



***Stephanostomum* spp. (Digenea: Acanthocolpidae) from scombrids and carangids (Perciformes) from the Great Barrier Reef, with the description of two new species**

***Stephanostomum* spp. (Digenea: Acanthocolpidae) de escómbridos y carángidos (Perciformes) del arrecife de la Gran Barrera, con descripción de dos especies nuevas**

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Abstract. Two new species and 4 *Stephanostomum* spp. as new host and/or locality records from Perciformes from the Great Barrier Reef are described: *Stephanostomum lamothei* n. sp. from *Grammatorcynus bilineatus* (type-host) and *G. bicarinatus*, Lizard Island and Swain Reefs, is characterised by its 50-55 circum-oral spines and >than 20% of the hindbody length lacking vitelline follicles; *Stephanostomum tupatupa* n. sp. from *Caranx papuensis*, Lizard Island, is characterised by its 34-36 circum-oral spines and <8% of the hindbody length lacking vitelline follicles; *Stephanostomum ditrematis* (Yamaguti, 1939) is reported from *Gnathanodon speciosus*, Heron Island and Lizard Island; *Stephanostomum hawaiiense* Yamaguti, 1970 and *Stephanostomum carangi* Liu, 1998 are reported from *Carangoides fulvoguttatus*, Lizard Island; *Stephanostomum nyoomwa* Bray and Cribb, 2003 is reported from *Caranx sexfasciatus*, Lizard Island.

Key words: Digenea, Acanthocolpidae, *Stephanostomum*, Great Barrier Reef, Carangidae, Scombridae.

Resumen. Se describen 2 especies nuevas del género *Stephanostomum* y se redescubren 4 más parásitos de perciformes del arrecife de la Gran Barrera australiana. *Stephanostomum lamothei* n. sp., parásito de *Grammatorcynus bilineatus* (hospedero-tipo) y de *G. bicarinatus*, de la isla Lizard y de los arrecifes Swain, se caracteriza por sus 50-55 espinas circunorales y por carecer de folículos vitelinos en más del 20% de la longitud del cuerpo; *Stephanostomum tupatupa* n. sp. de *Caranx papuensis* de la isla Lizard, exhibe como rasgos diagnósticos 34-36 espinas circunorales y folículos vitelinos en menos del 8% de la longitud del cuerpo; *Stephanostomum ditrematis* (Yamaguti, 1939) se registra en *Gnathanodon speciosus* de las islas Heron y Lizard; *Stephanostomum hawaiiense* Yamaguti, 1970 y *Stephanostomum carangi* Liu, 1998 se recolectaron en *Carangoides fulvoguttatus* y finalmente, *Stephanostomum nyoomwa* Bray and Cribb, 2003 se encontró parasitando a *Caranx sexfasciatus*, ambos peces de la isla Lizard.

Palabras clave: Digenea, Acanthocolpidae, *Stephanostomum*, arrecife de la Gran Barrera, Carangidae, Scombridae.

Introduction

This is a further report on our studies of the members of the large genus *Stephanostomum* Looss, 1899, documenting species found in the waters of the Great Barrier Reef (Bray and Cribb, 2003; Bray and Cribb, 2004; Bray and Cribb, 2006; Bray et al., 2007). A large proportion of *Stephanostomum* Looss, 1899 species are reported in fishes of the family Carangidae and all but 1 of the species described here are from fishes of that family, the other, a new species, being from scombrids.

Materials and methods

Digeneans collected from freshly killed fish were fixed by being pipetted into nearly boiling saline and immediately preserved in formalin or 70% ethanol. Whole-mounts were stained with Mayer's paracarmine, cleared in beechwood creosote and mounted in Canada balsam. Measurements were made through a drawing tube on an Olympus BH-2 microscope, using a Digicad Plus digitising tablet and Carl Zeiss KS100 software adapted by Imaging Associates, and are quoted in micrometres, with the range and the mean in parentheses (Table 1). The following abbreviations are used: BMNH, the British Museum (Natural History) Collection at the Natural History Museum, London, UK; QM, Queensland Museum Collection, Brisbane, Australia.

