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Diplectanids (Monogenea) parasitic on the gills of the coralgroupers *Plectropomus laevis* and *P. leopardus* (Perciformes, Serranidae) off New Caledonia, with the description of five new species and the erection of *Echinoplectanum* n. g.

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Abstract

Echinoplectanum n. g. is erected for diplectanids which have a male copulatory organ comprising a tubular sclerotised penis with a muscular reservoir at its proximal extremity and an protrusible cirrus, often with spiny ridges, at its distal extremity, and a female copulatory organ comprising a sclerotised vaginal sac, often with two thin tubes. All species have similar squamodiscs made of rows of rodlets, with the central rows forming closed circles, and haptoral parts with a similar shape but different measurements; they are distinguished on the basis of the size and morphology of the male copulatory organ and sclerotised vagina. Five new species are included in *Echinoplectanum* and are all parasites of coralgroupers, *Plectropomus* spp., off New Caledonia, South Pacific. Two are from *P. laevis* (Lacépède): *E. laeve* n. sp. (type-species) has a large elongate penis, 53 μm in length, a cirrus with spiny ridges and a spherical vagina with two long thin tubes; and *E. chauvetorum* n. sp. has a large elongate penis, 51 μm in length, a cirrus with thin spiny ridges, and a pear-shaped vagina with two short thin tubes. Three species are from *P. leopardus* (Lacépède): *E. leopardi* n. sp. has an elongate penis, 36 μm in length, an unspiny cirrus and a triangular vagina; *E. pudicum* n. sp. has a very small elongate penis 14 μm in length and no visible vagina; and *E. rarum* n. sp. has a short thick penis 18 μm in length and a ring-shaped vagina with two thin tubes. In addition, *Diplectanum plectropomi* Young, 1969, from *P. maculatus* off Western Australia, and *D. echinophallus* Euzet & Oliver, 1965 from *Epinephelus marginatus* in the Mediterranean Sea and Senegal, West Africa, both herein redescribed from the type-specimens, are transferred to *Echinoplectanum*, as *E. plectropomi* n. comb. and *E. echinophallus* n. comb., respectively. Six of the seven species of *Echinoplectanum* are parasitic in members of *Plectropomus* from the South West Pacific, but one (*E. echinophallus*) is a parasite of *Epinephelus marginatus* and has been recorded only from the Mediterranean and East Atlantic; it is suggested that *Echinoplectanum* is associated with *Plectropomus*, a basal genus among the epinephelines, and that host-switching to *Epinephelus marginatus* occurred, whose distribution extends from Europe to the Indian Ocean. Morphological characteristics of the copulatory organs suggest that a ''chastity belt versus spiny penis'' sperm competition pattern prevails in *Echinoplectanum* spp.

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Résumé

Echinoplectanum n. g. est créé pour des Diplectanidae qui ont un organe copulateur mâle comprenant un pénis tubulaire sclérifié avec un réservoir musculaire à son extrémité proximale et un cirre évaginable, souvent avec crêtes épineuses, à son extrémité distale, et un appareil copulateur femelle comprenant un sac vaginal sclérifié, souvent avec deux tubes fins. Toutes les espèces ont des squamodisques similaires formés de rangées d'osselets, dont les rangées centrales forment des cercles, et des pièces du hapteur de forme similaire, mais avec des mesures différentes ; elles sont différenciées à partir de la taille et de la morphologie de l'organe copulateur mâle et du vagin sclérifié. Cinq nouvelles espèces sont incluses dans *Echinoplectanum* et sont toutes parasites de *Plectropomus* spp. au large de la Nouvelle-Calédonie, Pacifique Sud. Deux sont parasites de *P. laevis* (Lacépède) : *E. laeve* n. sp. (espèce-type) a un grand pénis allongé, long de 53 µm, un cirre portant des crêtes épineuses, et un vagin sphérique avec deux longs tubes fins ; *E. chauvetorum* n. sp. a un grand pénis allongé, long de 51 µm, un cirre portant de fines crêtes épineuses, et un vagin en forme de poire avec deux courts tubes fins. Trois espèces sont parasites de *P. leopardus* (Lacépède) : *E. leopardi* n. sp. a un pénis allongé long de 36 µm et un cirre inerme, et un vagin triangulaire ; *E. pudicum* n. sp. a un pénis allongé très petit, long de 14 µm, et son vagin n'est pas visible ; *E. rarum* n. sp. a un pénis court et épais, de longueur 18 µm, et un vagin en anneau avec deux tubes fins. De plus, *Diplectanum plectropomi* Young, 1969, de *P. maculatus* à l'Ouest de l'Australie, et *D. echinophallus* Euzet & Oliver, 1965 d'*Epinephelus marginatus* de Mer Méditerranée et Sénégal, Afrique de l'Ouest, tous deux redécrits ici à partir des spécimens-types, sont transférés dans *Echinoplectanum* respectivement comme *E. plectropomi* n. comb. et *E. echinophallus* n. comb. Six des sept espèces d'*Echinoplectanum* sont parasites d'espèces de *Plectropomus* du Sud Ouest Pacifique, mais une (*E. echinophallus*) est parasite d'*Epinephelus marginatus* et a été rapportée uniquement de la Méditerranée et de l'Atlantique Est ; on fait l'hypothèse que le genre *Echinoplectanum* est associé à *Plectropomus*, un genre basal parmi les Epinephelinae, et qu'un changement d'hôte est survenu vers *Epinephelus marginatus*, dont l'aire s'étend de l'Europe jusqu'à l'Océan Indien. Les caractéristiques morphologiques de l'appareil copulateur suggèrent qu'une compétition spermatique de type « ceinture de chasteté contre pénis épineux » prévaut chez *Echinoplectanum* spp.

Introduction

Diplectanids parasitic on the gills of epinepheline fish (Serranidae) mostly belong to *Pseudorhabdosynochus* Yamaguti, 1958; more than 25 species have been described in this genus (lists in Santos et al., 2000; Justine, 2005a) and many others are still undescribed. These are characterised by a sclerotised quadriloculate male organ. However, the diplectanids found in the coralgroupers *Plectropomus laevis* (Lacépède) and *P. leopardus* (Lacépède) off New Caledonia cannot be attributed to this genus because their male copulatory organ does not have four sclerotised chambers but instead a tubular sclerotised penis associated with a protrusible cirrus, which is sometimes spiny. We describe here these species and create a new genus for them; two species previously attributed to *Diplectanum*, one from a *Plectropomus* from Australia, and another from an *Epinephelus* from the Mediterranean Sea and Africa, are transferred to the new genus. Hypotheses on the role of the spiny cirrus in sperm competition and host-switching from *Plectropomus* to *Epinephelus* are proposed.

Materials and methods

Specimens of *Plectropomus laevis* ('blacksaddled coralgrouper'; local name: 'saumonée gros points') and *P. leopardus* ('leopard coralgrouper'; local name: 'saumonée') were caught with hand-lines or spear-fished in various places off Nouméa, New Caledonia (see list of stations). Fish were kept in a container with seawater and immediately taken back to the laboratory. All fish were measured, weighed and photographed. A unique number (JNC) was assigned to each fish. The parasitological material was then assigned a corresponding JNC linked to the respective fish host. In the lists of material examined, measurements of hosts are abbreviated as FL (fork length) in millimetres and W (weight) in grams, for possible future comparison of parasite prevalence and host age in other localities. Age was determined, from observation of the otoliths, by Claude Chauvet.

Stations list. These stations, except for Stn E5 which is within the lagoon, are along the barrier reef, at a distance of about 20 km from the shore and with a depth of 5–20 m. Stn E1, Passe de Dumbéa, 22°20′S, 166°15′E, spear-fished by Claude Chauvet, Jean-Louis Pagnon and Mathias Chauchat, 8 November, 2003; Stn E2, off Bancs de l'Ouest, 22°26′30″S, 166°28′00″E, spear-fished by Jean-Louis Menou, 15 December, 2003; Stn E3, near Ever Prosperity wreck, 22°27′30″S, 166°21′45″E, fished by Jean-Louis Pagnon and Claude Chauvet, 23 January, 2004; Stn E4, Récif Le Sournois, 22°31′40″S, 166°26′00″E, line fished from N/O 'Coris', 8 July, 2004; Stn E5, Ilôt Signal (Te Ndu), 22°18′S, 166°17′E, spear-fished by Gérard Mou Tham, 12 October, 2004; Stn E6, Passe de Dumbéa, spear-fished by Claude Chauvet, 15 October, 2004.

Records and infection indices (Table 1). Two *P. laevis* examined: JNC963, FL 790, W 7500, age 14–16 years according to otoliths, stn E1; JNC1037, FL 880, W 9600, age 10 years according to otoliths, stn E3. Six *P. leopardus* examined: JNC1012, FL 465, W 1700, stn E2; JNC1191, FL 527, W 2100, stn E4; JNC1391, FL 290, W 344, stn E5, diplectanids observed alive, no slide kept; JNC1392, FL 380, W 775, stn E5; JNC1393, FL 355, W 555, stn E5; JNC1394, FL 440, W 1250, stn E6.

Remarks on the hosts: *P. laevis* and *P. leopardus* are abundant species off New Caledonia (Laboute & Grandperrin, 2000). *P. laevis* is a large species and adults, off New Caledonia, prefer the barrier reef; its geographical distribution ranges from Eastern Africa to the Austral Islands, but does not reach the Asian coast (Heemstra & Randall, 1993). *P. leopardus* is smaller and specimens can be seen from shallow waters around Nouméa city, even close to bathing beaches, to the external slope of the barrier reef; its geographical distribution is the Western Pacific, from southern Japan to Australia, and is limited in the east to Fiji (Heemstra & Randall, 1993). A third species, *P. areolatus* Rüppell, has been recorded off New Caledonia (Rivaton et al., 1990), but it is rare and we encountered none.

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 prepared according to the 'Carmine' of 'Picrate' methods (see Justine, 2005a). For the 'Carmine' method, monogeneans were put live in a drop of sea-water on a microscope slide placed in a Petri dish. The drop was covered with a 18×18 mm cover-slip obliquely arranged so that

Table 1. Records of species of *Echinoplectanum* n. g. on *Plectropomus* spp.

Parasite species Fish specimen	*E. laeve* n. sp.	*E. chauvetorum* n. sp.	*E. leopardi* n. sp.	*E. pudicum* n. sp.	*E. rarum* n. sp.
P. laevis					
JNC963	23	8			
JNC1037	53	22			
Total	76 (71%)	30 (28%)			
P. leopardus					
JNC1012			10	40	0
JNC1191			69	5	0
JNC1392			11	2	1
JNC1393			10	2	1
JNC1394			28	18	2
Total			128 (64%)	67 (34%)	4 (2%)

Exhaustive collection for JNC1394, non-exhaustive for all others. Only identifiable specimens included; immature and dubious not included. Total number of *Echinoplectanum* specimens identified 305. Total number of diplectanids per fish estimated to be 300–400 for *P. laevis*, 200 for *P. leopardus*.

it overlapped the edge of the slide (this facilitates removal the cover-slip later). A small lead weight (2 g) was placed on the cover-slip and 70% ethanol was poured into the Petri dish. After 24 h or more, the cover-slip was removed and the monogeneans were picked up using a woodcock feather, placed in a small dish and stained with Schneider's Carmine diluted with 70% alcohol. The progress of the staining was followed under a dissecting microscope. A few specimens were not stained. Specimens were rinsed in 70% ethanol, dehydrated through 95% (5 min) and 100% ethanol (5 min), cleared in clove oil (5 min or more) and mounted in Canada balsam dissolved in toluene. For the 'Picrate' method, monogeneans were put live in a small drop of sea-water on a microscope slide, then a tiny drop of ammonium picrate-glycerine (Malmberg, 1957) was deposited with a syringe in (or close to) the drop, and the drop of seawater was immediately covered by a round 15 mm cover-slip. Under a dissecting microscope, water was then aspirated from the edges of the cover-slips with filter paper until the monogeneans were flattened. Slides were immediately examined for the soft internal organs and hooklets. The slides were later sealed with Canada balsam.

Monogeneans were examined and drawn using a BH2 microscope equipped with a camera lucida and DIC optics, which greatly helps with the observation of unstained sclerotised parts. Measurements were taken on the pencil drawings with the help of a custom-made transparent rule, previously calibrated with a stage micrometer. The measurements of the haptoral hard-parts are as in Justine (2005a); the means of the measurements of the right-hand haptoral hard-parts and left-hand equivalents were compared using the Student t-test to ascertain that no bilateral asymmetry was present, and measurements from both sides were then pooled. All measurements are given in micrometres as: holotype, mean of specimens ± standard deviation when appropriate, with range and number in parentheses. Measurements in ammonium picrate preparations and in specimens flattened in ethanol vary for hollow sclerotised organs, the male copulatory organ and sclerotised vagina (Justine, 2005a), and are presented separately for these organs when appropriate. Drawings were scanned and redrawn on a computer with Adobe Illustrator; similar structures for all species, including whole worms, are drawn at similar scales.

In the squamodiscs of the species described here, most rodlets bear "spurs" ("éperons" of Euzet & Oliver, 1965); these are superficial, anteriorly directed structures, often overlapping the rodlet of the previous row; in most drawings, only the basic shape of the rodlets was figured and the spurs were omitted for clarity.

