2). Dorsal hamulus with indistinct guard, outer length h 38, c 39 (36–40, n = 17), p 40 (n = 2), inner length h 24, c 24 (22–26, n = 17), p 24 (n = 2). Dorsal (lateral) bars straight, with flattened medial extremity and cylindrical lateral extremity, length h 51, c 51 (46–54, n = 18), p 55 (n = 2), maximum width h 15, c 15 (13–17, n = 8), p 16 (n = 2). Ventral bar flat, with slightly constricted median portion and pointed extremities, length h 78, c 79 (74–

86, n = 9), p 90, maximum width h 14, c 14 (14–15, n = 3), p 13; groove visible on its ventral side.

Pharynx subspherical, length h 32, c 32 (28–36, n = 9), width h 30, c 31 (28–36, n = 9). Oesophagus apparently absent, such that intestinal bifurcation immediately follows pharynx. Caeca simple, terminate blindly at level of posterior margin of vitelline field.

Testis subspherical, intercaecal, length h 39, c 54 (39–68, n = 6), width h 43, c 54 (34–75, n = 6). Vas deferens inconspicuous; seminal vesicle in middle region of body, transforms into duct; duct forms bends then enlarges into small pyriform organ, then connects with quadriloculate organ. Prostatic reservoir small, connects with quadriloculate organ. Quadriloculate organ with fourth (posterior) chamber slightly more sclerotised than 3 anterior chambers; fourth chamber ends in long sclerotised cone, prolonged by sclerotised tube; end of tube prolonged by thin unsclerotised filament of variable length. Inner length of quadriloculate organ h 33, c 34 (32–36, n = 9), p 44; cone length h 17, c 17 (16–20, n = 9), p 16; tube length h 15, c 14 (12–15, n = 9), p 15; tube diameter h 2, c 2 (2–3, n = 9), p 2; filament length h 2, c 0–14 (n = 9), p 0.

Ovary subequatorial, intercaecal, pre-testicular, encircles right caecum. Ovary width h 42, 47 (37–60, n = 6). Oviduct passes medially to form oötype, surrounded by inconspicuous Mehlis' gland; oötype short, opens into uterus. Uterus dextral. Unsclerotised vagina inconspicuous. Duct from sclerotised vagina to oötype inconspicuous. Vitelline fields extend posteriorly from posterior to pharyngeal level in 2 lateral bands, confluent in post-testicular region and terminate anterior to peduncle. Bilateral connections from vitelline fields to oötype inconspicuous. Egg unknown.

Sclerotised vagina (nomenclature of parts according to Justine 2007a, see Figure 20). Sinistral, a complex sclerotised structure; aspect slightly changes according to specimen and orientation (Figure 18). Sclerotised vagina comprises anterior trumpet, followed by primary canal, and distal heavily sclerotised part including primary chamber and secondary chamber; primary canal cylindrical, coiled or bend once in its anterior part and straight in its posterior part; wall of anterior part thin, wall of posterior part slightly thicker; canal in continuity with primary chamber; primary chamber globular; thin internal wall in primary chamber, inserted posteriorly of obliquely, visible in certain specimens (Figure 17C, 18A,E,F); secondary canal very short; secondary chamber small, sometimes with two parts; accessory structure weakly sclerotised, curved, inserted on secondary chamber. Duct from sclerotised vagina to oötype inconspicuous. Total length of sclerotised vagina (measured from anterior extremity to posterior extremity of distal sclerotised part, i.e. not taking in account curved length along bend and coil of canal) h 45, c 43 (40–46, n = 9), p 44. Orientation of sclerotised vagina: bend of primary canal always anterior.

Differential diagnosis. *P. manifestus*, *P. huitoe*, *P. serrani*, and *P. shenzhenensis* share with *P. maaensis* the general structure of the vagina, with a long primary canal with anterior bend and primary and secondary chamber small in a common sclerotised part. However, proportions are very different: *P. maaensis* is characterised by a cylindrical (vs conical in the four other species) primary canal, with constant diameter along its length. Its vagina is longer than all four other species (Table 2). In addition, *P. maaensis* has small squamodiscs with a small number of rodlets.

***Pseudorhabdosynochus* cf. *shenzhenensis* Yang, Zeng & Gibson, 2005**
(Figure 19)

Host: *Epinephelus malabaricus* Bloch & Schneider (Serranidae).

Type-Host: *Epinephelus coioides* (Hamilton)

Locality: Lagoon of New Caledonia.

Site: Between secondary gill lamellae.

Material examined: 2 specimens in picrate, MNHN JNC2130A5, JNC2130A6, Baie Maa, New Caledonia (22°12'780S, 166°19'933E, 9.iii.2007)

Prevalence: 50% (1/2).

Intensity: See Table 1. A rare species (1.5% of the diplectanids).

Description. Body length 370–420, width 220–250. Tegumental scales apparently absent. Anterior region with 2 pairs of eye-spots; distance between outer margins of anterior eye-spot pair 36, of posterior eye-spot pair 30–32.

Haptor differentiated from rest of body, width 170–230, provided with 2 similar squamodiscs, 2 pairs of lateral hamuli, 3 bars and 14 marginal hooklets. Squamodiscs deformed in available specimens, made up of rows of rodlets; central rows forming almost closed ovals; rodlets progressively thinner from centre to periphery; rodlets adjacent in central rows, separated in peripheral rows; last row with very thin, separated rodlets; ventral and dorsal squamodiscs similar; ventral squamodisc length 28–29, width 40–50 with 9 rows of rodlets and 1 closed oval, total number of rodlets 64; dorsal squamodisc, length 38, width 26, with 10 rows of rodlets and 1 closed oval, total number of rodlets 55. Ventral hamulus with distinct handle and guard, outer length 45, inner length 35. Dorsal hamulus with indistinct guard, outer length 38, inner length 22. Dorsal (lateral) bars straight, with flattened medial extremity and cylindrical lateral extremity, length 63–66, maximum width 19. Ventral bar flat, with slightly constricted median portion and pointed extremities, length 68–75, maximum width 15–16; groove visible on its ventral side.

Pharynx subspherical, length 30–35, width 26–29. Caeca not seen in picrate specimens.

Testis subspherical, intercaecal, length 70, width 45. Vas deferens, seminal vesicle, prostatic reservoir not seen. Quadriloculate organ with fourth (posterior) chamber as sclerotised as 3 anterior chambers; fourth chamber ends in elongate sclerotised cone, prolonged by sclerotised tube; end of tube prolonged by thin unsclerotised filament of variable length. Inner length of quadriloculate organ 40–42; cone length 15–16; tube length 12–13; tube diameter 2; filament length 4–10.

Ovary subequatorial, intercaecal, pre-testicular. Ovary width 80. Uterus dextral. Unsclerotised vagina inconspicuous. Duct from sclerotised vagina to oötype inconspicuous. Vitelline fields extend posteriorly from posterior to pharyngeal level in 2 lateral bands and terminate anterior to peduncle. Egg unknown.

Sclerotised vagina (nomenclature of parts according to Justine 2007a, see Figure 20). Sinistral, a complex sclerotised structure. Sclerotised vagina comprises anterior trumpet, followed by primary canal, and distal heavily sclerotised part; primary canal conical, bent once in its anterior part and once in its posterior part; wall of primary canal progressively thinner from trumpet to posterior extremity; primary chamber embedded in distal heavily sclerotised part; secondary chamber and secondary canal not seen; accessory structure weakly sclerotised, connects to distal sclerotised part. Total length of sclerotised vagina (measured from anterior to posterior extremity, i.e. not taking in account curved length along bend and coil of canal) 20–22. Orientation of sclerotised vagina: trumpet anterior.

Remarks. Only two specimens of this species could be examined, and they were both picrate slides. We are not completely convinced that these specimens are conspecific with *P. shenzhenensis* Yang, Zeng & Gibson, 2005, described from *E. coioides* off South China, and identification as *P.* cf *shenzhenensis* is only provisional. Observations of more numerous

specimens, and particularly of carmine preparations, could reveal that this is a new species. The structure of the vagina, with conical bent primary canal and small chambers, is similar to that of *P. shenzhenensis*, but not exactly the same: the primary chamber seems more elongate in *P. shenzhenensis* than in this material.

Genus *Diplectanum* Diesing

Diplectanum maa n. sp.

(Figs 21–22)

Type-host: *Epinephelus malabaricus* Bloch & Schneider (Serranidae).

Type-locality: Lagoon of New Caledonia.

Site: Between secondary gill lamellae.

Type-specimens: Holotype, JNC2130A59, Baie Maa, New Caledonia (22°12'780S, 166°19'933E, 9.iii.2007).

Material examined: 29 specimens: 22 'carmine' (c), 7 'picrate' (p).

Material deposited: Holotype (c) and 26 paratypes (19 c, 7 p), MNHN; 1 paratype (c), BMNH 2007.6.1.6; 1 paratype (c), USNPC 99871; 1 paratype (c), HCPI M-441.

Prevalence: 50% (1/2).

Intensity: See Table 1. A relatively abundant species (22% of the diplectanids) in one of the fish examined.

Etymology: refers to type locality; indeclinable.

Description. Body elongate; length h 520, c 475 (440–550, n = 10), width at level of ovary h 250, c 209 (160–250, n = 11). Tegument apparently smooth (no tegumental scales). Anterior region with 3 pairs of head organs and 2 pairs of eye-spots; distance between outer margins of anterior eye-spot pair h 40, c 34 (24–42, n = 12), of posterior eye-spot pair h 36, c 31 (23–42, n = 12).