Table 1. Dimensions of *Stephanostomum* spp. from Perciformes from the Great Barrier Reef

Measurement, count or ratio descriptor	<i>Stephanostomum lamothei</i>	<i>Stephanostomum lamothei</i>	<i>Stephanostomum lamothei</i>
Host	<i>Grammatocyclus bilineatus</i>	<i>Stephanostomum lamothei</i>	<i>Grammatocyclus bicarinatus</i>
Locality	Lizard Island	Swain Reefs	Lizard Island
n	5	1	8
Overall dimensions	2 461-4 263 × 220-366 (3 248 × 293)	4 204 × 284	3 006-4 425 × 226-342 (3 735 × 295)
Width as % of length	7.48-11.9 (9.15)	6.76	6.65-9.83 (7.95)
Body-spines: anterior mid-ventral	about 8-12 long	about 14 long	about 14-19 long
Body-spines: longest	up to 26 long	up to 18 long	up to 21 long
Oral sucker	121-150 × 144-198 (132 × 168)	150 × 190	74-188 × 155-213 (124 × 184)
Oral sucker length as % of body-length	3.17-5.50 (4.21)	3.58	2.09-4.44 (3.31)
Circum-oral spine counts	51-53 (52)	50	51-55 (52)
Circum-oral spines: antero-ventral	26-41 (34)	24	13-43 (30)
Circum-oral spines: postero-ventral	30-47 (37)	33	27-54 (37)
Circum-oral spines: antero-dorsal	12-21 (16)	18	13-47 (26)
Circum-oral spines: postero-dorsal	13-26 (17)	31	18-55 (36)
Ventral sucker	209-320 × 174-291 (256 × 225)	291 × 246	206-273 × 169-231 (239 × 205)
VS length as % of body-length	7.10-10.2 (7.98)	6.93	5.29-7.56 (6.47)
Sucker-length ratio	1:1.73-2.37 (1.92)	1:1.94	1:1.33-3.35 (2.08)
Sucker-width ratio	1:1.21-1.60 (1.34)	1:1.29	1:0.92-1.38 (1.12)
Forebody	408-545 (486)	621	437-596 (499)
Forebody as % of body-length	11.6-17.5 (15.3)	14.8	10.8-15.7 (13.5)
Hindbody	1 803-3 448 (2 507)	3 292	2 358-3 694 (2 997)
Hindbody as % of body-length	73.2-80.9 (76.7)	78.3	77.7-83.9 (80)
Prepharynx	68-135 (110)	196	60-233 (147)
Prepharynx length as % of body-length	1.81-4.61 (3.49)	4.67	1.70-5.78 (3.97)
Pharynx	99-125 × 91-124 (109 × 104)	124 × 119	121-181 × 59-109 (155 × 79)
Pharynx length as % of body-length	2.43-4.38 (3.49)	2.95	3.15-5.16 (4.20)
Oesophagus	37-73 (54)	36	0-30 (23)
Intestinal bifurcation to ventral sucker	50-116 (74)	125	0-127 (49)
Anterior testis	124-366 × 109-229 (200 × 140)	282 × 182	229-492 × 94-244 (321 × 169)
Anterior testis as % of body-length	4.28-8.57 (6.01)	6.71	5.98-11.1 (8.61)
Posterior testis	158-436 × 113-234 (240 × 142)	303 × 182	277-581 × 97-239 (368 × 176)
Posterior testis as % of body-length	5.46-10.2 (7.28)	7.21	7.23-13.1 (9.86)