Monogenean material was deposited in the Muséum National d'Histoire Naturelle, Paris (MNHN), the Natural History Museum, London (BMNH) and the United States National Parasite Collection, Beltsville, USA (USNPC).

Echinoplectanum n. g.

Diagnosis

Diplectanidae. Diplectaninae. Two squamodiscs made up of rows of rodlets; first row forms closed circle; most rodlets with anteriorly directed spurs. Male copulatory organ: straight or slightly arched tubular penis, with proximal extremity a muscular reservoir limited by 4 muscular layers and its distal extremity a cirrus, sometimes with acute ridges resembling spines; no accessory piece. Seminal vesicle and prostatic reservoir both connected laterally to muscular reservoir. Vagina a slightly sclerotised sac, often with 2 small sclerotised tubes. Seminal receptacle present or absent. Parasites of marine Perciformes (Serranidae).

Type-species: *E. laeve* n. sp.
Other species: *E. echinophallus* (Euzet & Oliver, 1965) n. comb.; *E. plectropomi* (Young, 1969) n. comb.; *E. chauvetorum* n. sp.; *E. leopardi* n. sp.; *E. pudicum* n. sp.; *E. rarum* n. sp.
Etymology: The suffix '*plectanum*' is used as in *Diplectanum* ('*plectos*', Greek for plaited, twisted) and refers to the squamodiscs; '*echinos*' (Greek for hedgehog) refers to the cirral spines. Gender neuter.

Remarks

Oliver (1987) and others have grouped within *Cycloplectanum* Oliver, 1968 all diplectanines in which the first row of rodlets of the squamodisc is closed. We do not accept this system and consider that all species attributed by Oliver to *Cycloplec-*

tanum should rather be included in *Diplectanum* Diesing, 1858, *Pseudorhabdosynochus* Yamaguti, 1958 or *Echinoplectanum* n. g.

Echinoplectanum n. g. is distinguished from other genera by the morphology of its male copulatory apparatus. Synapomorphies for the new genus are: a muscular reservoir with four layers of thin muscles at the anterior extremity of the penis, and the presence of a spiny cirrus. The presence of two thin tubes associated with the vagina could be an additional synapomorphy for *Echinoplectanum* (but see below the remark on 'double vaginal tubes').

Diplectanum currently contains species with various forms of the male terminal genitalia and might be polyphyletic. Comparison is here restricted to the type-species, *D. aequans* Wagener, 1857. *D. aequans* has been redescribed by Oliver (1987): the male copulatory organ is composed of a tubular sclerotised penis with a muscular bulb at its anterior extremity; the muscular bulb has a thick muscular wall with crossed fibres; and the vas deferens and prostatic canal connect with the terminal (anterior) part of the bulb. *Echinoplectanum* thus can be distinguished from this structure by its muscular reservoir with four thin muscular layers and the lateral position of the connections of the vas deferens and prostatic canal.

Pseudorhabdosynochus has a characteristic male quadriloculate organ with four chambers separated by sclerotised walls. *Echinoplectanum* thus can be distinguished by absence of transverse sclerotised walls in the penis.

Laticola Yang et al., 2006 has recently been described for parasites of *Lates calcarifer* (Centropomidae). The male organ is spoon-shaped with concentric incomplete 'ridges' in the base (Yang et al., 2006). Muscle layers of the muscular reservoir of *Echinoplectanum* are distinct from these 'ridges', because they are complete and because the origins of all muscular layers in *Echinoplectanum* are at the anterior extremity of the penis, whereas the origins of the 'ridges' of *Laticola* are at different levels within the sclerotised organ; in addition, there is no spiny cirrus in *Laticola*. We have observed undescribed members of *Laticola* from *Epinephelus* spp. off New Caledonia and confirm that morphologies of male organs are different. Yang et al. (2006) mentioned 'double vaginal tubes' between the vagina and the seminal receptacle in certain species of *Laticola*; this is reminiscent of the double thin canals seen in several species of *Echinoplectanum*.

***Echinoplectanum laeve* n. sp.**

Type-host: *Plectropomus laevis* (Lacépède) (Perciformes: Serranidae).
Type-locality: Off Nouméa, 22°27′30″S, 166°21′45″E, New Caledonia.
Site: Gills, between secondary gill filaments.
Type-specimens: Holotype, from host MNHN JNC1037B26, near Ever Prosperity wreck, 22°27′30″S, 166°21′45″E, 23 January, 2004; 68 paratypes from hosts JNC963 and JNC1037.
Material studied: In addition to the deposited material, several fresh, unpreserved specimens were examined.
Type-material: MNHN, holotype, Carmine, and 68 paratypes, Carmine, on 17 slides from host JNC963 and 51 slides from host JNC1037; BMNH No. 2005.7.20.7, paratype (from host JNC1037); USNPC 97111, paratype (from host JNC1037).
Records and infection indices: See Table 1.
Etymology: Named after the type-host; in addition, the epithet *laeve* (Latin for smooth) is not inappropriate for a diplectanid without tegumental body scales.

Description (Figures 1–2)

Body length 650, 740 ± 104 (550–950, n = 42), width 370, 330 ± 50 (190–430, n = 45). Tegument smooth. Anterior region with 3 pairs of head-organs and 2 pairs of eye-spots; distance between outer margins of anterior eye-spot pair 47, 47 ± 7 (32–60, n = 37), between posterior eye-spot pair 37, 39 ± 6 (30–53, n = 38).

Haptor differentiated from rest of body, width 290, 269 ± 29 (200–330, n = 39), provided with 2 similar squamodiscs, 2 pairs of lateral anchors, 3 bars and 14 marginal hooklets. Squamodiscs round in shape, made up of rows of separate rodlets, with 3 central rows forming closed circles and fourth row almost closed; rodlets interlocking and robust in inner rows, progressively becoming thin and separate in peripheral rows; most rodlets, except those of central circle, bear single spur; spurs external, directed anteriorly, often overlapping rodlet of previous row; ventral squamodisc, length 80, 77 (65–86, n = 18), width 80, 79 (68–88, n = 18), with 13, 13 (n = 20) rows of rodlets including 3, 3 (n = 22) rows forming closed circles; dorsal squamodisc, length 80, 78 (68–94, n = 12), width 73, 75 (70–81, n = 12), with 14, 13

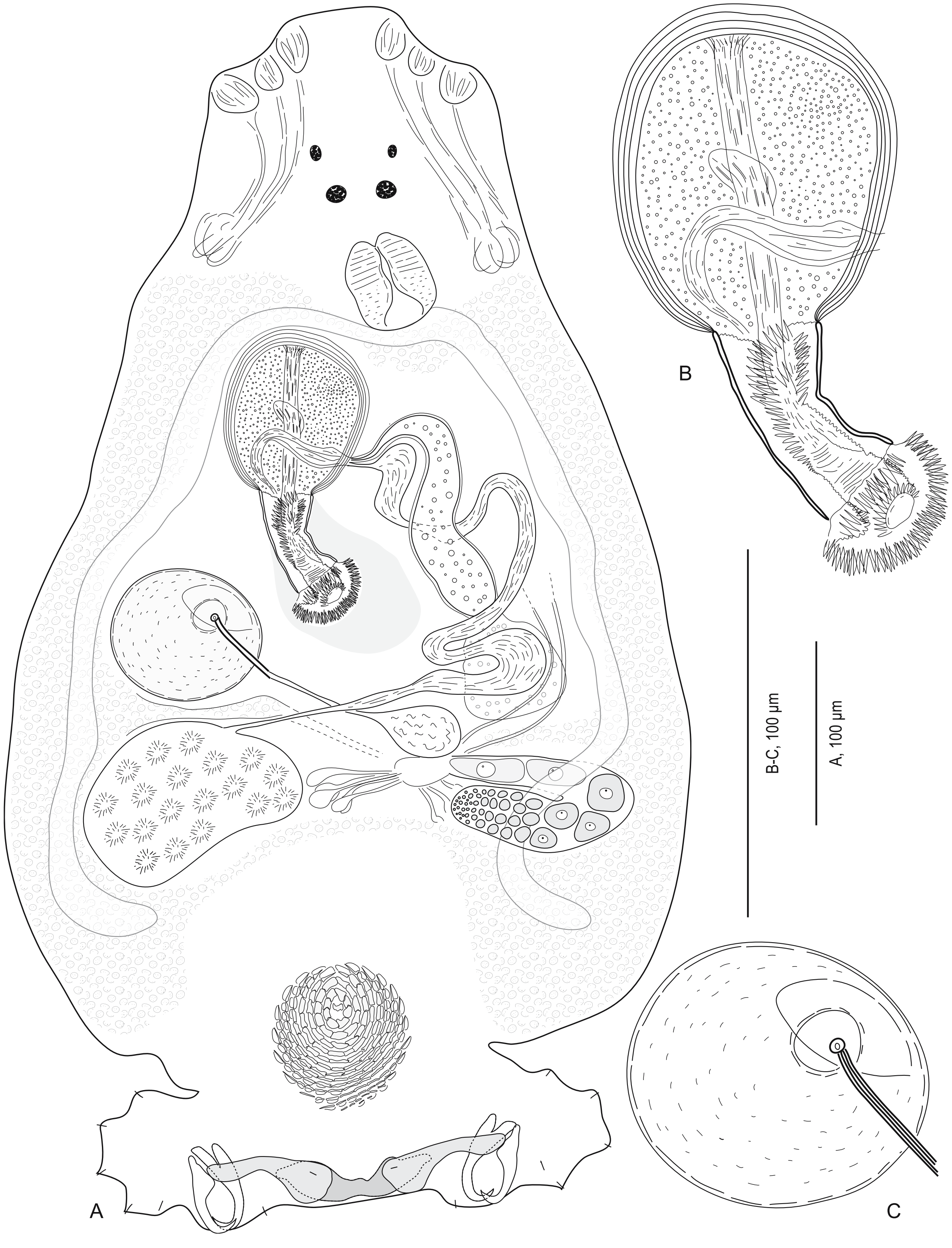

Figure 1. Echinoplectanum laeve n. sp.: A. Habitus (dorsal view; composite drawing from holotype and observations of other specimens); B. Male copulatory organ, holotype; C. Vagina, holotype. All Carmine.

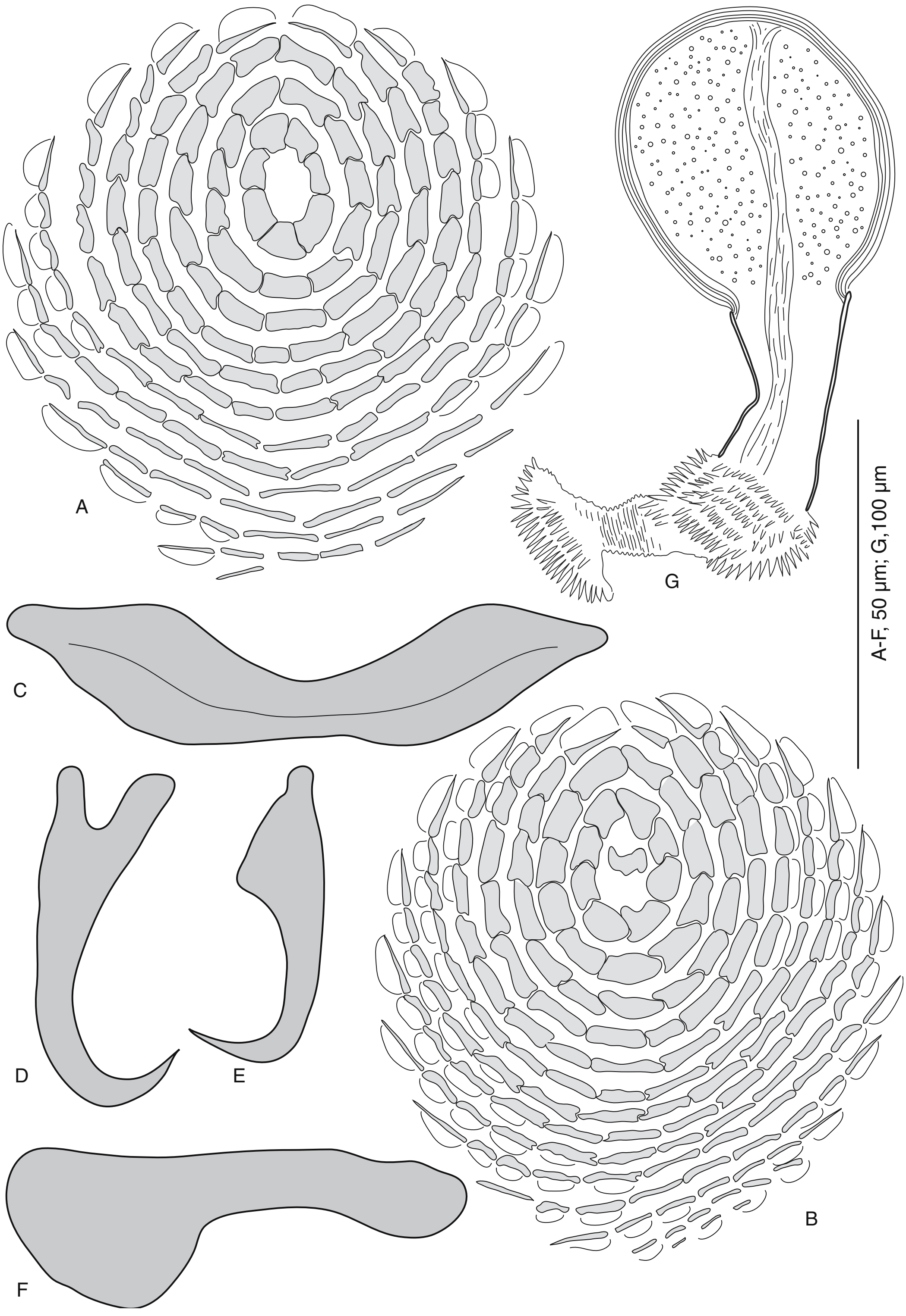

Figure 2. *Echinoplectanum laeve* n. sp.: A. Dorsal squamodisc, holotype; B. Ventral squamodisc, holotype; spurs on rodlets present but not figured for clarity; C. Ventral bar; D. Ventral anchor. E. Dorsal anchor. F. Dorsal bar. G. Male copulatory organ in a paratype specimen with protruded cirrus showing two regions with spines. All Carmine.