Haptor differentiated from rest of body, less wide than body, width h 180, c 171 (140–210, n = 10), provided with 2 similar squamodiscs, 2 pairs of lateral hamuli, 3 bars and 14 marginal hooklets. Squamodiscs small, made up of rows of small rodlets; central rows forming almost closed ovals; rodlets progressively thinner from centre to periphery; rodlets adjacent in central rows, separated in peripheral rows; ventral squamodisc round in shape, length h 34, c 33 (28–35, n = 3), width h 27, c 30 (27–34, n = 3), with 9–12 rows of rodlets (n = 3) with 0–1 closed oval, total number of rodlets h 65; dorsal squamodisc round in shape, length h 29, c 33 (28–36, n = 4), width h 33, c 34 (32–35, n = 4), with 10–12 rows of rodlets (n = 4) with 0–1 closed oval, total number of rodlets h 64. Ventral hamulus with distinct guard and handle, outer length h 45, c 46 (42–50, n = 22), p 49 (48–51, n = 8), inner length h 40, c 40 (37–43, n = 22), p 40 (31–43, n = 8). Dorsal hamulus with indistinct guard and handle, outer length h 41, c 41 (38–42, n = 22), p 42 (39–43, n = 8), inner length h 24, c 24 (23–25, n = 22), p 26 (23–30, n = 8). Dorsal (lateral) bars with flattened medial extremity and cylindrical lateral extremity, length h 57, c 57 (54–62, n = 22), p 60 (55–62, n = 8), maximum width h 19, c 18 (14–21, n = 22), p 19 (16–23, n = 7). Ventral bar flat, massive with blunt extremities, length h 66, c 72 (66–78, n = 11), p 77 (73–81, n = 3), maximum width h 18, c 18 (16–20, n = 9), p 19 (18–19, n = 3); groove visible on its ventral side.

Pharynx subspherical, length h 38, c 40 (35–46, n = 12), width h 41, c 39 (34–48, n = 12). Oesophagus apparently absent, such that intestinal bifurcation immediately follows pharynx. Caeca simple, terminate blindly at level of posterior margin of vitelline field.

Testis subspherical, intercaecal, length h 34, c 35 (25–55, n = 11), width h 62, c 57 (39–85, n = 11). Sclerotised male copulatory organ (MCO) a small tubular penis; no accessory part. Penis 'spoon-shaped', a funnel, made up of anterior cone and straight posterior tube of regular diameter; tube oriented in same axis as cone or slightly oblique. Within penis anterior cone, 4 very thin transverse walls limit 4 chambers. Posterior protruding cirrus visible in certain specimens (Figure 22A,G). Penis length h 36, c 36 (34–38, n = 12), p 34 (31–36, n = 5); maximum diameter h 14, c 13 (12–15, n = 12), p 12 (11–14, n = 5); tube diameter h 4, c 4 (4–5, n = 12), p 4 (4–5, n = 5).

Ovary subequatorial, intercaecal, pre-testicular, encircles right caecum. Ovary width h 102, c 78 (65–102, n = 11). Oviduct passes medially to form oötype, surrounded by Mehlis' gland; oötype short, opens into uterus. Uterus dextral. Vitelline fields extend posteriorly from posterior to pharyngeal level in 2 lateral bands, confluent in post-testicular region and terminate anterior to peduncle. Bilateral connections from vitelline fields to oötype inconspicuous. Egg unknown.

Differential diagnosis and generic status. This species belongs to a group of diplectanids from groupers (Epinephelinae) which are provisorily attributed (Justine 2007a) to *Diplectanum* Diesing. The group already includes three species: *D. grouperi* Bu, Leong, Wong, Woo & Foo, 1999 from *E. coioides* off Malaysia and South China, *D. uitoe* Justine, 2007 from *E. maculatus* off New Caledonia, and a species from *Cephalopholis sonnerati* (Justine 2007b). In this group, the MCO is similar to the spoon-shaped or funnel-shaped penis of members of *Laticola* Yang, Kritsky, Sun, Zhang, Shi & Agrawal, 2006, but the described species of *Laticola* have much larger male copulatory organs (Yang *et al*. 2006; Journo & Justine 2006) and a characteristic vaginal structure, not seen in this group.

Table 4 compares the species of diplectanids from groupers provisorily attributed to *Diplectanum*.

D. grouperi is different from *D. maa* by its shorter MCO.

D. uitoe has a MCO of similar length but can be differentiated from *D. maa* by larger squamodiscs, more numerous rodlets, and presence of 'spurs' on the rodlets; in addition, its ventral and dorsal hamuli are smaller.

The species from *C. sonnerati* can be distinguished from *D. maa* by shorter MCO, smaller body size, and a dorsal squamodisc very different from the ventral; in addition, the dorsal and ventral bars are thinner and more elongate, and the ventral and dorsal hamuli are smaller.

D. maa can thus be differentiated from all species already described of this group of '*Diplectanum'* from groupers; characters of the squamodiscs and haptoral hard parts are necessary to identify these species, which have inconspicuous female organs and very similar male organs.

Comments on the monogenean fauna of *E. malabaricus* and a comparison with other groupers

Size of monogeneans and of their attachment apparatus might be an important factor for their repartition. Table 3 shows that the *Pseudorhabdosynochus* species of *E. malabaricus* can be separated in two groups: a group of five 'large' species (*P. manifestus*, *P. malabaricus*, *P. maternus*, *P. manipulus*, *P. marcellus*) and a group of two 'small' species (*P. maaensis* and *P.* cf. *shenzhenensis*) with smaller body length (395–198 vs 564–665 µm), smaller ventral hamuli (42–45 vs 54–60 µm) and shorter ventral bar (72–79 vs 109–135 µm). We collected

monogeneans at random and did not record exact location of specimens; it might be that these two groups exploit each a specific region of the secondary gill lamellae.

As concerns relative abundance of species, the monogenean fauna of *E. malabaricus* consists of an abundant species (*P. manifestus*) and a series of rare species (*P. malabaricus*, *P. maternus*, *P. manipulus*, *P. marcellus*, *P. maaensis*, *P.* cf. *shenzhenensis*, *Haliotrema* sp. 2, and *Pseudomegalocotyla* sp.). *D. maa* and *Haliotrema* sp.1 are intermediary in that each one was absent in one fish but represented a relatively abundant species (22% and 17% of the monogeneans, respectively) in the other fish. Although obtained from a significant number of monogeneans (more than 300) our results concern only two fish and generalization from these species should be avoided. However, it is interesting to note that in *E. maculatus*, with results based on 10 fish and almost 800 monogeneans (Justine 2007a), there was clearly a similar situation, with a single dominant species (the diplectanid *Laticola dae* Journo & Justine, 2006) and a series of 11 rare species, in which none represented more than 7.5% of the total number of monogeneans. In *E. cyanopodus* (Richardson), on an abundant sampling of more than 1000 monogeneans, we found again a similar repartition, with a single abundant diplectanid species and a series of rare species (Sigura & Justine unpublished). This was also the case in *E. coeruleopunctatus* (Bloch), with a single abundant diplectanid species and three rare species (Sigura *et al.* 2007). It thus seems that the presence of a single dominant species accompanied by a series of rare species is a general situation in diplectanid fauna of large (> 1 kg) groupers. In smaller groupers, the general case seems to be presence of one abundant species and one rare species (*E. fasciatus*, Justine 2005b, Hinsinger & Justine 2006b; *E. merra*, *E. rivulatus*, *E. howlandi*, Hinsinger & Justine 2006b). These observations cast a doubt on reports of a single species of *Pseudorhabdosynochus* in certain grouper species, especially the big species; it is likely that a thorough examination of the monogenean fauna would reveal several additional rare species. Incomplete studies artificially diminish evaluation of parasite biodiversity.

Table 1 shows that the species found in our two specimens of *E. malabaricus* were not the same. Only *P. manifestus*, the abundant species, was found in both specimens. Two possible hypotheses may explain these very different monogenean faunae. One is that repartition of the rare species is at random, and that an insufficient sampling of two specimens can only provide incomplete information. Another is that the monogenean fauna in *E. malabaricus* changes with age, as our two specimens were of very different age and size. Such a phenomenon has been shown in *E. howlandi*, in which specimens smaller than 300 mm show only one species of *Pseudorhabdosynochus*, while greater specimens have another species (Hinsinger & Justine 2006a, b). Additional fish specimens are needed to know which hypothesis, or a mixing of both, explain these differences.

Parasites recorded from *E. malabaricus* and parasite biodiversity in groupers

Table 5 gives a list of all monogeneans mentioned from *E. malabaricus*. Four nominal species of capsalids have been reported prior to our study. The mention of six undescribed diplectanid species in Heron Island, Eastern Australia (identification by Klaus Rohde, listed in Lester & Sewell 1989) probably concerns the same species as the ones described here from New Caledonia. In Indonesia, Koesharyani *et al.* (1998) apparently differentiated a *Pseudorhabdosynochus* sp. and a *Diplectanum* sp.; this suggests that *Diplectanum maa* is present and relatively abundant in this locality. Finally, after elimination of dubious references, *E. malabaricus* probably harbours 5 capsalids, 2 ancyrocephalids and 8 diplectanids, a total of 15 monogeneans.

Digeneans are listed in Table 6. Among this list of 14 species, *Telorhynchus arripidis* is dubious in this host, and the *Prosorhynchus* species probably all belong to *P. maternus*; the final total is 11 different species.

Cestodes recorded from *E. malabaricus* include unidentified tetraphyllidean larvae (Leong & Wong 1988; Ruangpan & Tubkaew 1993) and larvae of the pseudobothriid trypanorhynch *Pseudotobothrium dipsacum* (Linton) from the Coast of East Africa (Beveridge *et al.* 2000). In New Caledonia, we also found larvae of *P. dipsacum* (identification by I. Beveridge, Melbourne, Australia) and of the grillotiid *Pseudogilquinia pillersi* (see Beveridge *et al.* 2007).