Table 1. Continues

Distance between testes	0-14 (6)	17	0-19 (4)
DBT as % of body-length	0-0.47 (0.17)	0.39	0-0.55 (0.12)
Post-testicular region	289-574 (411)	465	95-441 (214)
PTR as % of body-length	11.2-13.9 (12.6)	11.1	2.16-11.5 (5.90)
Cirrus-sac	768-1 395 x 77-136 (996 x 94)	1 311 x 136	709-1 221 x 59-113 (932 x 83)
Cirrus-sac length as % of body-length	26.6-37.5 (30.8)	31.2	18.6-34.9 (25.2)
Distance from anterior end of CS to VS	117 overlapping to 7 posterior	16 overlapping	117 overlap to 173 posterior
Distance from posterior end of CS to VS	644-1 071 (832)	1 016	592-1 140 (834)
Above dimension as % of VS to Ovary	50.8-60.9 (54.8)	51.1	37.8-51.9 (43.8)
Length of internal male duct	805-1 308 (1 001)	1 302	726-1 297 (932)
Seminal vesicle	170-362 (228)	224	168-349 (234)
SV as % of internal male duct	16.0-27.6 (22.6)	17.2	20.4-29.7 (25.1)
Pars prostatica	161-289 (223)	301	135-411 (236)
PP as % of internal male duct	16.9-25.9 (22.2)	23.1	16.4-31.7 (25.0)
Ejaculatory duct	444-657 (550)	777	346-622 (462)
EJ as % of internal male duct	50.2-58.5 (55.2)	59.6	43.7-61.1 (49.8)
Genital atrium	75-351 (228)	303	123-457 (303)
Ovary	72-157 x 69-127 (95 x 88)	101 x 98	99-169 x 90-139 (128 x 105)
Ovary length as % of body length	2.19-3.68 (2.93)	2.40	2.57-4.37 (3.47)
Ovary to ventral sucker	1 057-1 946 (1 530)	1 990	1 402-2 736 (1 911)
Ov-VS as % of body-length	43.0-49.8 (47.0)	47.33	46.6-62.1 (50.7)
Ovary to anterior testis (Ov-AT)	0-43 (9)	75	0-53 (16)
Ov-AT as % of body-length	0-1.17 (0.23)	1.77	0-1.76 (0.45)
Eggs	61-74 x 30-37 (69 x 33)	70 x 35	73-79 x 31-38 (76 x 35)
Anterior limit of vitellarium to VS	529-820 (693) posterior to VS	762 posterior to VS	485-973 (714) posterior to VS
Above dimension as % of HB-length	23.6-30.1 (28.1)	23.1	18.8-27.1 (23.7)
Measurement, count or ratio descriptor	<i>Stephanostomum ditrematis</i>	<i>Stephanostomum ditrematis</i>	<i>Stephanostomum tupatupa</i>
Host	<i>Gnathanodon speciosus</i>	<i>Gnathanodon speciosus</i>	<i>Caranx papuensis</i>
Locality	Heron Island	Lizard Island	Lizard Island
n	3	1	5
Overall dimensions	4 608-6 513 x 226-266 (5 395 x 250)	6 866	2 576-3 358 x 328-413 (3 110 x 368)
Width as % of length	4.08-5.60 (4.71)	344	11.3-12.7 (11.9)