(n = 9) or 14 (n = 7) rows of rodlets including 3, 3 (n = 16) rows forming closed circles. Ventral anchors with handle and distinct guard, outer length 48, 48 ± 2 (43–53, n = 85), inner length 47, 47 ± 2 (38–52, n = 83). Dorsal anchors with indistinct guard, outer length 43, 43 ± 2 (35–48, n = 85), inner length 27, 27 ± 2 (23–32, n = 81). Dorsal (lateral) bars curved, with flattened medial extremity and roughly cylindrical lateral extremity, length 68, 67 ± 4 (53–78, n = 92), maximum width 21, 20 ± 3 (13–26, n = 91). Ventral bar flat, with constricted median portion with broad anteromedial process and pointed extremities, length 84, 80 ± 6 (64–90, n = 46), maximum width 20, 17 ± 2 (13–22, n = 46); groove visible on its ventral side. Hooklets 9–10 in length.

Mouth subterminal. Pharynx subspherical, length 51, 50 ± 4 (40–60, n = 42), width 40, 42 ± 5 (35–52, n = 42). Oesophagus apparently absent, such that intestinal bifurcation immediately follows pharynx. Intestinal caeca simple, terminate blindly at level of posterior margin of vitelline field.

Testis subspherical, intercaecal, length 80, 82 ± 16 (40–130, n = 37), width 120, 124 ± 22 (80–180, n = 37). Vas deferens passes antero-dextrally from testis, dilates to form seminal vesicle in middle right region of body; seminal vesicle forms loop; male duct then narrows, loops prostatic reservoir from dorsal to ventral side; no ejaculatory bulb. Prostatic glands, ventral to seminal vesicle, enter prostatic reservoir. Penis a sclerotised cylinder, longer than wide, slightly constricted in its centre; length 48, 53 ± 5 (42–65, n = 46), distal diameter 25, 26 ± 3 (17–32, n = 46), minimum diameter 18, 20 ± 2 (16–28, n = 46); prominent muscular reservoir at proximal (anterior) extremity of penis with 4 muscular layers of similar width; muscular reservoir length 80, 79 ± 7 (50–92, n = 46), width 80, 71 ± 6 (58–80, n = 46); longitudinal muscular structure central in muscular reservoir; protrusible cirrus extends from distal (posterior) extremity of penis; cirrus with numerous folds and acute ridges looking like spines; in certain specimens with protruding cirrus, 2 spined regions are visible (Figure 2G). Male duct and anterior extremity of prostatic vesicle enter muscular reservoir at same place on its right side.

Ovary subequatorial, dextral, intercaecal, at same level as testis, grades into oviduct, loops right caecum from dorsal to ventral side. Ovary width 100, 105 ± 20 (70–160, n = 38), length 50, 54 ± 15 (25–80, n = 38). Oviduct passes medially to form oötype, surrounded by Mehlis' gland; oötype short, opens into uterus. Uterus dextral. Sclerotised vagina sinistral, a slightly sclerotised sac, round or oval in shape, length 80, 77 ± 15 (40–105, n = 30), width 90, 75 ± 12 (40–90, n = 30); from centre of sac, 2 thin, parallel sclerotised tubes end together in single unsclerotised duct; duct crosses vas deferens ventrally, passes postero-dextrally to seminal receptacle. Seminal receptacle spherical, just anterior to oviduct and oötype. Vitelline fields extend posteriorly from posterior to pharyngeal level in 2 lateral bands, confluent in thin band just posterior to testis and ovary, and terminate anterior to peduncle, leaving large free space around squamodiscs. Bilateral connections (transverse vitelloducts) from vitelline fields to oötype inconspicuous; left between testis and vaginal sac; right anterior to oviduct. Egg not known.

Differential diagnosis

This species is readily distinguished from other species of the same genus by its large size and the large size of its male copulatory organ, with very visible spiny ridges on the cirrus, and the shape of its sclerotised vagina with two long thin tubes.

Remarks

This species is apparently the most abundant *Echinoplectanum* species in *Plectropomus laevis.*

A few specimens were found with a deformed male copulatory apparatus, containing various structures highly stained by carmine. However, the vaginal structure in these specimens was typical, with the two characteristic tubes. These specimens were interpreted as abnormal or possibly pathological specimens, and were excluded from the type-series.

See below the paragraph on a hypothesis on sperm competition for a remark about spines on the male cirrus and the biology of fertilisation.

***Echinoplectanum chauvetorum* n. sp.**

Type-host: *Plectropomus laevis* (Lacepède) (Perciformes, Serranidae).
Type-locality: Off Nouméa, 22°27′30″S, 166°21′45″E, New Caledonia.
Site: Gills, between secondary gill filaments.

Type-specimens: Holotype, MNHN JNC1037B32, near Ever Prosperity wreck, 22°27′30″S, 166°21′45″E, 23 January, 2004; 30 paratypes from hosts JNC963 and JNC1037.

Material examined: In addition to the material deposited, several fresh unpreserved specimens were studied.

Type-material: MNHN, holotype, Carmine, and 30 paratypes, Carmine, in 8 slides from host JNC963 and 22 slides from host JNC1037; BMNH No. 2005.7.20.6, paratype (from host JNC1037); USNPC 97112, paratype (from host JNC1037).

Records and infection indices: See Table 1.

Etymology: Named for Professor Claude Chauvet, a renown specialist of grouper biology, and his wife Gisèle Chauvet, who kindly provided, among many other fish, several of the fish hosts used in this study.

Description (Figures 3–4)

Body length 670, 719 (530–950, n = 21), width 340, 337 (240–410, n = 23). Tegument smooth. Anterior region with 3 pairs of head organs and 2 pairs of eye-spots; distance between outer margins of anterior eye-spot pair 41, 45 (30–54, n = 20), between posterior eye-spot pair 34, 40 (26–48, n = 23).

Haptor differentiated from rest of body, width 270, 258 (205–320, n = 22), provided with 2 similar squamodiscs, 2 pairs of lateral anchors, 3 bars and 14 marginal hooklets. Squamodiscs round in shape, made up of rows of separate rodlets, with 3 central rows forming closed circles; rodlets interlocking and robust in inner rows, becoming progressively thinner and separate in peripheral rows; most rodlets, except those of central circle, bear single spur; spurs external, directed anteriorly, often overlapping rodlet of previous row; ventral squamodisc, length 70, 71 (62–82, n = 10), width 70, 76 (70–87, n = 10), with 13, 13 (n = 9) or 12 (n = 2) rows of rodlets including 3, 3 (n = 12) rows forming closed circles; dorsal squamodisc, length 75, 72 (68–75, n = 9), width 73, 68 (65–73, n = 9), with 14, 13 (n = 5) or 14 (n = 4) rows of rodlets including 3, 3 (n = 10) rows forming closed circles. Ventral anchors with handle and distinct guard, outer length 48, 48 ± 3 (43–53, n = 42), inner length 47, 47 ± 2 (44–52, n = 40). Dorsal anchors with indistinct guard, outer length 43, 42 ± 2 (38–46, n = 42), inner length 27, 26 ± 1 (23–29, n = 41). Dorsal (lateral) bars curved, with flattened medial extremity and roughly cylindrical lateral extremity, length 64, 64 ± 3 (58–72, n = 42), maximum width 23, 21 ± 2 (15–26, n = 42). Ventral bar flat, with constricted median portion with broad anteromedial process and pointed extremities, length 74, 74 (67–80, n = 21), maximum width 18, 16 (13–19, n = 21); groove visible on its ventral side. Hooklets 9–10 in length.

Mouth subterminal. Pharynx subspherical, length 51, 48 (32–55, n = 23), width 41, 42 (32–50, n = 23). Oesophagus apparently absent, such that intestinal bifurcation immediately follows pharynx. Intestinal caeca simple, terminate blindly at level of posterior margin of vitelline field.

Testis subspherical, intercaecal, length 50, 78 (40–130, n = 21), width 130, 111 (55–170, n = 21). Vas deferens passes antero-dextrally from testis, dilates to form seminal vesicle in dextro-medial region of body; seminal vesicle forms loop; male duct then narrows, loops prostatic reservoir from dorsal to ventral side; no ejaculatory bulb. Prostatic glands ventral to seminal vesicle, enter prominent prostatic reservoir. Penis a sclerotised cylinder, longer than wide, slightly wider at its proximal (anterior) extremity; length 65, 51 (40–65, n = 23), proximal diameter 38, 29 (22–40, n = 23), distal diameter 22, 17 (10–25, n = 23); prominent muscular reservoir at proximal (anterior) extremity of penis with 4 muscular layers of similar width; size of muscular reservoir and width of muscular layers vary in different specimens, apparently according to degree of replenishment (Figures 3B, 4J); muscular reservoir length 95, 79 (60–100, n = 23), width 70, 65 (48–85, n = 23); longitudinal muscular structure central in muscular reservoir; protrusible cirrus within penis; cirrus with numerous folds, including tiny spine-shaped folds. Male duct and anterior extremity of prostatic vesicle enter muscular reservoir at same place on its right side.

Ovary subequatorial, dextral, intercaecal, at same level as testis, grades into oviduct, loops right caecum from dorsal to ventral side. Ovary width 115, 110 (80–135, n = 19), length 50, 46 (30–65, n = 19). Oviduct passes medially to form oötype, surrounded by Mehlis' gland; oötype short, opens into uterus. Sclerotised vagina sinistral, a slightly sclerotised sac, pear-shaped, length 115, 119 (77–165, n = 21), width 65, 45 (30–70, n = 21); pointed (posterior) extremity of sac finishes in

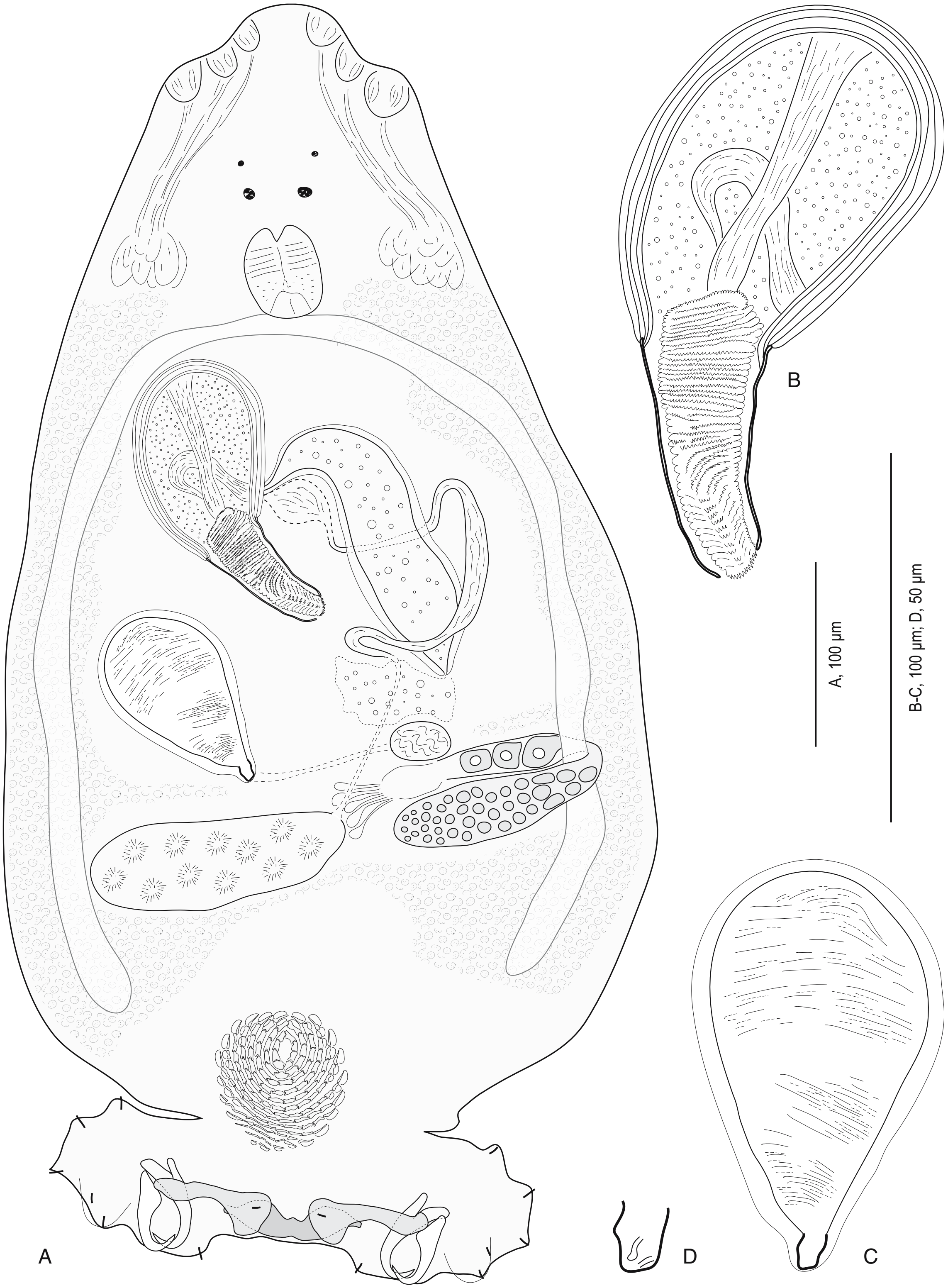

Figure 3. Echinoplectanum chauvetorum n. sp.: A. Habitus (dorsal view; composite drawing from holotype and observations on other specimens); B. Male copulatory organ, holotype; C. Vagina, holotype. D. Extremity of vagina showing small tubes. All Carmine.