Nematodes reported from *E. malabaricus* include only larvae of anisakids (*Contracoecum* sp. and *Raphidascaris* sp., Malaysia, Leong & Wong 1988; *Terranova* sp., Indian Ocean and West Australian Coast, Doupé *et al*. 2003, Eastern Australia, Lester & Sewell 1989) and a gnathostomid larva (*Echinocephalus* sp., Malaysia, Leong & Wong 1988); all these larvae are common in fish and generally cannot be identified at the species level. Published records include four 'species' but identification of anisakids at the species level would probably at least double this number.

Several copepods were listed for *E. malabaricus* by Johnson *et al.* (2004) from various locations: these include five species of *Caligus*, *Lepeophtheirus* sp. and *Ergasilus* sp. In New Caledonia, we found the hatschekiid *Hatschekia* sp. and the caligid *Lepeophtheirus* sp. (identification by G. Boxshall, The Natural History Museum, London). A total of 8 copepods species is thus recorded from this fish.

Larval gnathiid isopods (*Gnathia* sp.) were mentioned from Thailand, as well as an unidentified Hirudinea and an acanthocephalan (Ruangpan & Tubkaew 1993).

Finally, parasite records from *E. malabaricus* include at least 15 monogeneans, 11 digeneans, 3 larval cestodes, 4 larval nematodes, 8 copepods, 1 larval isopod, 1 acanthocephalan and 1 hirudinean, with a grand total of 44 parasite species (Table 7). This number, although impressive, is certainly an underestimate of parasite biodiversity in this fish. No larval digenean (metacercariae) have been mentioned, probably because they have not been sought for or collected; Moravec *et al*. (1997) recorded 17 species of digeneans from *E. morio* off Mexico, including 9 different metacercariae. The number of tetraphyllidean cestodes might also be impressive but this requires detailed morphological studies, even if species names cannot be attributed to the morphs found; such a study (Muñoz *et al*. 2007) revealed 31 tetraphyllidean species in labrids. Anisakid nematodes have not been identified at species level, but probably include a number of species. We can safely speculate that less than half of the parasite species of *E. malabaricus* have been recorded; many of the present identifications are at the genus level only and precise identification of all species is far from completed.

Comparison of parasite biodiversity in *E. malabaricus* with two other species of groupers examined in New Caledonia, *E. cyanopodus* and *E. maculatus* (Table 7) shows that total parasite biodiversity observed in New Caledonia ranges 18–25 species, and global biodiversity compiled from literature ranges 26–44. Numerical estimation of parasite biodiversity in fish species which have been the subject of an extensive literature in a wide geographic area can reach 40–60 parasite species per fish (i.e. *Boops boops*, Pérez-del Olmo *et al*. 2007; *Seriola lalandi*, Hutson *et al*. 2007). The three grouper species listed in Table 7 were certainly not subjected to such a sampling effort. As for *E. malabaricus*, it is a safe prediction that less than half of the parasites have been recorded in the two other grouper species in Table 7, and parasite biodiversity might well reach 100 species for each of these three species.

E. malabaricus is an important species for aquaculture in South-East Asia. In addition to viral, bacterial and other diseases (Supamattaya *et al*. 1990; Danayadol *et al*. 1995; review in Bondad-Reantaso *et al*. 2002), helminth parasites are a threat for this industry and proper species identification of these numerous pathogens is a prerequisite for an adapted treatment of the diseases they might provoke.

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TABLE 1. Number of monogeneans collected. Percentages shown are percentages of the total number of monogeneans (m) or of the total number of diplectanids (d)

	Diplectanids										Ancyrocephalids			Capsalids	
Host	*P. manifestus*	*P. malabaricus*	*P. maternus*	*P. manipulus*	*P. marcellus*	*P. maaensis*	*P.* cf. *shen-zhenensis*	*D. maa*	indet.	Total	*Haliotrema* sp. 1	*Haliotrema* sp. 2	Total	*Pseudome-galocotyla*	TOTAL
JNC 1536	**133** 80.6% d 66.5% m	**9** 5.5% d 4.5% m	**11** 6.7% d 5.5% m	**9** 5.5% d 4.5% m	**2** 1.2% d 1.0% m	**0**	**0**	**0**	**1** 0.6% d 0.5% m	**165** 82.5% m	**29** 14.5% m	**3** 1.5% m	**32** 16% m	**3** 1.5% m	**200**
JNC 2130	**87** 64.9% d 64.9% m	**0**	**0**	**0**	**0**	**10** 7.5% d 7.5% m	**2** 1.5% d 1.5% m	**29** 21.6% d 21.6% m	**6** 4.5% d 4.5% m	**134** 100% m	**0**	**0**	**0**	**0**	**134**
Total	**220** 73.6% d 65.9% m	**9** 3.0% d 2.7% m	**11** 3.7% d 3.3% m	**9** 3.0% d 2.7% m	**2** 0.7% d 0.6% m	**10** 3.3% d 3.0% m	**2** 0.7% d 0.6% m	**29** 9.7% 8.7% m	**7** 2.3% d 2.1% m	**299** 89.5% m	**29** 8.7% m	**3** 1% m	**32** 9.6% m	**3** 0.9% m	**334**
Prevalence	100%	50%	50%	50%	50%	50%	50%	50%			50%	50%		50%	

TABLE 2. Selected measurements and abbreviated vagina characteristics for three species resembling *P. manifestus* and *P. maaensis*. From Yang *et al.* (2005) and Justine (2007a).

Characteristic	*P. huitoe*	*P. shenzhenensis*	*P. serrani*	*P. manifestus* **n. sp.**	*P. maaensis* **n. sp.**
Body Length	440	314–519	434	665	498
Dorsal Bar Length	84	72	79	84	51
Ventral Bar Length	119	81	113	117	79
Ventral Hamulus Outer Length	45 *	41	42	57	42
Dorsal Hamulus Outer Length	37 *	33	34	48	39
Ventral Squamodisc Diameter	50	43	52–63	60	44
Dorsal Squamodisc Diameter	49	40	52	55	40
Squamodisc Rows	9–12	9–11	9–11	10–12	10–13
Quadriloculate Organ Internal Length	45	43	28	57	34
Vagina Length	25	30 (16 in voucher)	39 (26 in voucher)	34	43
Vagina Primary Canal	conical	conical	conical	conical	cylindrical
Vagina Primary Canal Wall	thin	thin	without ring	with ring	thin
Tegumental scales	Posterior region	Only on peduncle **	Only on peduncle	Posterior region	Posterior region

Measurements indicated are means from carmine specimens; * These measurements were misprinted in the text of the original description (Justine, 2007a p. 112) but were correct in the comparative Table (p. 113). ** confirmed by examination of voucher.

TABLE 3. Selected characteristics of the seven species of *Pseudorhabdosynochus* from *E. malabaricus*.

Character	*P. manifestus*	*P. malabaricus*	*P. maternus*	*P. manipulus*	*P. marcellus*	*P. maaensis*	*P.* cf. *shenzhenensis*
Body Length	665	543	564	600	585	498	395
Quadriloculate Organ Internal Length	57	52	45	60	42	34	41
Quadriloculate Organ Cone Length	19	11	10	17	25	17	16
Quadriloculate Organ Tube Length	22	16	18	19	21	14	13
Quadriloculate Organ Tube Diameter	3	3	3	4	3	2	2
Vagina Total Length	34	38	28	38	34	43	21
Ventral Hamuli Outer Length	57	58	58	60	54	42	45
Ventral Hamuli Inner Length	49	42	44	50	46	35	35
Dorsal Hamuli Outer Length	48	48	47	50	47	39	38
Dorsal Hamuli Inner Length	30	30	29	30	29	24	22
Dorsal Bar Length	84	113	106	93	88	51	65
Ventral Bar Length	117	132	135	132	109	79	72
Squamodisc Row Number	10–12	10–12	10–12	10–12	9–10	10–13	9–10
Ventral Squamodisc Rodlet Number	87	147	153	105	59	72	64
Dorsal Squamodisc Rodlet Number	86	133	147	109	46	76	55
Ventral Squamodisc Length × Width	60 × 61	63 × 77	61 × 68	65 × 69	44 × 50	44 × 45	28 × 45
Dorsal Squamodisc Length × Width	54 × 56	64 × 71	58 × 65	64 × 63	44 × 36	44 × 37	38 × 26

Measurements are generally means from carmine specimens.

TABLE 4. Measurements of species resembling *Diplectanum maa* **n. sp.**

	D. grouperi	*D. uitoe*	*Diplectanum*	*D. maa* **n. sp.**
Host	*E. coioides*	*E. maculatus*	*C. sonnerati*	*E. malabaricus*
Body Length	641	405	240	475
MCO Length	26	35	24	36
Ventral Hamulus Outer Length	44 *	37	35	46
Dorsal Hamulus Outer Length	37 *	33	31	41
Dorsal Bar Length	50 *	58	50	57
Ventral Bar Length	70 *	75	67	72
Ventral Squamodisc Length × Width	44 × 38 **	61× 58	30 × 30	33 × 30
Dorsal Squamodisc Length × Width	44 × 38 **	57 × 53	21 × 20	33 × 34
Ventral Squamodisc Rodlet Number	?	124	84	65
Dorsal Squamodisc Rodlet number	?	111	41	64

Measurements are generally means from carmine specimens; * from redescription by Justine (2007a); ** dorsal and ventral squamodiscs measurements not separated in original description.

TABLE 5. Monogeneans previously reported in *Epinephelus malabaricus*.