Table 1. Continues

Body-spines: anterior mid-ventral	about 15-19 long	about 10 long	about 15-26 long
Body-spines: longest	up to about 26-29 long	up to about 15	up to about 27-30 long
Oral sucker	126-141 x 128-143 (132 x 134)	101 x 126	63-92 x 174-214 (77 x 192)
Oral sucker length as % of body-length	1.94-3.07 (2.52)	1.47	2.23-2.85 (2.46)
Circum-oral spine counts	34-37 (35)	36	34-36 (36)
Circum-oral spines: antero-ventral	42-48 (45)	30	21-39 (28)
Circum-oral spines: postero-ventral	30-51 (41)	22	21-45 (31)
Circum-oral spines: antero-dorsal	43-68 (51)	43	27-41 (31)
Circum-oral spines: postero-dorsal	49-68 (56)	39	27-36 (32)
Ventral sucker	202-211 x 179-201 (205 x 188)	168 x 164	173-228 x 174-210 (207 x 193)
VS length as % of body-length	3.11-4.57 (3.89)	2.45	6.19-7.14 (6.67)
Sucker-length ratio	1:1.49-1.61 (1.55)	1:1.66	1:2.47-3.20 (2.73)
Sucker-width ratio	1:1.29-1.57 (1.41)	1:1.31	1:0.95-1.10 (1.01)
Forebody	818-1 085 (933)	984	983-1 164 (1 098)
Forebody as % of body-length	16.7-17.7 (17.4)	14.3	32.9-38.1 (35.5)
Hindbody	3 580-5 226 (4 258)	5 713	1 422-2 042 (1 805)
Hindbody as % of body-length	77.7-80.2 (78.8)	83.2	55.2-60.9 (57.9)
Prepharynx	421-605 (500)	461	493-628 (585)
Prepharynx length as % of body-length	9.13-9.33 (9.25)	6.71	18.0-20.8 (18.9)
Pharynx	188-214 x 97-117 (201 x 105)	152 x 67	171-192 x 130-153 (180 x 141)
Pharynx length as % of body-length	2.88-4.65 (3.83)	2.21	5.41-6.62 (5.83)
Oesophagus	37-113 (78)	149	151-226 (187)
Intestinal bifurcation to ventral sucker	0-17 (6)	87	46-93 (63)
Anterior testis	358-482 x 145-182 (402 x 162)	391 x 209	109-179 x 130-163 (159 x 147)
Anterior testis as % of body-length	7.07-7.94 (7.47)	5.69	4.24-5.57 (5.09)
Posterior testis	377-490 x 135-185 (437 x 158)	415 x 212	141-217 x 141-170 (195 x 153)
Posterior testis as % of body-length	7.45-9.61 (8.19)	6.04	5.46-7.20 (6.26)
Distance between testes	153-180 (163)	243	0
DBT as % of body-length	2.40-3.56 (3.10)	3.54	0
Post-testicular region	169-238 (210)	574	303-438 (375)
PTR as % of body-length	3.34-5.16 (3.97)	8.35	10.1-14.7 (12.1)
Cirrus-sac	548-902 x 74-90 (677 x 83)	921 x 98	301-497 x 40-70 (62)
Cirrus-sac length as % of body-length	11.4-13.9 (12.4)	13.4	11.7-14.8 (13.8)
Distance from anterior end of CS to VS	413-837 (599)	736	always dorsal to ventral sucker
Distance from posterior end of CS to VS	948-1 725 (1 262)	1 527	160-216 (191)