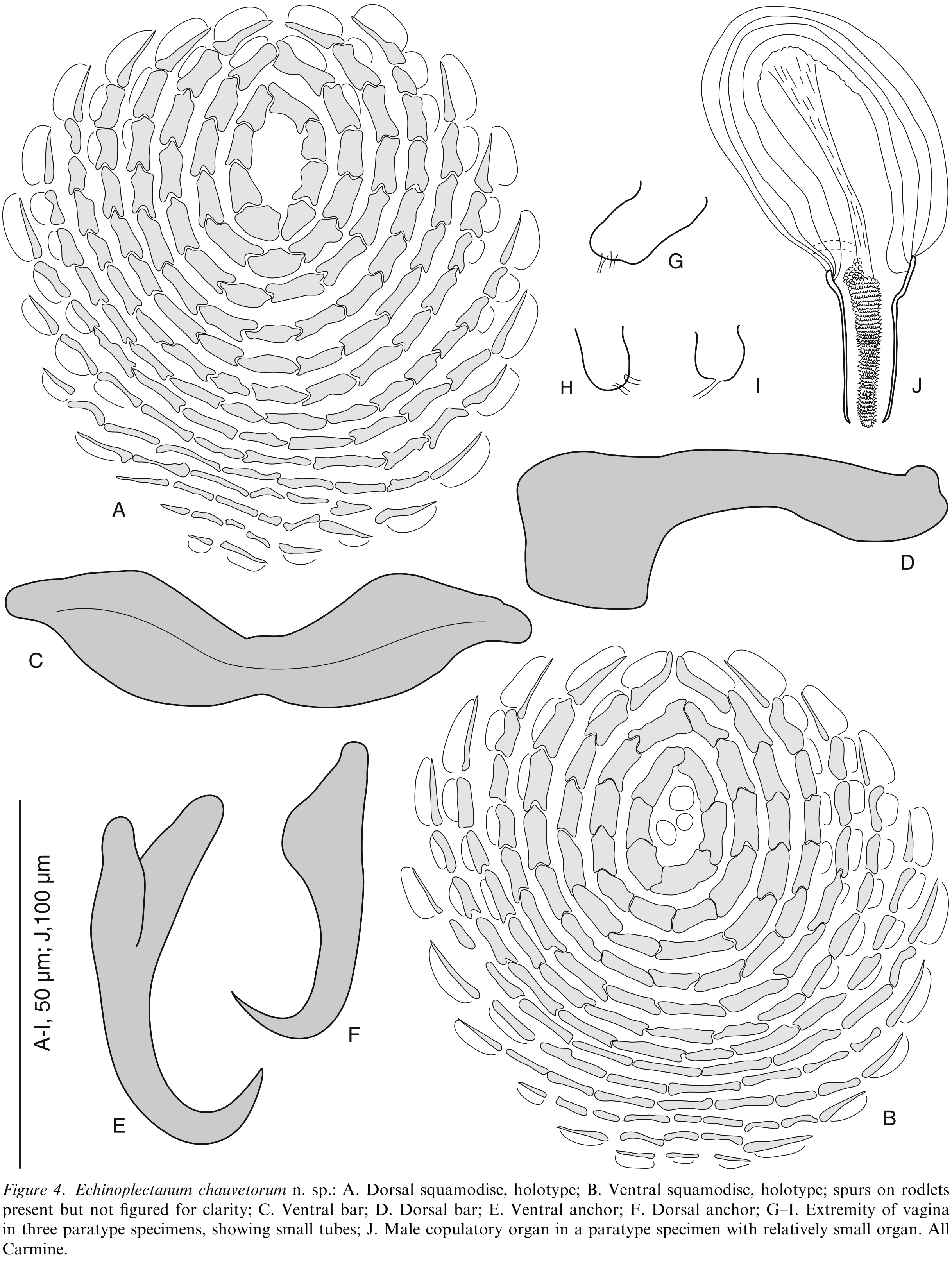

Figure 4. *Echinoplectanum chauvetorum* n. sp.: A. Dorsal squamodisc, holotype; B. Ventral squamodisc, holotype; spurs on rodlets present but not figured for clarity; C. Ventral bar; D. Dorsal bar; E. Ventral anchor; F. Dorsal anchor; G–I. Extremity of vagina in three paratype specimens, showing small tubes; J. Male copulatory organ in a paratype specimen with relatively small organ. All Carmine.

blind cup-shaped sclerotised structure with two thin sclerotised tubes (Figures 3D, 4G–I). Unsclerotised duct from vagina crosses vas deferens ventrally, passes postero-dextrally to seminal receptacle. Seminal receptacle spherical, located just anterior to oviduct and oötype. Vitelline fields extend posteriorly from posterior to pharyngeal level in 2 lateral bands, confluent in thin band just posterior to testis and ovary, and terminate anterior to peduncle, leaving large free space around squamodiscs. Bilateral connections (transverse vitelloducts) from vitelline fields to oötype inconspicuous; left between testis and vaginal sac; right anterior to oviduct. Egg unknown.

Differential diagnosis

This species is readily distinguished from other species of the same genus by the size and shape of its male and female copulatory organs.

Remarks

This species is apparently the less abundant *Echinoplectanum* species found on *P. laevis*.

Specimens exhibited spectacular variations in the size of the muscular reservoir of the male copulatory organ, which might be related to its pre- or post-copulation status. This was not seen to such an extent in other species. See below the paragraph on an hypothesis on sperm competition for remarks on the size of the male accessory glands and the biology of fertilisation.

***Echinoplectanum leopardi* n. sp.**

Type-host: *Plectropomus leopardus* (Lacépède) (Perciformes, Serranidae).
Type-locality: Off Nouméa, 22°31′40″S, 166°26′00″E, New Caledonia.
Site: Gills, between secondary gill filaments.
Type-specimens: Holotype, MNHN JNC1191A8, Récif Le Sournois, 22°31′40″S, 166°26′00″E, 8 July, 2004; 47 Paratypes from hosts JNC1012, JNC1191, JNC1392, JNC1393 and JNC1394.
Other material examined: In addition to the material deposited, several fresh unpreserved specimens, and about 50 specimens in Carmine and Picrate were studied but excluded from the type-series.
Type-material: MNHN, holotype, Carmine, and 47 paratypes: 2 on 2 Carmine slides from host JNC1012; 10 in 10 Carmine slides from host JNC1191; 11 on 3 Picrate slides from host 1392; 10 on 2 Picrate slides from host 1393; 14 on 7 Picrate slides from host 1394; BMNH No. 2005.7.20.4, paratype (from host JNC1012); USNM 97113, paratype (from host xxxxxxx).
Records and infection indices: See Table 1.
Etymology: The specific epithet *leopardi* is the genitive form of *leopardus* and relates to the type-host.

Description (Figure 5)

Body length 580, 570 ± 152 (235–1100, n = 41), width 170, 247 ± 75 (140–400, n = 39). Tegument smooth. Anterior region with 3 pairs of head organs and 2 pairs of eye-spots; distance between outer margins of anterior eye-spot pair 37, 40 ± 9 (22–58, n = 40), between posterior eye-spot pair 30, 35 ± 9 (14–55, n = 43).

Haptor differentiated from rest of body, width 130, 182 ± 38 (100–230, n = 34), provided with 2 similar squamodiscs, 2 pairs of lateral anchors, 3 bars and 14 marginal hooklets. Squamodiscs round in shape, made up of rows of separate rodlets, with 2–3 central rows forming closed circles; rodlets interlocking and robust in inner rows, progressively becoming thinner and separate in peripheral rows; most rodlets, except those of central circle, bear single spur; spurs external, directed anteriorly, often overlapping rodlet of previous row; ventral squamodisc, length 45, 48 (35–60, n = 20), width 48, 52 (40–60, n = 20), with 12, 12 (n = 8), 11 (n = 7) or 10 (n = 3) rows of rodlets including 3, 3 (n = 11) or 2 (n = 9) rows forming closed circles; dorsal squamodisc, length 43, 49 (41–65, n = 16), width 46, 50 (44–58, n = 16), with 12, 12 (n = 12), 11 (n = 3) or 10 (n = 1) rows of rodlets including 3, 3 (n = 9) or 2 (n = 8) rows forming closed

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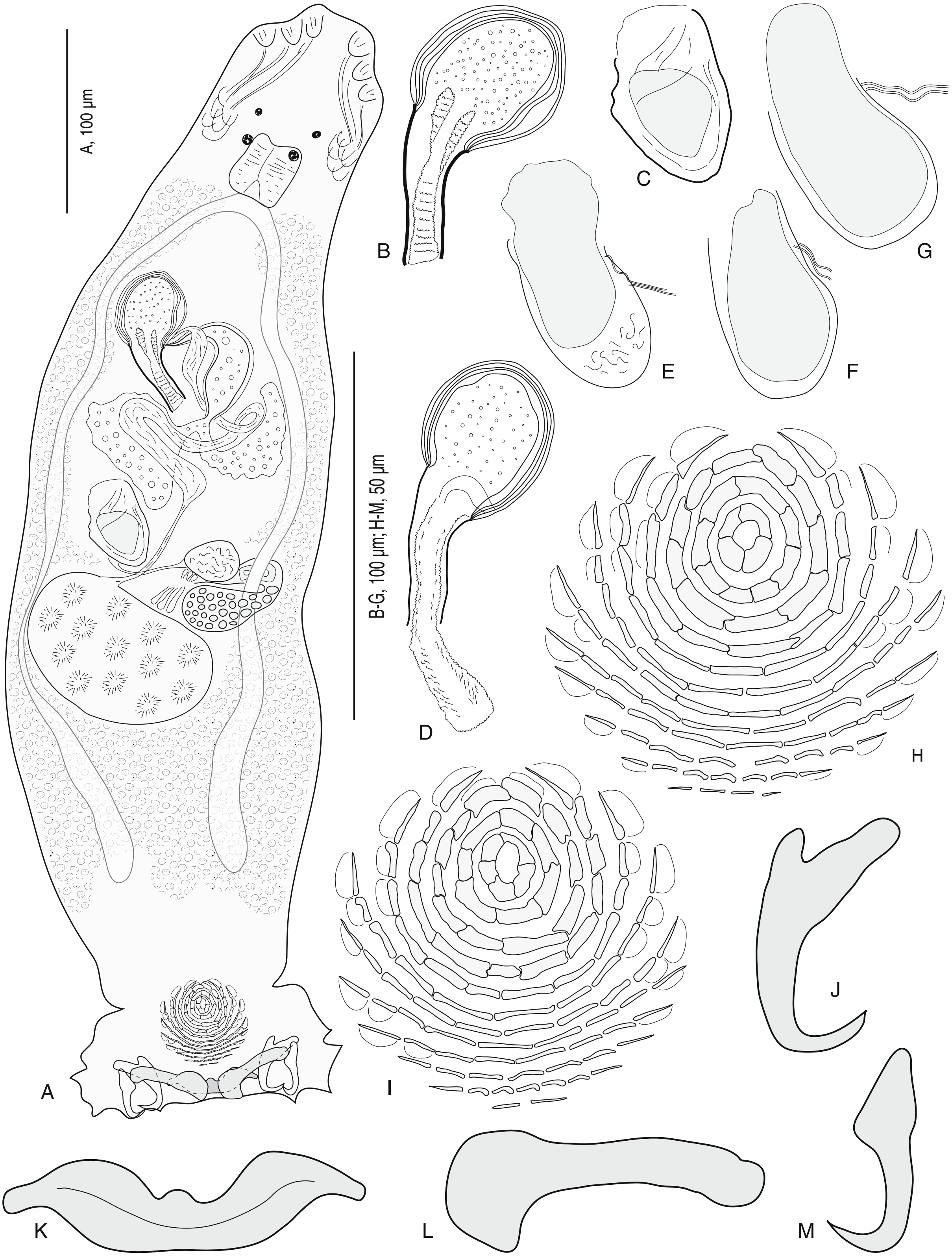
Figure 5. Echinoplectanum leopardi n. sp.: A. Habitus (dorsal view; composite drawing from holotype and observations on other specimens); B. Male copulatory organ, holotype; C. Vagina (holotype); D. Male copulatory organ with protruded cirrus, paratype; E–G. Aspects of vaginal sac and thin tubes in three paratypes; H. Dorsal squamodisc, paratype; I. Ventral squamodisc, paratype; spurs on rodlets present but not figured for clarity; J. Ventral anchor; K. Ventral bar; L. Dorsal bar; M. Dorsal anchor. All Carmine.