Family, Species	Locality	Reference
Ancyrocephalidae		
Undetermined (1)	Eastern Australia	Lester & Sewell 1989
Haliotrema sp. 1	New Caledonia	This paper
Haliotrema sp. 2	New Caledonia	This paper
Capsalidae		
Benedenia sp. or *Neobenedenia* sp.	Indonesia	Koesharyani *et al*. 1998
Neobenedenia girellae (Hargis)	Japan	Ogawa *et al*.1995
Megalocotyloides epinepheli Bychowsky & Nagibina	Eastern Australia	Lester & Sewell 1989 (2)
	South China Sea	Zhang, Yang, Liu & Ding 2003
	Malaysia	Leong & Wong 1988
	Thailand, Philippines	Leong & Wong 1990
Sprostonia longiphallus Lawler & Hargis	Eastern Australia	Lester & Sewell 1989
Pseudomegalocotyla sp.	New Caledonia	This paper (3)
Diplectanidae		
6 species, undescribed (4)	Eastern Australia	Lester & Sewell 1989
Pseudorhabdosynochus epinepheli (Yamaguti)	Malaysia, Philippines, Thailand	Leong & Wong 1988 (5)
	Thailand	Ruangpan & Tubkaew 1993 (5) (6)
Pseudorhabdosynochus sp.	Indonesia	Koesharyani *et al*. 1998
Diplectanum sp.	Indonesia	Koesharyani *et al*. 1998
Pseudorhabdosynochus manifestus	New Caledonia	This paper
Pseudorhabdosynochus malabaricus	New Caledonia	This paper
Pseudorhabdosynochus maternus	New Caledonia	This paper
Pseudorhabdosynochus manipulus	New Caledonia	This paper
Pseudorhabdosynochus marcellus	New Caledonia	This paper
Pseudorhabdosynochus maaensis	New Caledonia	This paper
Pseudorhabdosynochus cf. *shenzhenensis*	New Caledonia	This paper
Diplectanum maa	New Caledonia	This paper

(1) probably *Haliotrema* spp. as in the present study; (2) under the name *Allosprostonia tauvinae* Lawler & Hargis, junior synonym of *M. epinepheli* (see Hussey 1986); (3) identification by I. Whittington, The South Australian Museum, Adelaide; (4) probably corresponding to 6 of the species of the present study; (5) '*P. epinepheli*' probably correspond to one or several of the diplectanid species described in this paper but these records are not associated with descriptions, drawings or deposited specimens; (6) under the junior synonym *Cycloplectanum epinepheli*; (7) a mention of *Dactylogyrus* sp. in Thailand (Ruangpan & Tubkaew 1993) is considered dubious and not included in the Table.

TABLE 6. Digeneans reported in *E. malabaricus.*

Family, species	Locality	Reference
Acanthocolpidae		
Stephanostomum sp.	Malaysia	Leong & Wong 1988
Bucephalidae		
Prosorhynchus pacificus Manter (1)	Philippines	Leong & Wong 1990
	Thailand	Ruangpan & Tubkaew 1993
	Malaysia	Leong & Wong 1988, 1990
Prosorhynchus maternus Bray & Justine, 2006	New Caledonia	Bray & Justine 2006
Prosorhynchus maternus ? (2)	India	Hafeezullah & Siddiqi 1970
Telorhynchus arripidis Crowcroft (3)	Red Sea	Shalaby & Hassanine 1996
Cryptogonimidae		
Pseudometadena celebesensis Yamaguti	Malaysia	Leong & Wong 1988
Didymozoidae		
Gonapodasmius sp.	Thailand	Ruangpan & Tubkaew 1993
Hemiuridae		
Ectenurus sp.	Malaysia	Leong & Wong 1988, 1990
Erilepturus hamati (Yamaguti) Manter	Malaysia	Leong & Wong 1988 (4)
	Thailand	Ruangpan & Tubkaew 1993 (4)
	Thailand, Philippines	Leong & Wong 1990 (4)
Opecoelidae		
Allopodocotyle serrani (Yamaguti) (5)	Malaysia	Leong & Wong 1988
Pseudopecoeloides sp.	Thailand	Ruangpan & Tubkaew 1993
Helicometrina nimia Linton	Malaysia	Leong & Wong 1990
Cainocreadium sp.	New Caledonia	This paper (6)
Sanguinicolidae		
Cardicola sp.	Malaysia	Leong & Wong 1988, 1990
	Thailand	Leong & Wong 1990

(1) although no descriptions are available, it appears likely that these specimens are *P. maternus*; (2) as *Prosorhynchus atlanticu*s Manter; according to Bray & Justine (2006), the single specimen is more similar to *P. maternus* than to *P. atlanticus*; (3) this identification may be erroneous as *Telorhynchus arripidis* is usually reported from *Arripis trutta* from southern Australian and New Zealand waters (Crowcroft 1947; Manter 1954; Lebedev 1968); (4) as *Lecithochirium neopacificum*; Bray *et al*. (1993) examined a type-specimen of *L. neopacificus* Velasquez and concluded that it could not be distinguished from *E. hamati*; (5) Bray & Cribb (1989) thought that *A. serrani* was 'very similar and may be found indistinguishable' from *A. epinepheli* (Yamaguti); (6) identified by R. Bray (The Natural History Museum, London) from a single specimen from fish JNC1536.

TABLE 7. Biodiversity of parasites in three species of groupers. First number is the number of species recorded in New Caledonia; second number in parenthesis is the total number of species recorded in all locations (according to various sources, including the NHM host-parasite database [http://www.nhm.ac.uk/research-curation/projects/host-parasites/database/], Table 5 and 6, and Moravec & Justine 2005; Bray & Justine 2006, 2007; Journo & Justine 2006; Justine 2007a). 'Others' include Hirudinea and Acanthocephala.

	Monogenea	Digenea	Cestoda	Nematoda	Copepoda	Isopoda	Others	Total
E. maculatus	12 (12)	7 (7)	1 (2)	1 (1)	3 (3)	1 (1)	0 (0)	25 (26)
E. cyanopodus	6 (7)	4 (10)	2 (2)	4 (8)	5 (5)	2 (2)	0 (0)	23 (34)
E. malabaricus	11 (15)	2 (11)	2 (3)	1 (4)	2 (8)	0 (1)	0 (2)	18 (44)

Figure Legends

FIGURE 1. Methods of measurements (italics) and nomenclature of various sclerotised organs.

FIGURE 2. *Pseudorhabdosynochus manifestus* **n. sp. A.** Composite drawing; tegumental scales drawn only on edges. **B.** Quadriloculate organ. **C.** Sclerotised vagina. B, C, holotype; A–C, ventral view, carmine.

FIGURE 3. *Pseudorhabdosynochus manifestus* **n. sp.** Sclerotised vagina, variation according to specimen, orientation and fixation method. Note general shape reminding a "?", particularly in A–C. A–M, carmine, dorsal view; N–T, carmine, ventral view; U–Y, picrate, dorsal view; Z, picrate, ventral view. All paratypes.

FIGURE 4. *Pseudorhabdosynochus manifestus* **n. sp. A.** Ventral squamodisc, ventral view. **B.** Dorsal squamodisc, same individual, ventral view. **C.** Tegumental scales. **D.** Ventral bar. **E.** Dorsal bar. **F.** Ventral hamulus. **G.** Dorsal hamulus. A–C, holotype, carmine; D–G, paratype, picrate.

FIGURE 5. *Pseudorhabdosynochus manifestus* **n. sp.**, development of sclerotised copulatory organ in a juvenile. **A.** Silhouette of body. **B.** Quadriloculate organ. **C.** Sclerotised vagina. Dorsal view, carmine.

FIGURE 6. *Pseudorhabdosynochus malabaricus* **n. sp. A.** Composite drawing; tegumental scales drawn only on edges. **B.** Sclerotised vagina, holotype, carmine.

FIGURE 7. *Pseudorhabdosynochus malabaricus* **n. sp. A.** Quadriloculate organ. **B–G.** Sclerotised vaginae. **F–G.** Superposed plans of vagina drawn separately for two vaginae. A, holotype; B–G, paratypes. B–D, F, dorsal view; A, E, G, ventral view; all carmine.

FIGURE 8. *Pseudorhabdosynochus malabaricus* **n. sp. A.** Ventral squamodisc. **B.** Dorsal squamodisc, same individual. **C.** Ventral tegumental scales. **D.** Dorsal tegumental scales, same individual. **E.** Ventral hamulus. **F.** Dorsal hamulus. **G.** Ventral bar. **H.** Dorsal bar. A–D, holotype, ventral view, carmine; E–H, paratype, picrate.

FIGURE 9. *Pseudorhabdosynochus maternus* **n. sp. A.** Composite drawing; tegumental scales drawn only on edges. **B.** Quadriloculate organ. **C–E.** Sclerotised vagina, superposed planes drawn separately. A–E, holotype, carmine.

FIGURE 10. *Pseudorhabdosynochus maternus* **n. sp.** Sclerotised vagina, variation according to specimen, orientation and fixation method. Superposed planes drawn separately in certain specimens. A–C, G, carmine, ventral view; D–F, H–Q, carmine, dorsal view; R, picrate, dorsal view; all paratypes.

FIGURE 11. *Pseudorhabdosynochus maternus* **n. sp. A.** Dorsal squamodisc. **B.** Ventral squamodisc, same individual. **C.** Ventral tegumental scales. **D.** Dorsal tegumental scales. **E.** Dorsal hamulus. **F.** Ventral hamulus. **G.** Ventral bar. **H.** Dorsal bar. A–D, holotype, carmine; E–H, paratype, picrate.

FIGURE 12. *Pseudorhabdosynochus manipulus* **n. sp. A.** Composite drawing; tegumental scales drawn only on edges. **B.** Sclerotised vagina, holotype, carmine.

FIGURE 13. *Pseudorhabdosynochus manipulus* **n. sp. A.** quadriloculate organ. **C–H.** sclerotised vagina, variation according to specimen, orientation and fixation method. B, ventral view, carmine; C–F, ventral view, picrate; G–H, dorsal view, picrate; all paratypes.

FIGURE 14. *Pseudorhabdosynochus manipulus* **n. sp. A.** Ventral bar. **B.** Dorsal bar. **C.** Dorsal hamulus. **D.** Ventral hamulus. **E.** Ventral squamodisc. **F.** Dorsal squamodisc, same individual. **G.** Ventral tegumental scales. **H.** Dorsal tegumental scales. A–D, picrate, paratype; E–H, ventral view, holotype.