Table 1. Continues

Above dimension as % of VS to Ovary	43.6-46.9 (44.8)	42.3	18.5-22.8 (20.7)
Length of internal male duct	613-943 (726)	1 026	314-510 (445)
Seminal vesicle	165-233 (201) long	431 long	124-275 (190) long
SV as % of internal male duct	24.7-33.7 (28.3)	42.1	32.5-53.9 (42.1)
Pars prostatica	203-388 (265) long	221 long	58-135 (99) long
PP as % of internal male duct	32.7-41.2 (35.7)	21.6	15.3-28.9 (22.2)
Ejaculatory duct	202-322 (259)	373	132-182 (156)
EJ as % of internal male duct	33.0-40.8 (35.0)	36.4	26.8-42.0 (35.7)
Genital atrium	637-1 059 (819)	915	33-76 (58)
Ovary	113-143 x 176-345 (124 x 237)	152 x 144	111-160 x 121-157 (139 x 141)
Ovary length as % of body length	2.66-2.77 (2.73)	2.22	4.113-4.92 (4.47)
Ovary to ventral sucker	2 021-3 924 (2 834)	3 611	700-1 065 (928)
Ov-VS as % of body-length	43.9-60.3 (51.5)	52.6	27.2-31.7 (29.7)
Ovary to anterior testis	176-345 (237)	267	0-2 (0)
Ov-AT as % of body-length	3.74-5.30 (4.29)	3.88	0-0.06 (0.01)
Eggs	65-83 x 28-32 (74 x 30)	70 x 35	66-74 x 29-49 (71 x 37)
Anterior limit of vitellarium to VS	912-1 703 (1 263) posterior to VS	2 221 posterior to VS	84-154 (103) posterior to VS
Above dimension as % of HB-length	25.5-32.6 (29.2)	38.9	4.64-7.53 (5.72)
Measurement, count or ratio descriptor	<i>Stephanostomum carangi</i>	<i>Stephanostomum hawaiiense</i>	<i>Stephanostomum nyoomwa</i>
Host	<i>Carangoides fulvoguttatus</i>	<i>Carangoides fulvoguttatus</i>	<i>Caranx sexfasciatus</i>
Locality	Lizard Island	Lizard Island	Lizard Island
n	3	3	6
Overall dimensions	5 125-6 008 x 504-580 (3 451 x 539)	4 743-8 399 x 278-351 (6 517 x 326)	2 624-3 420 x 188-235 (3 092 x 212)
Width as % of length	9.66-10.2 (9.91)	4.18-5.85 (5.16)	6.06-7.49 (6.88)
Body-spines: anterior mid-ventral	about 24-27 long	about 10-18 long	about 16-23 long
Body-spines: longest	up to about 35-46 long	up to about 23-27	up to about 34-40 long
Oral sucker	253-261 x 362-421 (258 x 386)	94-130 x 163-199 (133 x 179)	126-156 x 184-230 (142 x 209)
Oral sucker length as % of body-length	4.35-5.06 (4.75)	1.54-1.99 (1.78)	4.26-5.02 (4.60)
Circum-oral spine counts	36-37 (37)	34-37 (36)	34-37 (36)
Circum-oral spines: antero-ventral	51-77 (62)	39-52 (44)	48-61 (53)
Circum-oral spines: postero-ventral	56-72 (67)	34-43 (37)	45-66 (53)