A, 100 µm
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circles. Ventral anchors with handle and distinct guard, outer length 32, 34 ± 3 (27–39, n = 81), inner length 32, 32 ± 1 (29–35, n = 82). Dorsal anchors with indistinct guard, outer length 28, 29 ± 2 (25–33, n = 83), inner length 17, 18 ± 1 (14–20, n = 81). Dorsal (lateral) bars curved, with flattened medial extremity and roughly cylindrical lateral extremity, length 46, 49 ± 5 (38–57, n = 84), maximum width 14, 15 ± 2 (12–19, n = 77). Ventral bar flat, with constricted median portion with broad anteromedial process and pointed extremities, length 43, 61 ± 9 (43–73, n = 42), maximum width 12, 12 ± 2 (8–18, n = 42); groove visible on its ventral side. Hooklets 9–10 in length.

Mouth subterminal. Pharynx subspherical, length 36, 40 ± 6 (28–58, n = 44), width 27, 38 ± 8 (27–64, n = 44). Oesophagus apparently absent, such that intestinal bifurcation immediately follows pharynx. Intestinal caeca simple, terminate blindly at level of posterior margin of vitelline field.

Testis subspherical, intercaecal, length 80, 79 ± 13 (55–110, n = 25), width 100, 97 ± 21 (60–150, n = 25). Vas deferens passes anteriorly from testis, dilates to form seminal vesicle in middle left region of body; seminal vesicle forms loop; male duct then narrows, loops prostatic reservoir from dorsal to ventral side; ejaculatory bulb absent. Prostatic glands, prominent, ventral to seminal vesicle and male duct, enter prostatic reservoir; length of prostatic reservoir 50, 56 (50–80, n = 7). Penis a sclerotised cylinder, longer than wide, slightly wider at its proximal (anterior) extremity; length 37, 36 ± 4 (30–47, n = 43), proximal diameter 18, 21 ± 2 (17–25, n = 42), distal diameter 10, 11 ± 2 (8–15, n = 42); measurements in Carmine (C) *vs* Picrate (P): lengths similar, proximal diameter 18 (C, n = 9) *vs* 22 (P, n = 33), distal diameter 9 (C, n = 9) *vs* 11 (P, n = 33); muscular reservoir at proximal (anterior) extremity of penis with 4 muscular layers of similar width; muscular reservoir length 40, 34 ± 10 (24–60, n = 43), width 37, 34 ± 9 (25–58, n = 43); cirrus with numerous folds within penis, sometimes exerted. Male duct and anterior extremity of prostatic vesicle enter muscular reservoir at same place on its right side.

Ovary dextral, subequatorial, intercaecal, at level of anterior extremity of testis, grades into oviduct, loops right caecum from dorsal to ventral side. Ovary width 64 ± 11 (50–80, n = 12), length 42 ± 18 (20–70, n = 12). Oviduct passes medially to form oötype, surrounded by Mehlis' gland. Sclerotised vagina sinistral, a sclerotised sac apparently open in its anterior extremity; sac length 45, 45 ± 6 (30–55, n = 42), width 32, 33 ± 9 (20–58, n = 42); measurements in Carmine (C) *vs* Picrate (P): lengths similar, width 28 (C, n = 10) *vs* 34 (P, n = 32); 2 thin sclerotised tubes visible on side of sac, their aspect variable according to specimen and orientation (Figures 5C,E–G). Vaginal sac often contains homogeneous mass which apparently closes sac; spermatozoa sometimes visible in blind end of sac (Figure 5E). Unsclerotised duct from vaginal sac crosses vas deferens ventrally, passes postero-dextrally to seminal receptacle. Seminal receptacle spherical, located just anterior to oviduct and oötype. Vitelline fields extend posteriorly from posterior to pharyngeal level in 2 lateral bands, confluent in large zone posterior to testis and ovary, terminate anterior to peduncle leaving large free space around squamodiscs. Bilateral connections from vitelline fields to oötype inconspicuous; left between testis and vaginal sac; right anterior to oviduct. Egg not known.

Differential diagnosis

This species is readily distinguished from other species of the same genus by the size and shape of its male and female copulatory organs.

Remarks

This species is apparently the most abundant species found in *P. leopardus*, except in the case of one host (Table 1).

The presence of an amorphous mass in the vaginal sac suggests the possibility of a spermatophore or copulatory plug being deposited by the male organ of the hermaphroditic partner to insure that no further copulation is possible with another sexual partner. See the paragraph below for an hypothesis on sperm competition in relation to remarks on copulatory plugs and the biology of fertilisation.

***Echinoplectanum pudicum* n. sp.**

Type-host: *Plectropomus leopardus* (Lacépède) (Perciformes, Serranidae).

Type-locality: Off Nouméa, 22°26′30″S, 166°28′00″E, New Caledonia.

Site: Gills, between secondary gill filaments.

Type-specimens: Holotype, MNHN JNC1012A11, off Bancs de l'Ouest, 22°26′30″S, 166°28′00″E, 15 December, 2003; 39 Paratypes from hosts JNC1012, JNC1191, JNC1392, JNC1393, and JNC1394.

Other material studied: In addition to the material deposited, several fresh unpreserved specimens and about 20 specimens in Picrate or Carmine which are excluded from the type-series were examined.

Material deposited: MNHN, Paris, holotype, Carmine, and 20 paratypes on 18 Carmine slides and 2 unstained slides from host JNC1012; 2 on 1 Picrate slide from host 1392; 2 on 1 Picrate slide from host 1393; 15 on 3 Picrate slides from host 1394; BMNH No. 2005.7.20.5, paratype (from host JNC1012); USNPC 97114, paratype (from host JNC1012).

Records and infection indices: See Table 1.

Etymology: The epithet *pudicum* (Latin, bashful, chaste) refers to the low level of development of the reproductive organs.

Description (Figure 6)

Body length 480, 417 ± 64 (320–570, n = 36), width 210, 211 ± 35 (130–280, n = 38). Tegument smooth. Anterior region with 3 pairs of head organs and 2 pairs of eye-spots; distance between outer margins of anterior eye-spot pair 38, 36 ± 9 (20–58, n = 31), between posterior eye-spot pair 32, 29 ± 7 (18–44, n = 36).

Haptor differentiated from rest of body, width 170, 166 ± 20 (120–205, n = 34), provided with 2 similar squamodiscs, 2 pairs of lateral anchors, 3 bars and 14 marginal hooklets. Squamodiscs round in shape, made up of rows of separate rodlets, with 2–3 central rows forming closed circles; rodlets interlocking and robust in inner rows, becoming progressively thinner and separate in peripheral rows; most rodlets, except those of central circle, bear single spur; spurs external, directed anteriorly, often overlapping rodlet of previous row; ventral squamodisc, length 54, 52 (37–65, n = 23), width 58, 53 (40–66, n = 22), with 11, generally 11 (n = 20) or 10 (n = 2), 12 (n = 1) rows of rodlets including 2, mostly 2 (n = 17) or 3 (n = 6) rows forming closed circles; dorsal squamodisc, length 48, 50 (38–65, n = 21), width 55, 54 (40–62, n = 20), with 10, generally 12 (n = 13) or 13 (n = 2), 11 (n = 4), 10 (n = 1) rows of rodlets including 2, 2 (n = 20) rows forming closed circles. Ventral anchors with handle and distinct guard, outer length 32, 31 ± 2 (27–37, n = 84), inner length 32, 31 ± 1 (28–33, n = 76). Dorsal anchors with indistinct guard, outer length 28, 28 ± 2 (22–32, n = 84), inner length 17, 17 ± 1 (15–18, n = 66). Dorsal (lateral) bars curved, with flattened medial extremity and roughly cylindrical lateral extremity, length 43, 43 ± 3 (36–50, n = 84), maximum width 15, 16 ± 2 (11–19, n = 77). Ventral bar flat, with constricted median portion bearing broad anteromedial process and pointed extremities, length 52, 52 ± 4 (43–59, n = 42), maximum width 13, 12 ± 1 (8–15, n = 41); groove visible on its ventral side. Hooklets 9–10 in length.

Mouth subterminal. Pharynx subspherical, length 33, 34 ± 5 (23–49, n = 40), width 30, 32 ± 6 (23–49, n = 40). Oesophagus apparently absent, such that intestinal bifurcation immediately follows pharynx. Intestinal caeca simple, terminate blindly at level of posterior margin of vitelline field.

Testis small, subspherical, intercaecal, length 35, 32 (25–50, n = 19), width 33, 30 (20–45, n = 19). Vas deferens not seen; seminal vesicle loops then narrows to form duct which enter male copulatory organ. Prostatic reservoir small. Penis very small, a thin-walled sclerotised cylinder, longer than wide, slightly wider at its proximal (anterior) extremity, length 14, 12 ± 2 (9–15, n = 38), proximal diameter 8, 7 ± 1 (5–8, n = 40), distal diameter 7, 6 ± 1 (5–8, n = 39), measurements similar in Carmine and Picrate; muscular reservoir at proximal (anterior) extremity of penis with muscular layers indistinct; muscular reservoir length 10, 12 ± 2 (8–15, n = 40), width 12, 13 ± 2 (10–17, n = 40). Male duct and anterior extremity of prostatic vesicle enter muscular reservoir laterally at same place.

Ovary dextral, subequatorial, intercaecal, at level of testis, grades into oviduct, loops right caecum from dorsal to ventral side, width 50, 63 (40–80, n = 19), length 40, 54 (27–90, n = 19). No sclerotised vagina. Other details of female ducts not seen. Vitelline fields extend posteriorly from posterior to pharyngeal level in 2 lateral bands, confluent posterior to testis and ovary, terminate

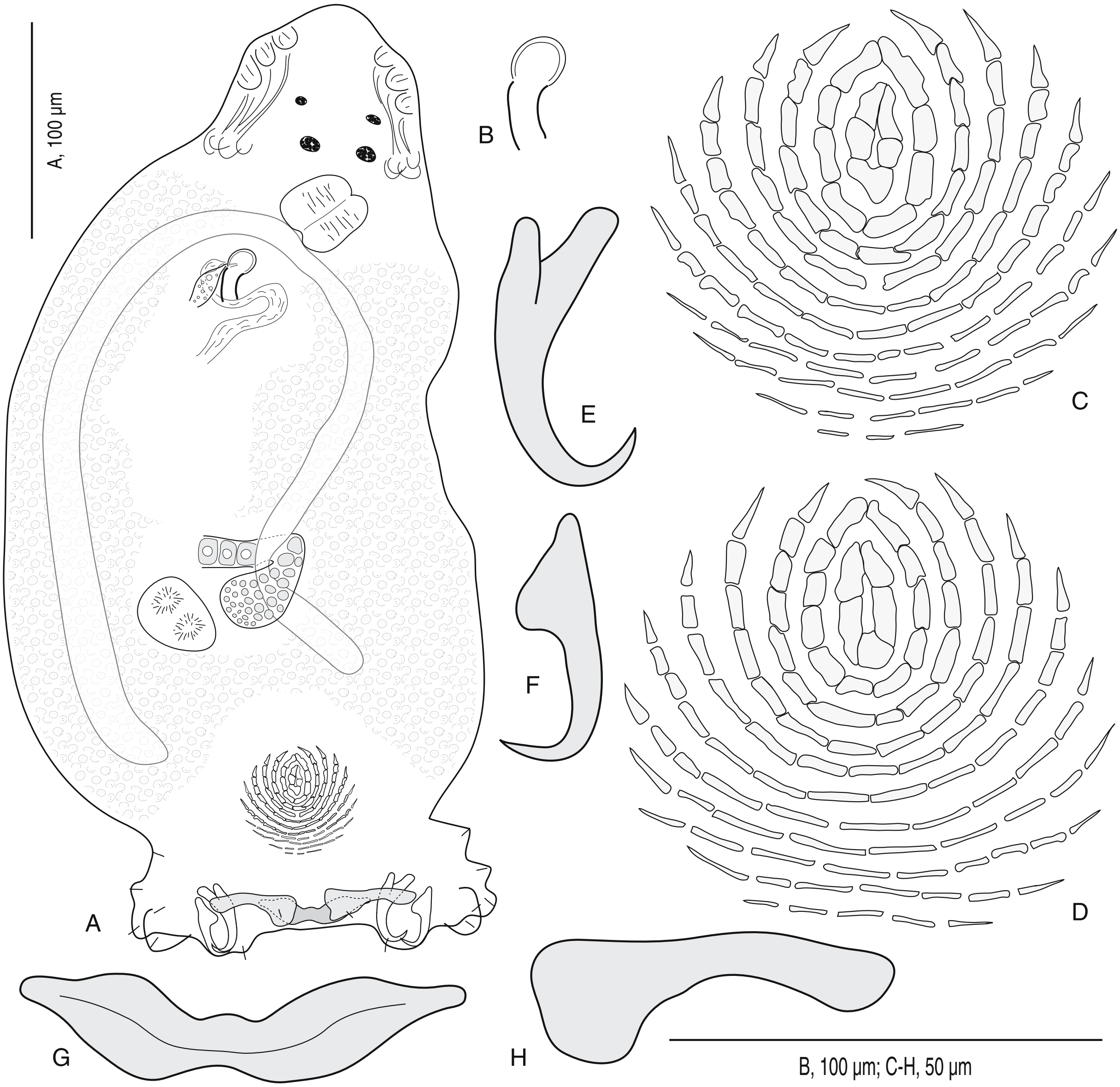

Figure 6. *Echinoplectanum pudicum* n. sp.: A. Habitus (dorsal view; composite drawing from holotype and observations on other specimens); B. Male copulatory organ, holotype; C. Dorsal squamodisc, paratype; D. Ventral squamodisc, paratype; spurs on rodlets present but not figured for clarity; E. Ventral anchor; F. Dorsal anchor; G. Ventral bar; H. Dorsal bar. All Carmine.

anterior to peduncle leaving large free space around squamodiscs. Bilateral connections from vitelline fields to oötype, anterior to testis (left) and oviduct (right). Egg: immature hatched egg seen once, 65×45, with filament 50 still within body.