FIGURE 15. *Pseudorhabdosynochus marcellus* **n. sp. A.** Composite drawing; tegumental scales drawn only on edges. **B.** quadriloculate organ. **C, D.** Sclerotised vagina. B, C, dorsal view, holotype, carmine; D, dorsal view, paratype, carmine.

FIGURE 16. *Pseudorhabdosynochus marcellus* **n. sp. A.** Dorsal bar. **B.** Ventral bar. **C.** Dorsal hamulus. **D.** Ventral hamulus. **E.** Dorsal squamodisc. **F.** Ventral squamodisc, same individual. **G.** Dorsal tegumental scales. A–D, paratype, picrate; E–G**,** holotype, carmine, dorsal view.

FIGURE 17. *Pseudorhabdosynochus maaensis* **n. sp. A.** Composite drawing; tegumental scales drawn only on edges. **B.** Quadriloculate organ. **C.** Sclerotised vagina. **D.** Ventral squamodisc. **E.** Dorsal squamodisc, same individual. **F.** Ventral hamulus. **G.** Dorsal hamulus. **H.** Dorsal bar. **I.** Ventral bar. B–E, holotype, carmine, dorsal view; F–I, paratype, picrate.

FIGURE 18. *Pseudorhabdosynochus maaensis* **n. sp.** Sclerotised vagina, variation according to specimen, orientation and fixation method. A–E, carmine, ventral view; F–H, carmine, dorsal view; I, picrate, ventral view; all paratypes.

FIGURE 19. *Pseudorhabdosynochus* cf. *shenzhenensis*. **A.** Composite drawing. **B.** Quadriloculate organ. **C, D.** Sclerotised vagina. **E.** Ventral squamodisc. **F.** Dorsal squamodisc, same individual. **G.** Ventral squamodisc, other individual. **H.** Ventral hamulus. **I.** Dorsal hamulus. **J.** Dorsal bar. **K.** Ventral bar. All picrate; A–C, H–K, dorsal view; D–G, ventral view.

FIGURE 20. *Pseudorhabdosynochus* spp: nomenclature and measurements (italics) of sclerotised vaginae. Abbreviations as in general diagram. *P. serrani* (voucher from *E. coioides*, MNHN JNA6A1) drawn for comparison with *P. manifestus*; *P. shenzhenensis* (voucher from *E. coioides*, MNHN JNA5A1) drawn for comparison with specimens from *E. malabaricus*. *pcid*, primary chamber internal diameter; *pced*, primary chamber external diameter; *scid*, secondary chamber internal diameter; *sced*, secondary chamber external diameter.

FIGURE 21. *Diplectanum maa* **n. sp. A.** Composite drawing. **B.** Ventral bar. **C.** Dorsal bar. **D.** Ventral hamulus. **E.** Dorsal hamulus. **F.** Ventral squamodisc. **G.** Dorsal squamodisc, same individual. **H.** Male copulatory organ. B–E, picrate, paratype; F–H, carmine, holotype.

FIGURE 22. *Diplectanum maa* **n. sp. A–J.** Male copulatory organs, variation according to specimen and orientation. **K.** method of measurements. A–H, ventral view; I, J, dorsal view; all carmine paratypes.