Table 1. Continues

Circum-oral spines: antero-dorsal	66-107 (83)	52-61 (55)	62-77 (71)
Circum-oral spines: postero-dorsal	119-134 (128)	49-65 (57)	85-97 (91)
Ventral sucker	317-379 x 309-357 (344 x 338)	199-263 x 175-257 (237 x 207)	122-144 x 109-148 (132 x 126)
VS length as % of body-length	6.19-6.43 (6.31)	3.13-4.20 (3.73)	3.88-4.92 (4.31)
Sucker-length ratio	1:1.22-1.45 (1.33)	1:2.03-2.14 (2.09)	1:0.80-1.15 (0.94)
Sucker-width ratio	1:0.73-0.96 (0.88)	1:1.08-1.29 (1.15)	1:0.53-0.72 (0.60)
Forebody	1 980-2 119 (2 047)	789-985 (895)	764-1 040 (872)
Forebody as % of body-length	34.0-41.3 (37.8)	11.7-16.6 (14.2)	24.2-32.3 (28.3)
Hindbody	2 689-3 586 (3 060)	3 754-7 151 (5 386)	1 731-2 412 (2 087)
Hindbody as % of body-length	52.5-59.9 (55.9)	79.2-85.1 (82.1)	63.8-71.7 (67.4)
Prepharynx	966-1 344 (1 108)	386-456 (427)	322-510 (399)
Prepharynx length as % of body-length	16.8-26.2 (20.5)	5.24-8.14 (6.83)	9.80-15.8 (13.0)
Pharynx	368-417 x 172-265 (394 x 207)	151-190 x 94-138 (172 x 115)	147-180 x 64-78 (161 x 72)
Pharynx length as % of body-length	6.63-7.99 (7.27)	2.26-3.18 (2.72)	4.84-5.84 (5.24)
Oesophagus	124-273 (191)	24-116 (77)	32-144 (89)
Intestinal bifurcation to ventral sucker	77-207 (123)	72-134 (103)	16-164 (82)
Anterior testis	399-534 x 184-355 (449 x 252)	279-503 x 120-310 (360 x 201)	209-261 x 96-167 (239 x 123)
Anterior testis as % of body-length	7.79-8.89 (8.20)	4.66-5.99 (5.51)	7.05-9.59 (7.78)
Posterior testis	455-661 x 194-386 (537 x 263)	297-530 x 116-293 (383 x 190)	220-323 x 113-200 (277 x 139)
Posterior testis as % of body-length	8.88-11.0 (9.78)	5.02-6.31 (5.86)	7.44-10.6 (8.98)
Distance between testes	0	327-676 (494)	0-21 (5)
DBT as % of body-length	0	6.89-8.05 (7.48)	0-0.61 (0.17)
Post-testicular region	448-666 (528)	402-805 (575)	144-200 (161)
PTR as % of body-length	8.75-11.1 (9.60)	8.08-9.59 (8.71)	4.38-6.09 (5.24)
Cirrus-sac	983-1 076 x 145-176 (1 030 x 156)	727-1 898 x 93-159 (1 195 x 115)	634-1 065 x 49-74 (888 x 60)
Cirrus-sac length as % of body-length	17.9-19.8 (19.0)	15.0-22.6 (17.6)	24.1-33.7 (28.6)
Distance from anterior end of CS to VS	always dorsal to ventral sucker	328*	always dorsal to ventral sucker
Distance from posterior end of CS to VS	442-606 (516)	785-1 506 (1 194)	443-676 (571)
Above dimension as % of VS to Ovary	37.2-41.7 (39.0)	39.2-44.9 (41.5)	42.7-49.5 (46.7)
Length of internal male duct	1 042-1 248 (1 140)	719-983 (851)	766-1 130 (943)
Seminal vesicle	311-531 (407) long	158-211 (184) long	260-390 (349)
SV as % of internal male duct	29.9-42.5 (35.3)	21.5-21.9 (21.7)	32.3-48.6 (37.3)
Pars prostatica	247-302 (266) long	318-355 (337) long	202-313 (242)
PP as % of internal male duct	20.0-26.7 (23.5)	36.2-44.3 (40.2)	24.2-27.7 (25.6)
Ejaculatory duct	450-484 (467)	243-417 (330)	210-434 (353)

Table 1. Continues

EJ as % of internal male duct	37.4-46.4 (41.2)	33.8-42.4 (38.1)	26.2-42.9 (37.1)
Genital atrium	75-152 (105)	286-590 (438)	17-47 (36)
Ovary	215-290 x 153-236 (255 x 191)	142-245 x 134-185 (184 x 155)	94-137 x 77-105 (116 x 86)
Ovary length as % of body length	4.20-5.00 (4.67)	2.60-2.99 (2.84)	3.19-4.06 (3.75)
Ovary to ventral sucker	1 188-1 452 (1 318)	1 939-3 845 (2 886)	943-1 490 (1 227)
Ov-VS as % of body-length	23.2-25.2 (24.2)	40.9-45.8 (43.8)	35.0-44.1 (39.5)
Ovary to anterior testis	0-12 (4)	298-526 (443)	0-87 (16)
Ov-AT as % of body-length	0-0.20 (0.07)	6.27-7.87 (6.81)	0-2.94 (0.53)
Eggs	70-77 x 31-44 (73 x 38)	52-74 x 31-36 (62 x 33)	55-70 x 29-40 (63 x 35)
Anterior limit of vitellarium to VS	76-238 (136) posterior to VS	806-1 660 (1 324) posterior to VS	359-678 (528) posterior to VS
Above dimension as % of HB-length	2.67-8.19 (4.56)	21.5-28.7 (24.5)	18.9-28.1 (25.1)

* In one specimen the ejaculatory duct is extruded through the genital pore as a cirrus, in this case the genital atrium reaches 244 into the hindbody, in another the ejaculatory duct is extruded within the genital atrium, which reaches 176 into the hindbody.