Differential diagnosis

This species is readily distinguished from all other species of the genus by the shape and small size of its male copulatory organ, and the apparent absence of a sclerotised vagina.

Remarks

This species was less abundant than *E. leopardi* n. sp. in most fish specimens but was the most abundant species in one (Table 1).

This species is characterised by the extremely small size of its male copulatory organ and

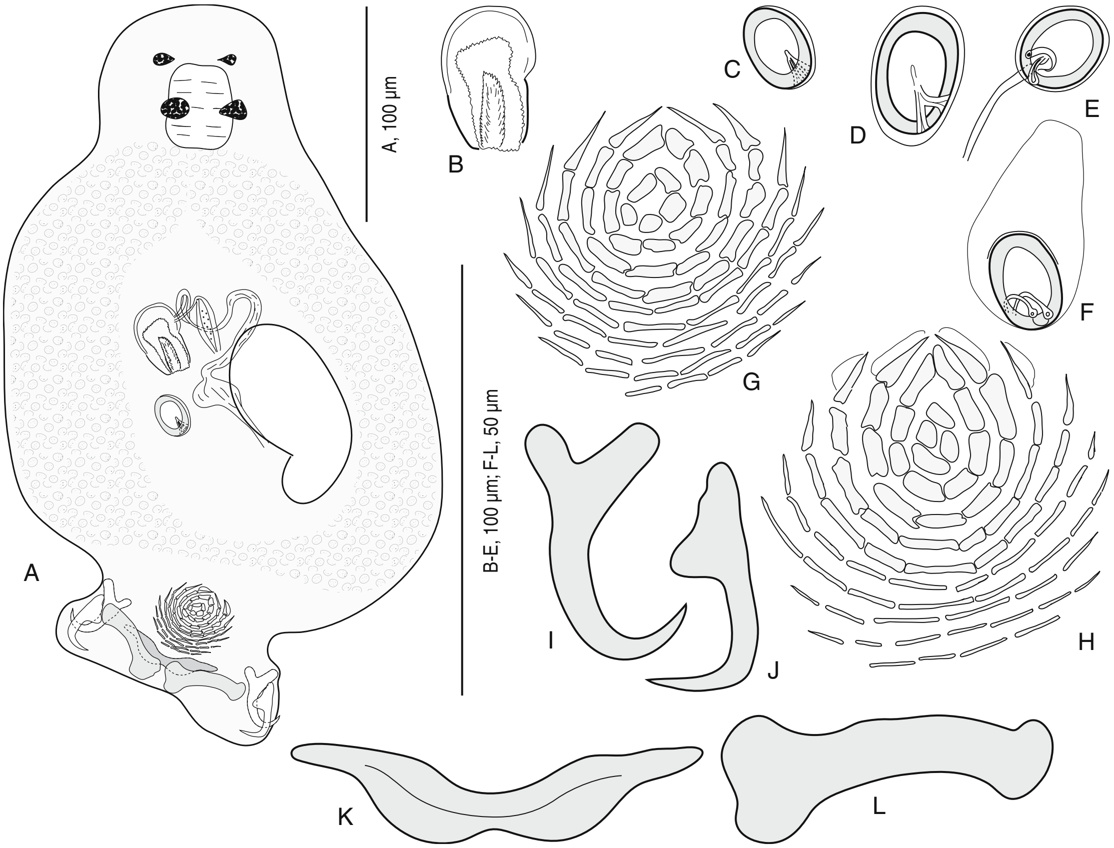

Figure 7. Echinoplectanum rarum n. sp.: A. Habitus, holotype; B. Male copulatory organ, holotype; C. Vagina, holotype; D–F. Aspects of sclerotised vagina and thin tubes in the three paratypes; G. Dorsal squamodisc, holotype; H. Ventral squamodisc, holotype; spurs on rodlets present but not figured for clarity; I. Ventral anchor; J. Dorsal anchor; K. Ventral bar; L. Dorsal bar. All Picrate.

generally the small size of all its reproductive organs, including the testis and ovary; however, the specimens were mature since one egg was observed *in utero*. No sclerotised or unsclerotised vagina was seen despite a thorough search; this is not so surprising if these organs are of a size related to the small male copulatory organ (Figure 10).

Echinoplectanum rarum n. sp.

Type-host: *Plectropomus leopardus* (Lacépède) (Perciformes, Serranidae).
Type-locality: Off Nouméa, 22°18′S, 166°17′E, New Caledonia.
Site: Gills, between secondary gill filaments.
Type-specimens: Holotype, MNHN JNC1393A2, Ilôt Signal (Te Ndu), 22°18′S, 166°17′E; 12 October, 2004; 3 paratypes on 3 slides from hosts JNC1392 and JNC1394.
Type-material: Muséum National d'Histoire Naturelle (MNHN), Paris, holotype, Picrate, and 3 paratypes on 3 Picrate slides JNC1392A1, JNC1394A2, JNC1394A7 (mixed with *E. pudicum* and *E. leopardi*).
Records and infection indices: See Table 1.
Etymology: The epithet ''rarus'' is Latin for rare.

Description (Figure 7)

[Based on only 4 specimens preserved in Picrate; since preservation of soft parts of body was suboptimal, description is based mainly on sclerotised parts.]

Body length 320, 450 (410–480, n = 3), width 190, 207 (150–240, n = 3). Tegument smooth. Anterior region with 2 pairs of eye-spots.

Haptor differentiated from rest of body, width 105, provided with 2 similar squamodiscs, 2 pairs of lateral anchors, 3 bars and 14 marginal hooklets. Squamodiscs round in shape, made up of rows of separate rodlets, with 2 central rows forming closed circles and third row almost closed; rodlets interlocking and robust in inner rows, becoming progressively thinner and separate in peripheral rows; certain rodlets bear single spur; spurs external, directed anteriorly, often overlapping rodlet of previous row; ventral squamodisc, length 39 (31–50, n = 2), width 40 (45–45, n = 2), with 10 (9–10) rows of rodlets including 2, 2 (n = 2) rows forming closed circles; dorsal squamodisc, length 34, 46, width 37, 40, with 10, 10 rows of rodlets including 2, 2 rows forming closed circles. Ventral anchors with handle and distinct guard, outer length 29, 31 (29–32, n = 6), inner length 27, 29 (27–30, n = 6). Dorsal anchors with indistinct guard, outer length 26, 27 (26–28, n = 6), inner length 16, 17 (16–17, n = 6). Dorsal (lateral) bars slightly curved, with flattened medial extremity and roughly cylindrical lateral extremity, length 38, 43 (38–47, n = 6), maximum width 15, 16 (16–17, n = 6). Ventral bar flat, with constricted median portion and pointed extremities, length 45, 49 (43–56, n = 3), maximum width 8, 9 (8–10, n = 3); groove visible on its ventral side.

Pharynx subspherical, length 38, 46 (42–50, n = 3), width 33, 43 (40–46, n = 3).

Testis small, intercaecal. Proximal part of vas deferens not seen; seminal vesicle loops then narrows to form duct which loops around prostatic reservoir and enters male copulatory organ. Prostatic reservoir small. Penis small; a sclerotised cylinder, as wide as long, slightly wider at its proximal (anterior) extremity, length 15, 18 (17–19, n = 3), proximal diameter 18, 19 (19–20, n = 3), distal diameter 13, 14 (14–15, n = 3); muscular reservoir at proximal (anterior) extremity of penis with indistinct muscular layers, length 18, 23 (20–25, n = 3), width 23, 26 (24–30, n = 3); thin prostrusible cirrus within penis. Male duct and anterior extremity of prostatic vesicle enter muscular reservoir laterally at same place.

Ovary dextral, subequatorial, intercaecal. Sclerotised vagina sinistral, a heavily sclerotised flat oval ring, greatest diameter 20, 21 (20–23, n = 3), smallest diameter 15, 16 (15–17, n = 3), with apparently hollow centre and 2 thin sclerotised tubes linked to periphery of ring; aspect of tubes varies according to specimen and orientation (Figures 7C–F). Vitelline fields extend posteriorly from posterior to pharyngeal level in 2 lateral bands, confluent posterior to testis and ovary, and terminate anterior to peduncle. Single immature egg seen in uterus of holotype on right side of body, apparently oval, 100×50.

Differential diagnosis

This species is readily distinguished from other species of the same genus by its very characteristic ring-shaped sclerotised vagina.

Remarks

This species is very rare (Table 1) and represented only 2% of the specimens of *Echinoplectanum* found in *P. leopardus*. The fact that a specimen was found with an egg shows that its occurrence on this host is not accidental and *P. leopardus* can justifiably be designated as its type-host.

***Echinoplectanum echinophallus* (Euzet & Oliver, 1965) n. comb.**

Syns *Diplectanum echinophallus* Euzet & Oliver, 1965; *Cycloplectanum echinophallus* (Euzet & Oliver, 1965) Oliver, 1968

Type-host: *Epinephelus marginatus* (Lowe) (Perciformes, Serranidae). Host designated as *E. gigas* (Brünnich) in Euzet & Oliver (1965) and *E. guaza* (Linnaeus) in Oliver (1987); according to Heemstra & Randall (1993) and Froese & Pauly (2005), both are synonyms of *E. marginatus*.

Type-locality: Off Banyuls, French Mediterranean Coast.

Other localities: Off Lavezzi Island, southern Corsica (Oliver, 1992); off Rosas, Spain (Oliver, 1987); off Kerkennah Island, Tunisia (Euzet, 1984). All previous localities are in the Mediterranean Sea. Off Dakar, Senegal, East Atlantic (new geographical record).

Site: Gills, between secondary gill filaments.

Type-specimens: 2 specimens on 2 slides 156 TZ 120 TB and 156TZ 121TB, MNHN. The original publication mentions that a type (singular) has been deposited in MNHN, but 2 type-slides, each with 1 specimen, are present. Specimen 120TB is the one represented in figure 2 of Euzet & Oliver (1965) and thus is here designated as the lectotype; specimen 121TB is thus paralectotype.

Material examined: The 2 MNHN type-slides; voucher specimens, from *Epinephelus marginatus*, off Dakar, Senegal, collected by André Raibaut (1989), in Louis Euzet's personal collection. Note: a voucher (not examined) in the USNPC, no. 77470, is mentioned by Oliver (1987).

Description (Figure 8)

[The original description (OD) is detailed and accurate, and the type-specimens are extremely well preserved. The description below is for homogeneity with other species, since Euzet & Oliver (1965) did not use exactly the same method for measurements (i.e. for anchors). Measurements are given for the lectotype and paralectotype, with measurements from OD in parentheses.]

Body length 950, 1,200 (OD 600–1,500) width 300, 350 (OD 150–350). Tegument smooth. Anterior region with 3 pairs of head organs and 2 pairs of eye-spots; distance between outer margins of anterior eye-spot pair 37, between posterior eye-spot pair 50, 55.

Haptor differentiated from rest of body, width 230, 250, provided with 2 similar squamodiscs, 2 pairs of lateral anchors, 3 bars and 14 marginal hooklets. Squamodiscs round in shape, made up of rows of separate rodlets, with 2 central rows forming closed circles; rodlets interlocking and robust in inner rows, progressively becoming thin and separate in peripheral rows; ventral squamodisc, length 65, width 65, with 10 rows of rodlets including 1 row (OD 2) forming closed circle; dorsal squamodisc, length 55, 63, width 55, 73 with 11 rows of rodlets including 2, 2 rows forming closed circles. In both ventral and dorsal squamodiscs, first circle leaves wide empty central space, diameter of first circle 23–26 (OD 25–30); most rodlets, except those of central circle, bear single spur ("éperon" in OD); spur is external and directed toward anterior end and often overlaps rodlet of previous row. Ventral anchors with handle and distinct guard, outer length 58–62, inner length 63–65. Dorsal anchors with indistinct guard, outer length 54–57, inner length 33–35. Dorsal (lateral) bars with flattened medial extremity and roughly cylindrical lateral extremity, length 68–72 (OD 90–100), maximum width 19–22. Ventral bar flat, with constricted median portion and pointed extremities, length 75, 83 (OD 100–110), maximum width 15–18; groove visible on its ventral side.