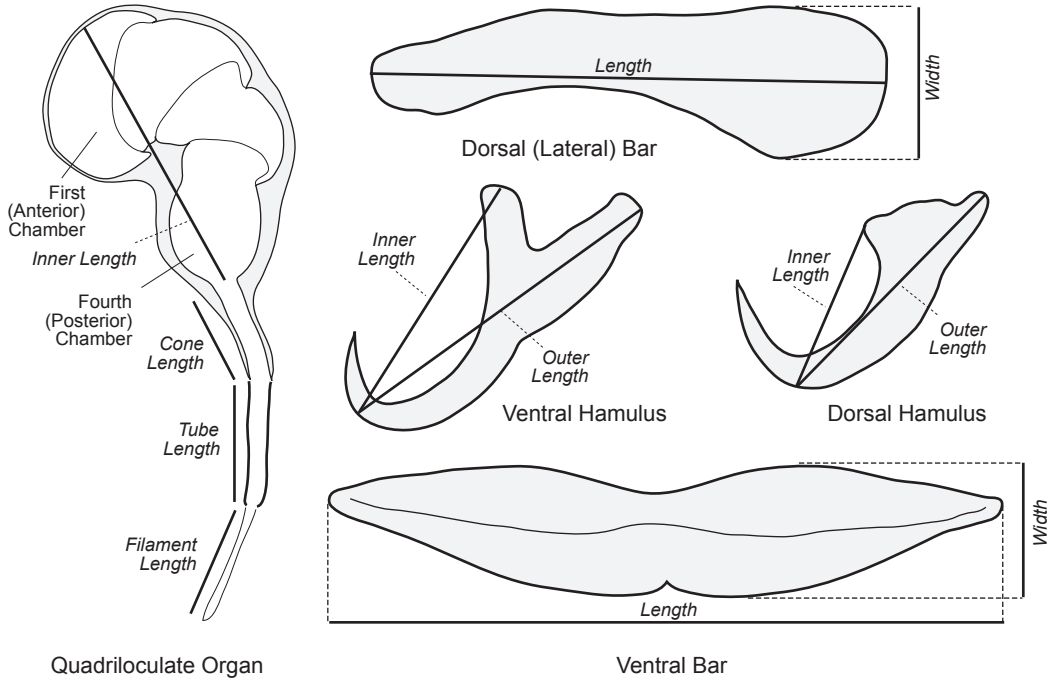

Figure 1: Measurements

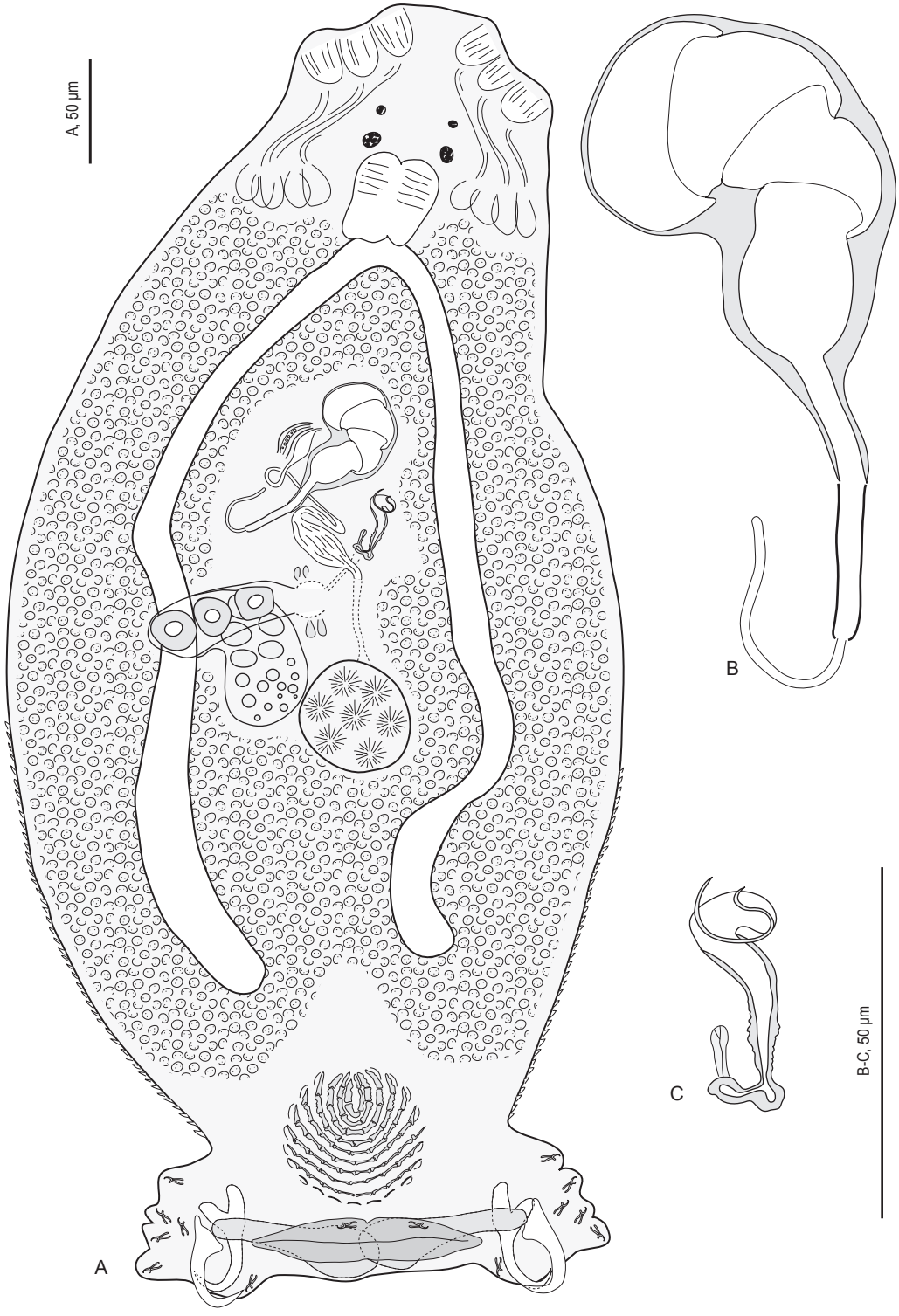

Figure 2 ***Pseudorhabdosynochus manifestus*** **n. sp.**

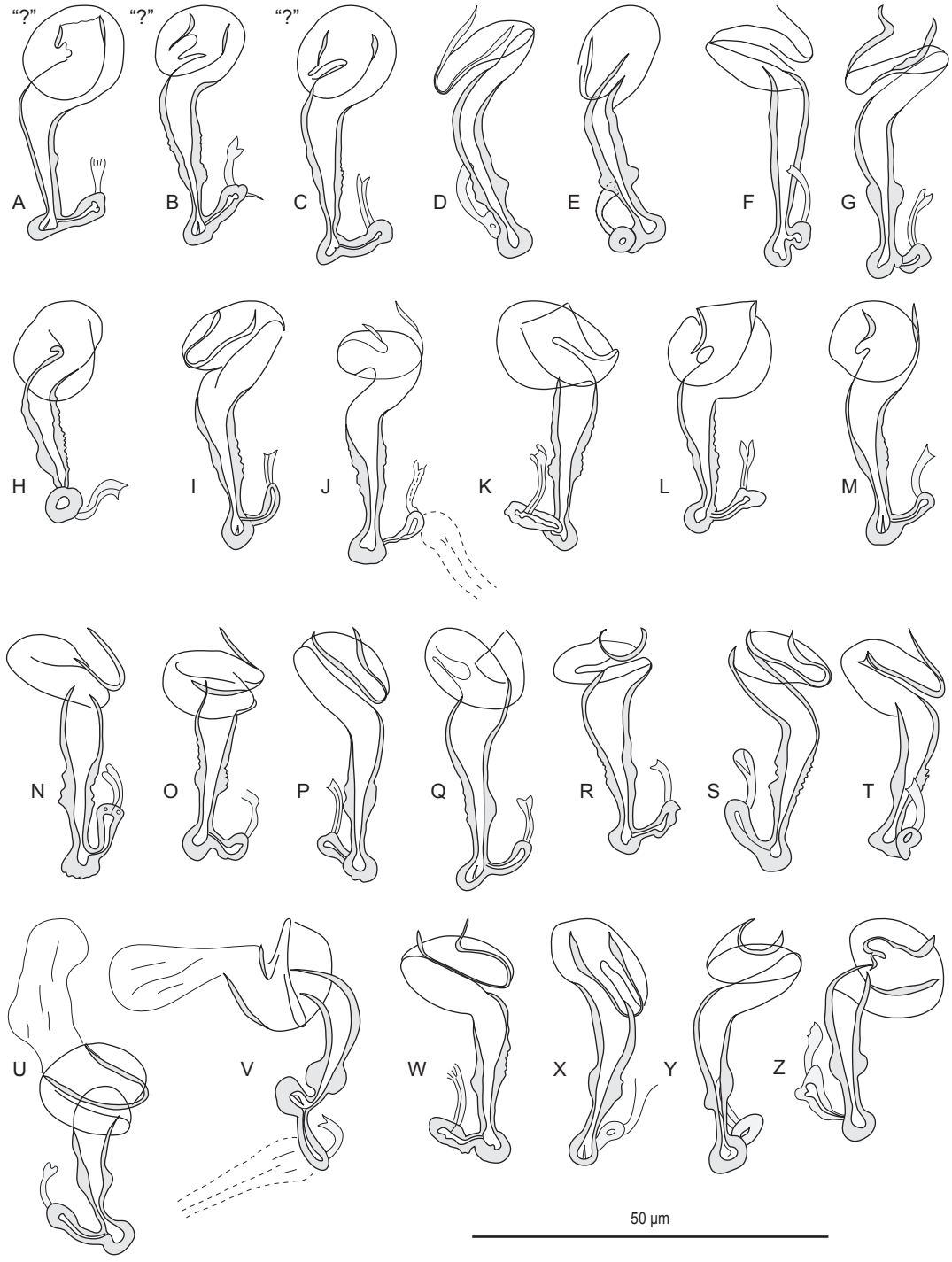

Figure 3 ***Pseudorhabdosynochus manifestus*** **n. sp.**

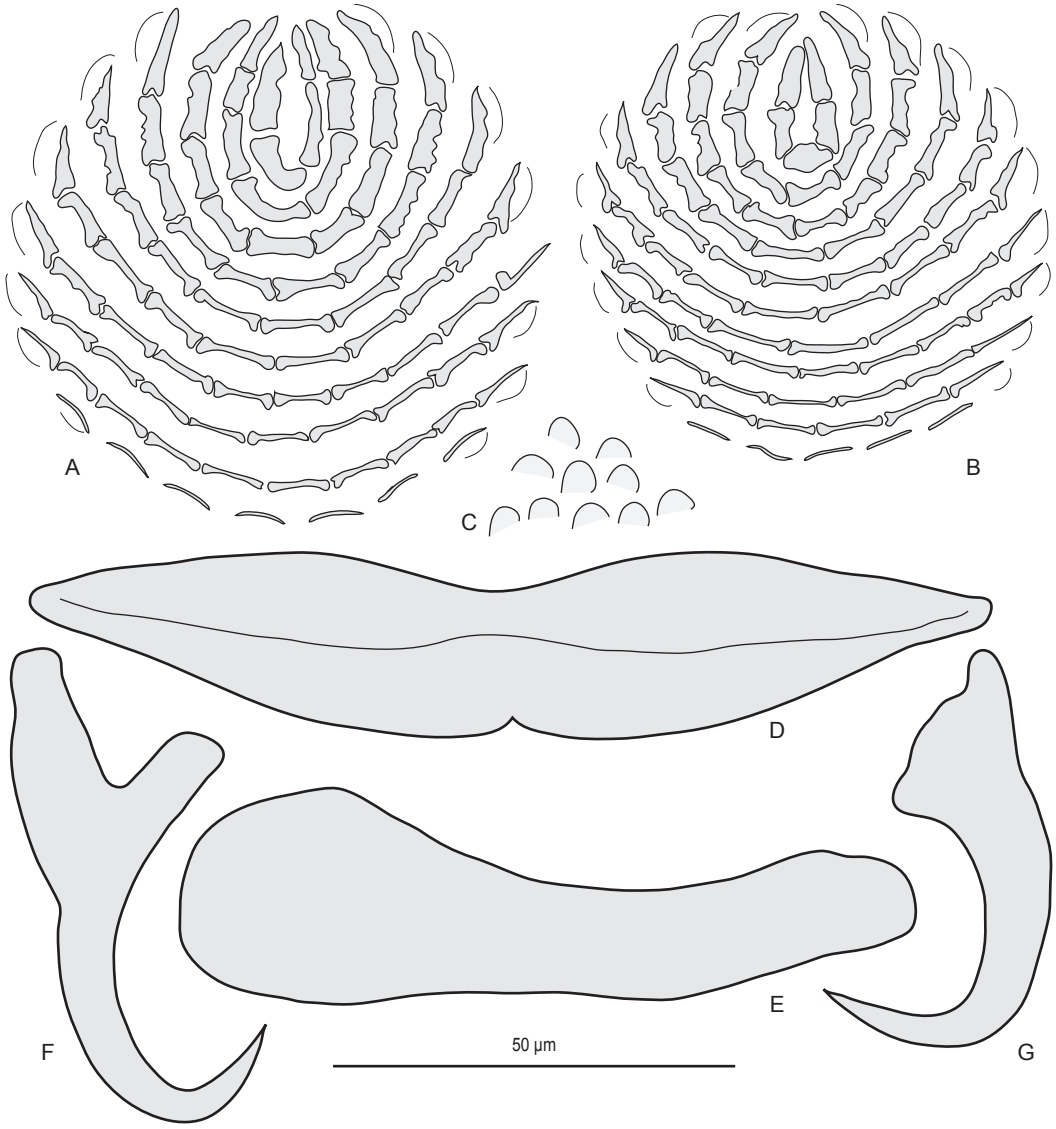

Figure 4 ***Pseudorhabdosynochus manifestus*** **n. sp.**

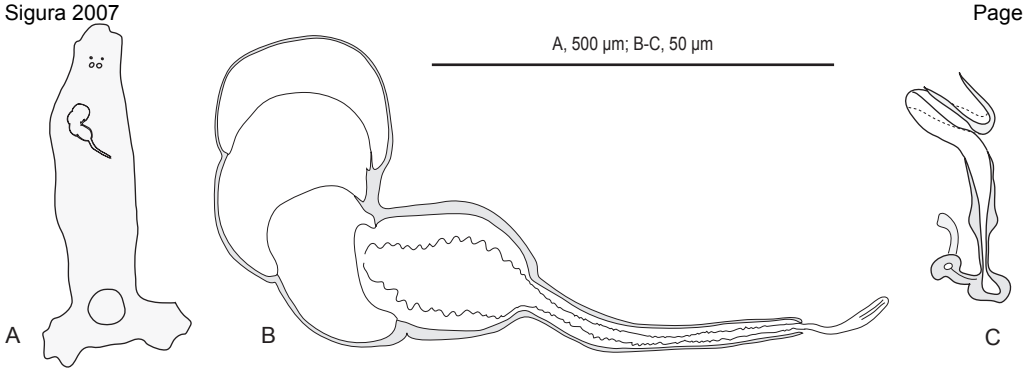

Figure 5 *Pseudorhabdosynochus manifestus* n. sp. (juvenile)