Pharynx subspherical, length 75, 80 (OD 90), width 75, 80 (OD 80). Oesophagus apparently absent, such that intestinal bifurcation immediately

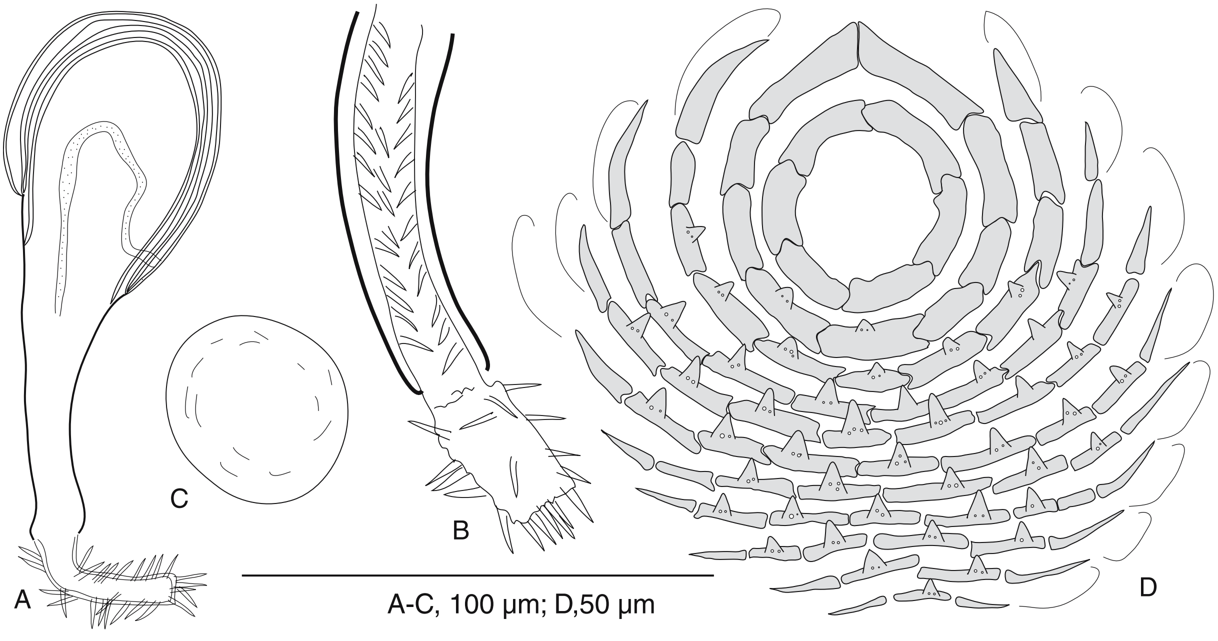

Figure 8. *Echinoplectanum echinophallus* (Euzet & Oliver, 1965) n. comb., type specimens: A. Male copulatory organ; B. Extremity of male copulatory organ showing prominent spiny ridges on cirrus; C. Sclerotised vagina; D. Dorsal squamodisc; spurs on rodlets figured. A, lectotype; B–D, paralectotype. All Carmine.

follows pharynx. Intestinal caeca simple, terminate blindly at level of posterior margin of vitelline field.

Testis intercaecal, length 120, 160, width 160, 160. Vas deferens directed anteriorly, forms seminal vesicle; seminal vesicle sinistral, narrows to form duct which loops around prostatic reservoir and enter male copulatory organ. Prostatic glands ventral, enter prostatic reservoir. Penis a sclerotised cylinder, longer than wide, wider at its proximal (anterior) extremity, length 63, 65 (OD 55–60), proximal diameter 30, 32, distal diameter 12, 12; muscular reservoir at proximal (anterior) extremity of penis with 4 (OD 3) muscular layers, length 50, 55, width 45, 48; thin protrusible cirrus within penis; cirrus with prominent acute ridges resembling spines; spine length 5–8. Male duct and anterior extremity of prostatic vesicle enter muscular reservoir laterally at same place.

Ovary subequatorial, intercaecal, anterior to testis. Oviduct passes medially to form oötype, surrounded by Mehlis' gland. Uterus dextral, directed anteriorly from oötype. Sclerotised vagina sinistral, a slightly sclerotised sac, length 38, 37, width 38, 41. No tubes seen in vagina. Wide unsclerotised duct runs directly from sclerotised vagina to oötype. Vitelline fields extend posteriorly from posterior to pharyngeal level in 2 lateral bands, confluent posterior to testis and ovary, terminate anterior to peduncle. Egg not known.

Differential diagnosis

This species is distinguished from other species of the genus by the shape and size of its male copulatory organ, especially the cirral spines, which are the most prominent in the genus. It is the only species of the genus in which the vaginal opening is on the side of the body (left). The original description mentions that the body sometimes narrows at the level of the vagina.

Remarks

We carefully sought the thin tubes in the vagina and could not find them; however, the type-specimens are feebly stained and the examination of more material is needed to ascertain the absence of the tubes in this species. A seminal receptacle was not seen, but it is not often visible in other species and this character should also be checked on other material.

Oliver (1987) classified this species in *Cycloplectanum*, but distinguished a morphological type for the male copulatory organ as "type à cirre avec bulbe non sclérifié et non divisé" ("type with cirrus with unsclerotised and undivided bulb") in which he also included *Diplectanum plectropomi* Young, 1969, thus clearly differentiating these species from other species with a quadriloculate male organ (now in *Pseudorhabdosynochus*).

The present mention of this species off Senegal (West Africa) is a new geographical record. Judging from the geographical distribution of the host, *Epinephelus marginatus* (Figure 11), this species should be found in many places, including off the entire west coast of Africa and eastern coast of South America, in addition to the Mediterranean Sea, where it has been recorded in several places.

This species is the only one in *Echinoplectanum* which is found in a serranid host which does not belong to *Plectropomus*; see the section below on host-switching. For this reason, although it is the oldest described species of *Echinoplectanum* and has all the characteristic features of the genus, we decided not to choose it as the type-species.

***Echinoplectanum plectropomi* (Young, 1969) n. comb.**

Syns *Diplectanum plectropomi* Young, 1969; *Cycloplectanum plectropomi* (Young, 1969) Oliver, 1984.

Type-host: *Plectropomus maculatus* (Bloch) (Perciformes: Serranidae).
Type-locality: Off Heron Island, Eastern Australia.
Site: Gills.
Type-specimens: USNPC, holotype no. 63141; paratypes no. 63142.
Material examined: Paratypes USNPC 63142, 5 slides 1003-20–1003-24, each with 1 specimen. The paratypes comprise 1 complete unstained specimen (1003-23) in which almost nothing is visible, 1 haemalum-stained specimen (1003-20) without a haptor and 3 complete haemalum-stained specimens (1003-21, 22, 24).

Description (Figure 9)

[The original description (OD) is good for many aspects. Anatomical details are hard to see in most of the paratype specimens and only details and a

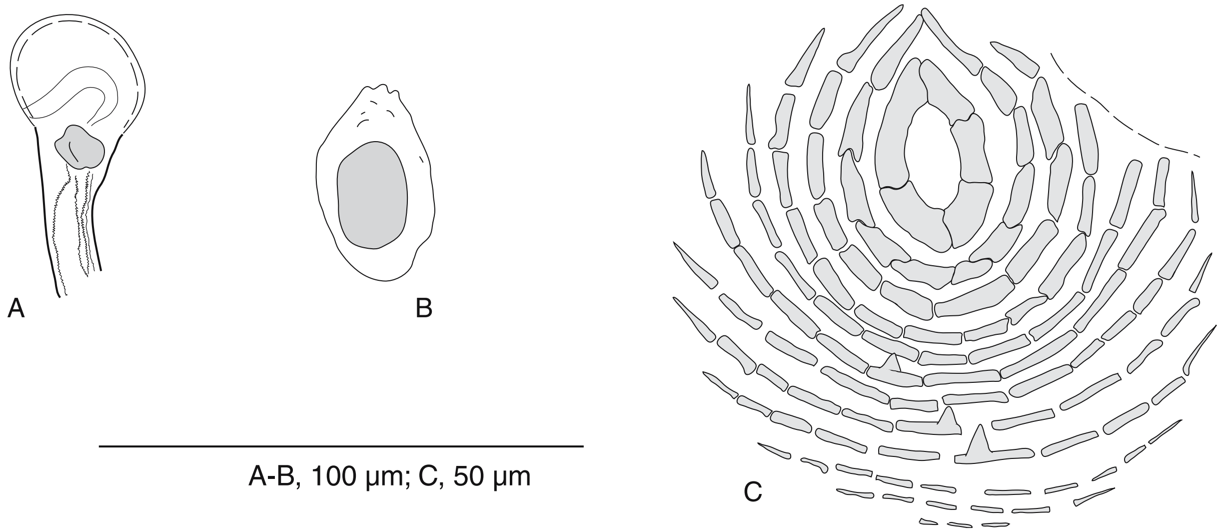

Figure 9. *Echinoplectanum plectropomi* (Young, 1969) n. comb., paratypes: A. Male copulatory organ; B. Sclerotised vagina; C. Squamodisc; a few spurs are visible on rodlets. A,B, USNPC 63142 1003-24; C, USNPC 63142 1003-21. All Haemalun.

few measurements are reported here. Measurements from OD are in parentheses.]

Body length 290–400 (OD 308–396), width 130–220 (OD 110–165).

Haptor width 120–160. Squamodiscs readily visible in specimen 1003-21, round in shape, made up of 12 rows of separate rodlets (OD 8–13), with 2 central rows forming closed circles (OD 4); rodlets interlocking and robust in inner rows, becoming progressively thinner and separating in peripheral rows; ventral squamodisc, length 53 (OD 51–62), width 55 (OD 50–61), with 12 rows of rodlets including 2 rows forming closed circles; dorsal squamodisc, length 63 (OD 48–58), width 68 (OD 43–66), with 12 rows of rodlets including 2 rows forming closed circles; in certain rodlets anteriorly-directed spur is visible. Ventral anchors with handle and distinct guard, outer length 34–36, inner length 35–38. Dorsal anchors with indistinct guard, outer length 27–33, inner length 18–22. Dorsal (lateral) bars with flattened medial extremity and roughly cylindrical lateral extremity, length 50–55 (OD 46–52), maximum width 14–16 (OD 12–16). Ventral bar flat, with constricted median portion and pointed extremities, length 63–64 (OD 54–61), maximum width 12–15; groove visible on its ventral side.

Penis a thinly sclerotised cylinder, longer than wide, wider at its proximal (anterior) extremity, length 33–36 (OD 32–40), proximal diameter 18–21, distal diameter 9–12; muscular reservoir at proximal (anterior) extremity of penis with muscular layers indistinct, its length 18–23 (OD 23–26), width 25–27; sclerotised mass, yellow in haemalum-stained specimens, is visible in wider, anterior region of penis; thin protrusible cirrus within penis; no spine seen.

Sclerotised vagina (''copulation canal'' in OD) dextral, located posterior to male copulatory organ, in form of slightly sclerotised sac, length 40–45 (OD 40–48), width 23–24. No tubes seen in vagina. Egg not known.

Differential diagnosis

This species is distinguished from other species of the same genus by the shape and size of its male copulatory organ and the position and shape of the sclerotised vagina.

Remarks

Young (1969) remarked that this species was similar to *D. echinophallus*. Oliver (1987) transferred this species to *Cycloplectanum*, but separated it in a special group with *D. echinophallus* (see above).

The staining and state of the type-specimens precludes any detailed observation of the vagina and absence of thin tubes should be checked on fresh material. The presence of a sclerotised globular element in the wide, anterior extremity of the penis was visible in Young's drawing but not mentioned in the text; it is confirmed here. This is the only species with such a sclerotised element within the male organ.

In the squamodiscs, spurs visible on the rodlets are similar to those of other species of *Echinoplectanum*. Our observations differ mainly from the OD regarding the number of closed circles in the squamodiscs (2 *vs* 4 in OD) but our observations are based on a single specimen. Fresh material is needed to clarify the structure of the squamodiscs; nevertheless, this species has been described with accuracy and is clearly distinct from the other species of the genus.

Size groups in *Echinoplectanum*

Several size groups may be distinguished within species of *Echinoplectanum* n. g. (Table 2).

According to Table 2, body size is related with the size of the squamodiscs and anchors. Species can be classified in three categories: (a) a 'giant' species, *E. echinophallus*; (b) two 'large' species: *E. laeve* n. sp. and *E. chauvetorum*; both are from *Plectropomus laevis*; (c) four 'small' species: *E. leopardi* n. sp., *E. rarum* n. sp. and *E. pudicum* n. sp. from *P. leopardus*, and *E. plectropomi* from *P. maculatus*.

Statistical tests show that key measurements are not signifciantly different between the two species of the 'large' group, *E. laeve* and *E. leopardi*. Differences between the species of the 'small' group are very small; statistical tests performed on the two species with enough data, *E. leopardi* and *E. pudicum*, show that measurements are different ($p < 0.05$) but the differences (1–3 μm) are very small.

The size of the attachment organs is apparently homogeneous within the species from a given host, suggesting that the structure of the host gill is a key evolutionary factor for the haptor.

'Spiny penis versus chastity belts': an hypothesis for sperm competition in *Echinoplectanum*

The homogeneous masses found in the vagina of *Echinoplectanum* spp. resemble spermatophores or copulatory plugs. Spermatophores are known in many phyla (Mann, 1984); they are sometimes very complex structures and serve to transfer sperm in a 'solid' form. Copulatory plugs have a different role, to prevent spermatozoa from being lost by backflow of semen from the vagina; they are formed by a mechanism similar to spermatophore production, usually implying the coagulation and solidification of semen. In certain cases, copulatory plugs have another role, i.e. to form in the female a barrier to re-mating and re-insemination, sometimes termed a 'chastity belt'.

Spermatophores have been mentioned in several monopisthocotylean monogeneans (lists in Justine, 1985; see also Lim, 2002). Silan et al. (1983) suggested that the dense masses found in the female ducts of *Diplectanum aequans* (Wagener, 1857) serve as copulatory plugs.

A cirrus with spines is uncommon within monopisthocotylean monogeneans. Species of *Echinoplectanum* exhibit a suite of morphological characteristics (presence of vaginal plugs, large size of male accessory glands, a muscular reservoir containing the abundant product of the prostatic glands, and especially a male copulatory organ with spines) which are known to be associated, in other groups, including mammals, with special features of sperm competition. In the primate *Lemur catta*, the same suite of characters is found: copulatory plugs are a major feature of copulation, males have the largest relative testes of their groups, and the penis has spines (Parga, 2003); after a first mating, the females display copulatory plugs, but at subsequent matings males displace the plug with their penis before ejaculation; sperm competition thus implies a competition between the plug (chastity belt) left by the first mating male and the penile spines of the subsequent mating male. Such behaviours and sperm competition are not uncommon in vertebrates such as mammals and reptiles (Shine et al., 2000) and are especially associated with the capacity of sperm to coagulate (Dixson & Anderson, 2002), and morphological adaptations of penises with spines or special terminal structures (Parga, 2003; Wallach & Hart, 1983).

We will certainly never be able to perform on *Echinoplectanum* species, tiny parasites hidden between the gill filaments of a large grouper, the extremely detailed behavioural observations carried out on terrestrial vertebrates. However, strong morphological similarities, which are apparently unique within diplectanids, suggest that *Echinoplectanum* species use sperm competition between

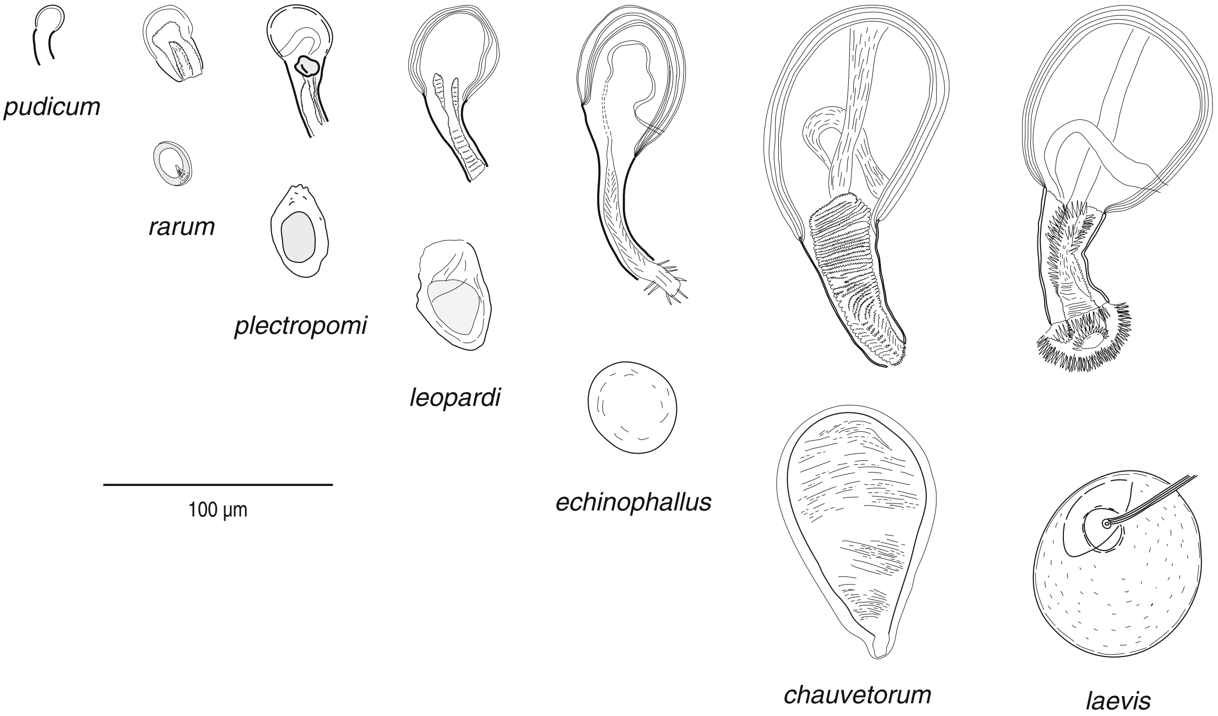

Figure 10. A comparison of size of copulatory organs in the seven species of *Echinoplectanum* n. g., ordered in a size sequence. No vagina was seen in *E. pudicum*. Note that the sizes of the male and female organs are correlated. In an hypothesis on sperm competition using spiny male organs against 'chastity belts', *E. pudicum* should be considered the most basal species, and species with large penises and cirral spines are derived.

chastity belts and spiny penises. This behaviour, and the morphological adaptations which are associated with it, are correlated with multiple-mating behaviour in terrestrial vertebrates; this is also probably the case for *Echinoplectanum*. This pattern of sperm competition has never been described in hermaphroditic animals; in *Echinoplectanum*, it is probably reciprocal between the two mating partners, just as the transfer of spermatophores is reciprocal in certain monogeneans (Lim, 2002).

If this sperm competition strategy prevails within *Echinoplectanum*, we may suggest that species with the smaller male copulatory organs are the most basal and that species with larger male copulatory organs are the most derived. Figure 10 is a diagram of comparative sizes of male and female parts in *Echinoplectanum* species; *E. pudicum* should be considered the most basal species, based on this hypothesis. Comparison of Table 2 and Figure 10 shows that species of the 'small' group have smaller copulatory organs than species of the 'large' group; however, the size of the copulatory organs is not directly related to body size: *E. echinophallus*, the 'giant' species with the largest haptoral parts, has copulatory organs smaller than the two species of the 'large' group.

Host-switching

Members of the new genus *Echinoplectanum* are mainly specific to members of *Plectropomus*, with a strict (oioxenous) species specificity (Table 1). *Plectropomus* is a genus restricted to warm coralian waters of the Indo Pacific ocean (Heemstra & Randall, 1993; see Figure 11). On the other hand, within the Serranidae, the diplectanid genus richest in species is *Pseudorhabdosynochus*, which is mainly associated with numerous species of *Epinephelus*, with occasional records on members of the genera *Mycteroperca* (see Vidal-Martinez & Mendoza-Franco, 1998; Neifar & Euzet, unpublished observations), *Variola* (see Justine 2005b)

Table 2. Size of key characters in *Echinoplectanum* spp.

Group	'giant'	'large'		'small'			
Species	*E. echinophallus*	*E. laeve*	*E. chauvetorum*	*E. leopardi*	*E. rarum*	*E. pudicum*	*E. plectropomi*
Host	*Ep. marginatus*	*P. laevis*	*P. laevis*	*P. maculatus*	*P. leopardus*	*P. leopardus*	*P. maculatus*
Body length	1,000	740^a	720^a	570	450	420	350
Squamodisc diameter	65	80	70	50	40	50	50
Ventral anchor length	60	48^b	48^b	34^d	31	31^d	35
Dorsal anchor length	56	43^c	43^c	29^e	27	28^e	29

Ep., Epinephelus; P., Plectropomus.
Species are ordered according decreasing body length.
Measurements are rounded.
$^{a\ b\ c}$ Means not significantly different; $^{d\ e}$ Means significantly different ($p < 0.05$) but difference very small.

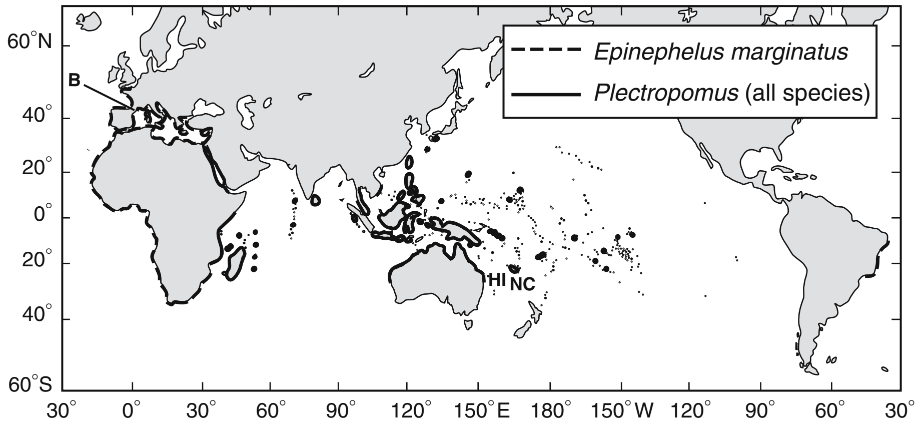

Figure 11. Geographical distribution of hosts and diplectanid parasites. Areas of all seven known species of *Plectropomus* (from Heemstra & Randall, 1993) are pooled. Areas of *Epinephelus marginatus* and *Plectropomus* spp. almost overlap off south-east Africa. Type-localities of *Echinoplectanum* spp: B, Banyuls, Mediterranean, *E. echinophallus* on *Epinephelus marginatus*; HI, Heron Island, Australia, *E. plectropomi*; NC, New Caledonia, *E. laeve*, *E. chauvetorum*, *E. leopardi*, *E. pudicum* and *E. rarum*.

and *Cephalopholis* (Justine, unpublished observations). *Pseudorhabdosynochus* has never been mentioned from members of *Plectropomus*, and we confirm that it is absent from the species of *Plectropomus* examined from off New Caledonia.

Therefore, if *Echinoplectanum* is associated with *Plectropomus*, how can we interpret the presence of a very characteristic member of the genus, *E. echinophallus*, in a grouper from a different genus, *Epinephelus*, from the Mediterranean and Eastern Atlantic? Although the localities appear remote, examination of the recorded areas of *Epinephelus marginatus* and *Plectropomus laevis* shows that they almost overlap off south-east Africa (Figure 11). Host-switching from a *Plectropomus* species to *E. marginatus* thus may have occurred in the overlapping region. Apparently, after host-switching, the species on *Epinephelus* evolved by increasing considerably in size (Table 2).

Echinoplectanum as a basal group

Echinoplectanum, *Pseudorhabdosynochus* and *Laticola* possess male copulatory organs with some morphological similarities. *Laticola* and *Pseudorhabdosynochus* are not sister-groups (Yang et al., 2006). The erection of *Echinoplectanum* and *Laticola*, and the transfer of species from *Pseudorhabdosynochus*, enhance the probability of *Pseudorhabdosynochus* being monophyletic. The acquisition of transverse walls in the penis, thus producing the typical morphology of the quadriloculate organ, is a synapomorphy which clearly separates *Pseudorhabdosynochus* from the two other genera. *Plectropomus* is considered a basal epinepheline in morphological (Heemstra & Randall, 1993) and molecular (Craig et al., 2001) studies. We sugggest that *Echinoplectanum*, which is associated with *Plectropomus*, represents a group basal to *Pseudorhabdosynochus*, which is associated with more derived epinephelines; relationships of *Echinoplectanum* with *Laticola* are less clear. Members of *Echinoplectanum* are probably good choices as outgroups for phylogenetic, including molecular, studies on the diplectanids from epinephelines.

Other gill parasites from *Plectropomus* spp. off New Caledonia

The following data include a few fish specimens in addition to the specimens recorded in this paper. No other diplectanid other than the species of *Echinoplectanum* described here was found on *Plectropomus laevis* and *P. leopardus*. No ancyrocephalid was found. In *P. leopardus*, a capsalid was found occasionally and belongs to an apparently new genus of the Trochopodinae (determination by I. Whittington); no capsalid was found in *P. laevis*. Copepods were found on *P. leopardus*, and include the dissonid *Dissonus manteri* Kabata, 1966, the lernanthropid *Sagum* sp. and the hatschekiid *Hatschekia* cf. *plectropomi* Ho & Dojiri, 1978 (determinations by G. Boxshall); no copepod was found on *P. laevis*. Both specimens of *P. laevis* had a corallanid isopod, *Argathona macronema* (Bleeker, 1857); no isopod was found on the specimens of *P. leopardus* cited in this study but *Argathona rhinoceros* (Bleeker, 1857) was found once on this fish (determinations by J.-P. Trilles). Finally, *P. laevis* had two monogeneans and one isopod; *P. leopardus* had four monogeneans, three copepods and one isopod, a total of eight parasite species on a single organ, the gill.

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