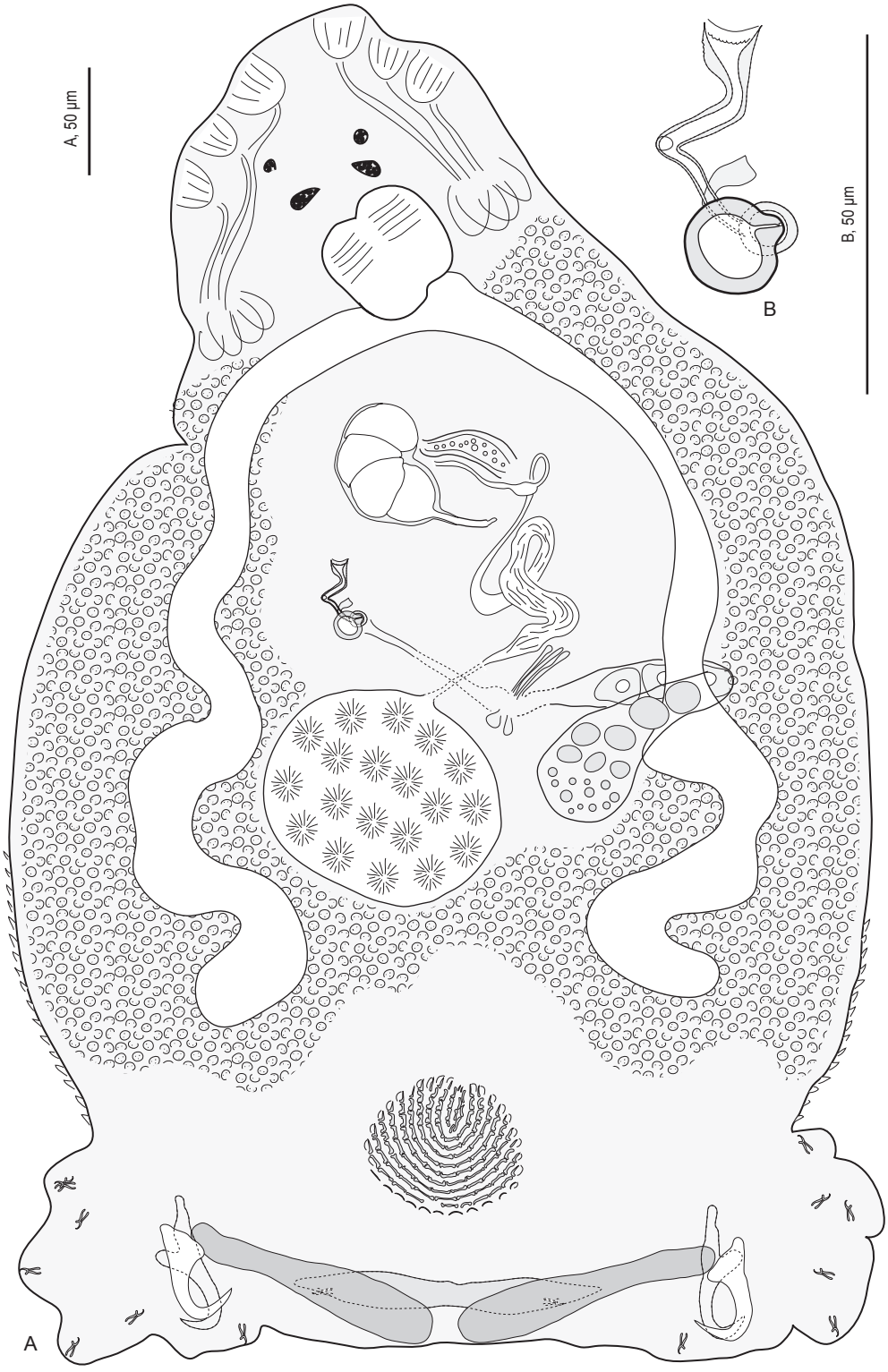

Figure 6 *Pseudorhabdosynochus malabaricus* n. sp.

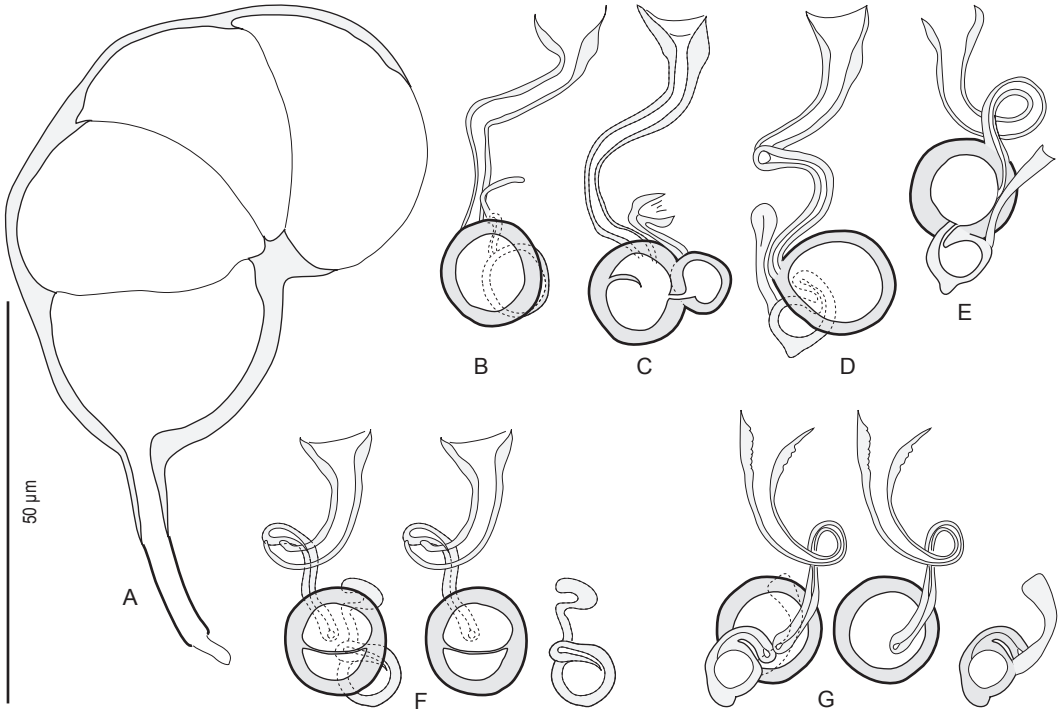

Figure 7 ***Pseudorhabdosynochus malabaricus*** **n. sp.**

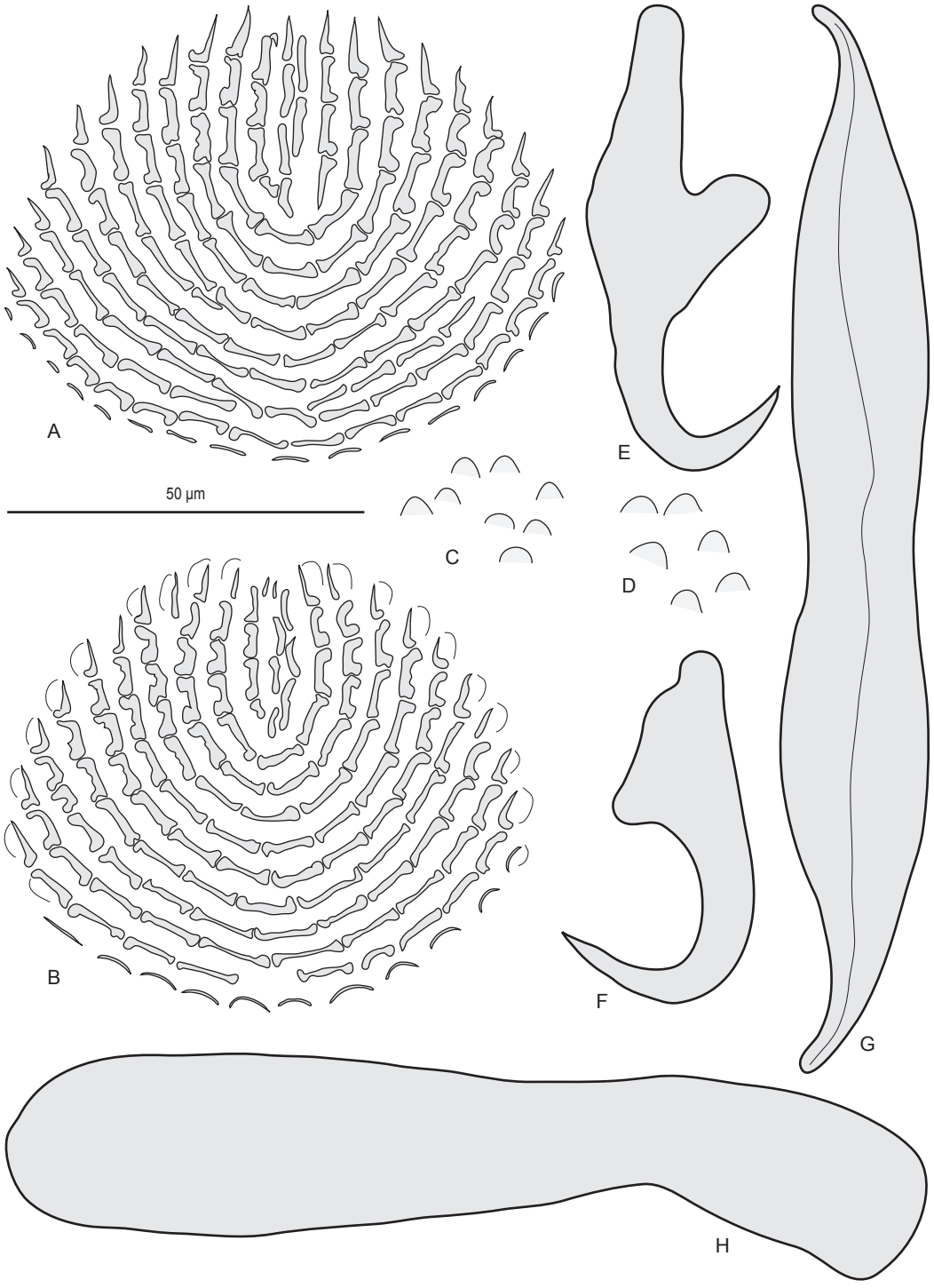

Figure 8 ***Pseudorhabdosynochus malabaricus*** **n. sp.**

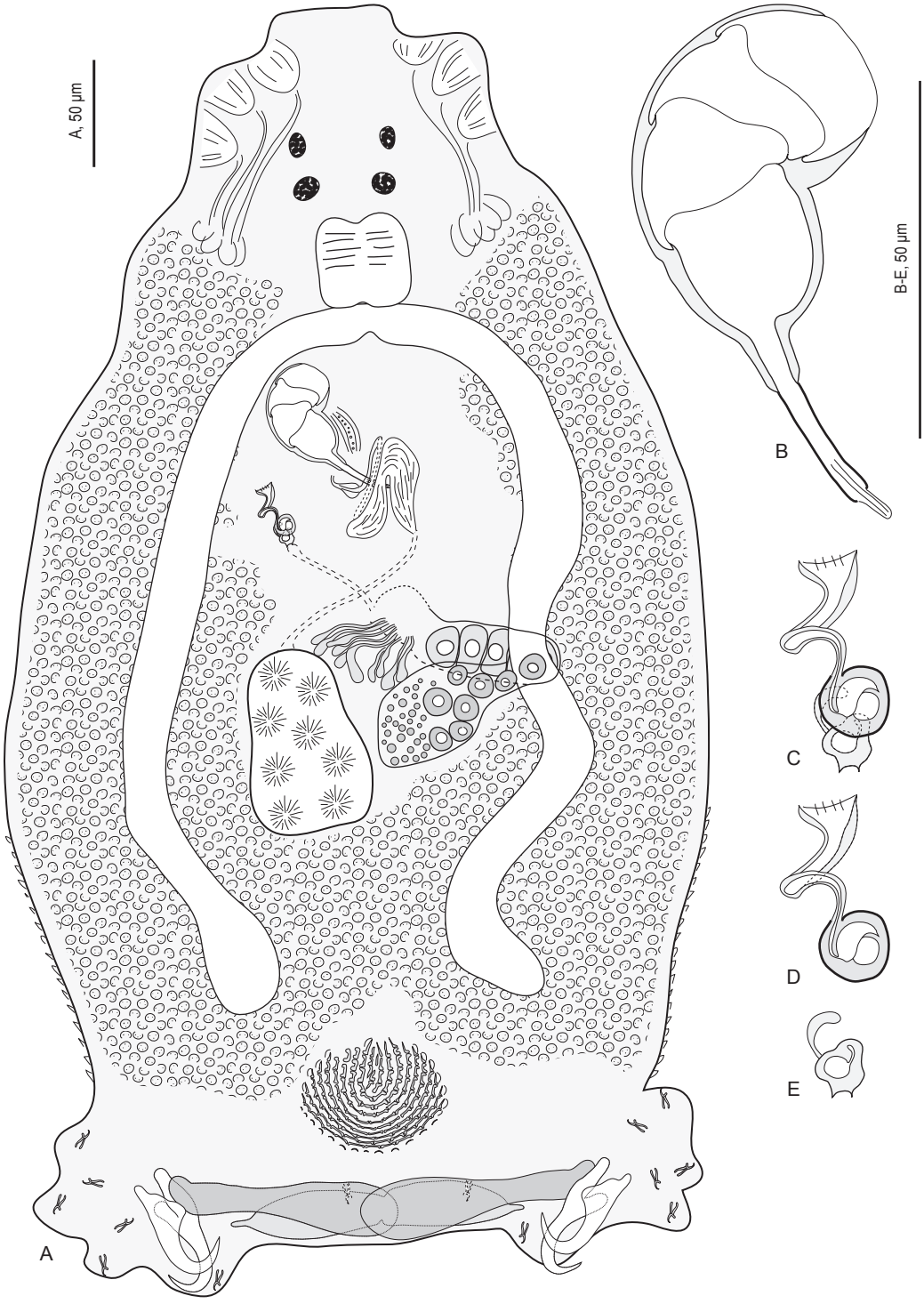

Figure 9 ***Pseudorhabdosynochus maternus*** **n. sp.**

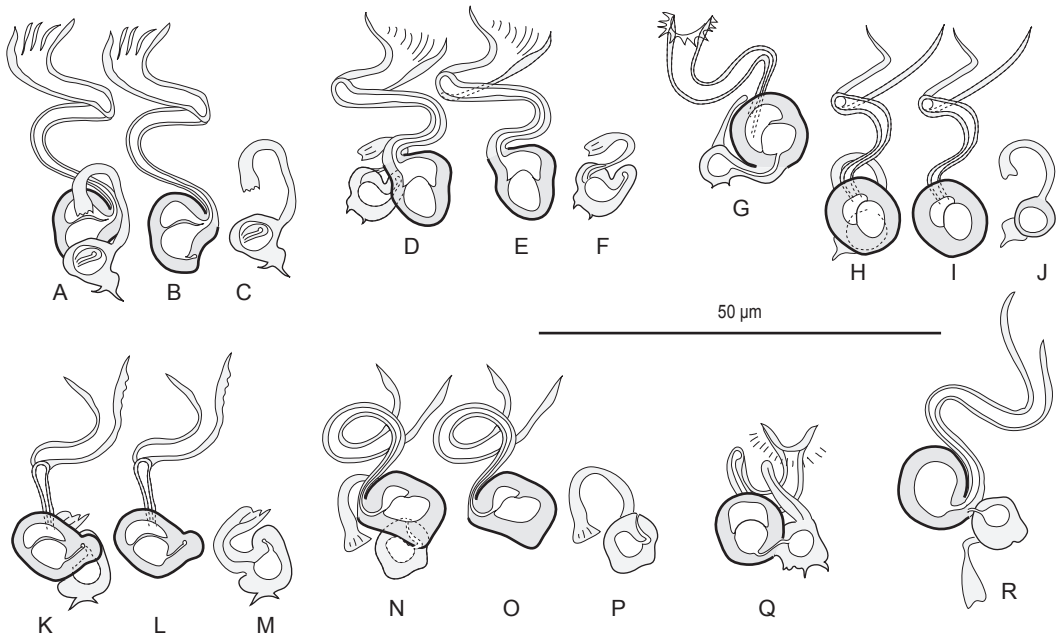

Figure 10 ***Pseudorhabdosynochus maternus*** **n. sp.**

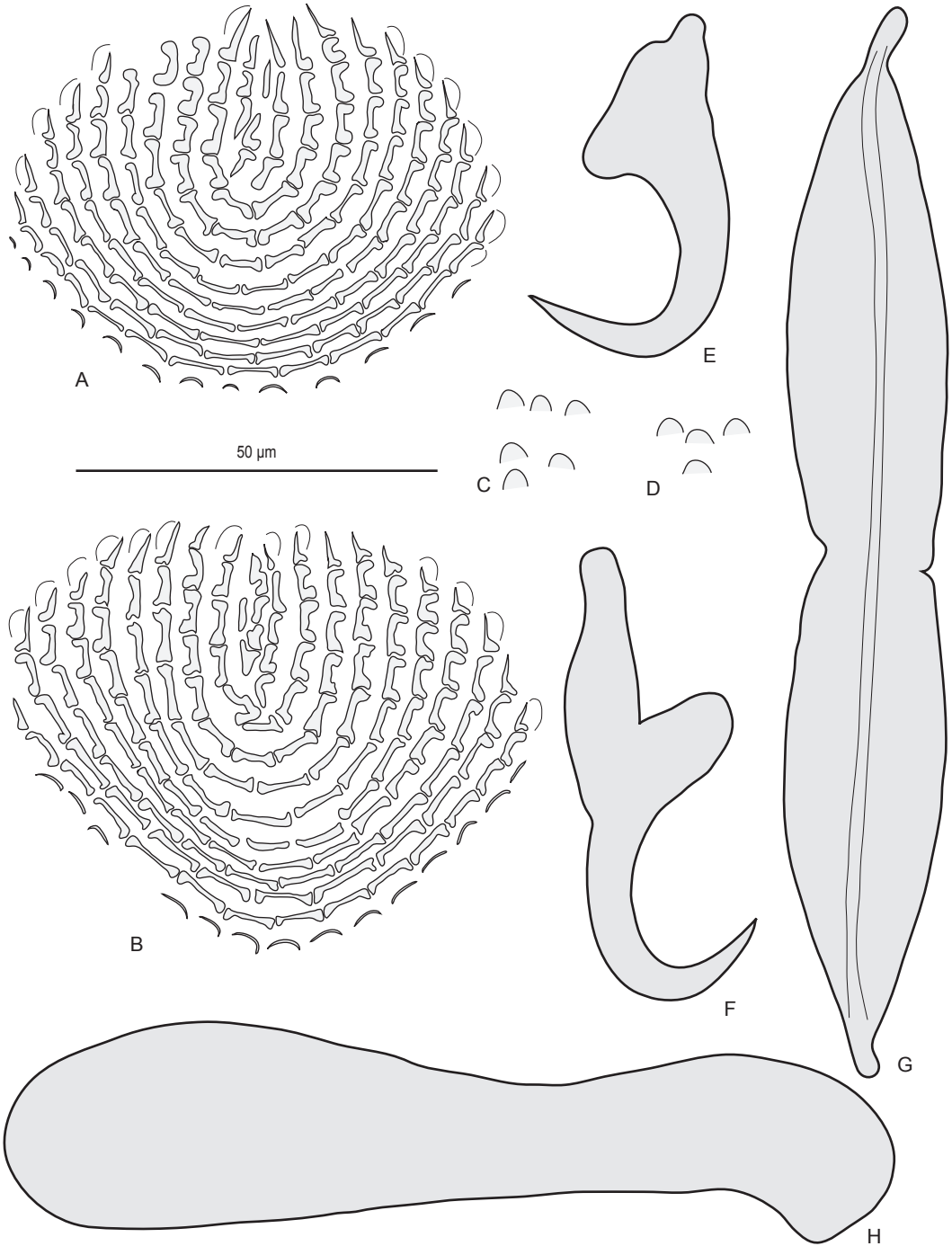

Figure 11 ***Pseudorhabdosynochus maternus*** **n. sp.**