Abbreviations used in table: CS, cirrus-sac; DBT, distance between testes; EJ, ejaculatory duct; HB, hindbody; Ov-AT, Ovary to anterior testis distance; Ov-VS, ovary to ventral sucker distance; PP, pars prostatica; PTR, post-testicular region; SV, seminal vesicle; VS, ventral sucker.

Descriptions

Family Acanthocolpidae Lühe, 1906
Genus *Stephanostomum* Looss, 1899

Stephanostomum lamothei n. sp. (Figs. 1-6)

Based on 18 whole-mount preparations from *Grammatorcynus bilineatus* and 24 from *G. bicarinatus*, 5 of which were from the Swain Reefs. Measurements and ratios in Table 1. Measurements are based on the relatively small number of specimens which we were able to mount dorso-ventrally, due to the ventral flexing of the forebody on fixation. Body elongate, narrow, widest in region of ventral sucker or testes (Figs. 1, 4). Tegument spinous, unarmed patch immediately posterior to oral sucker, spines small, scale-like and densely packed in forebody, smaller in hindbody, becoming sparse in hindbody, detectable to varying levels in hindbody, in some cases to posterior extremity. Oral sucker terminal, distinctly wider than long. Circum-oral spines in double ring, without ventral hiatus; spines frequently distorted, reduced to very small size or lost, counts only on clearly normal sets of spines (Figs. 2, 5). Ventral sucker oval, in anterior fifth of body. Prepharynx long. Pharynx pyriform. Oesophagus short. Intestinal bifurcation in posterior forebody. Caeca long, narrow, form uroproct.

Testes 2, oval, entire, tandem, contiguous. Post-testicular region short or very short, usually relatively shorter in worms from *G. bicarinatus*. Cirrus-sac elongate (Figs. 3, 6), reaches well into hindbody; anterior extremity in anterior hindbody or overlapping to about mid-ventral sucker. Seminal vesicle saccular, oval, undivided. Pars prostatica short, narrower distally, lined with anuclear cell-like bodies, surrounded by gland-cells. Ejaculatory duct long, wide, lined with closely packed small cupolas, with round bases seen as circles on wall of duct, with distinct naked region distally. Genital atrium long, reaching to mid-ventral sucker or just into hindbody. Genital pore median, slit-like, immediately anterior to ventral sucker.

Ovary oval, entire, usually slightly separated from anterior testis, occasionally contiguous. Mehlis' gland antero-dorsal to ovary. Laurer's canal opens dorsally to ovary. Uterine seminal receptacle in proximal uterus. Uterus narrow, intercaecal, pre-ovarian. Eggs large, tanned operculate. Metraterm slightly shorter than cirrus-sac, lining similar to ejaculatory duct. Vitellarium follicular, just overlaps posterior end of cirrus-sac; fields confluent or nearly so ventrally and dorsally to uterus, lateral to and slightly overlap gonads, confluent or nearly so dorsally and ventrally in post-testicular region.

Excretory pore terminal. Vesicle I-shaped, reaches to

mid-level of anterior testis.

Taxonomic summary

Type-host: *Grammatorcynus bilineatus* (Rüppell, 1836), Scombridae, double-lined mackerel.

Other host: *Grammatorcynus bicarinatus* (Quoy and Gaimard, 1825), Scombridae; shark mackerel.

Site of infection: intestine.

Type-locality: Lizard Island, Australia. (14°40'S, 145°28'E, Aug., 2002, May, June, 2005, April 2006).

Other locality: Swain Reefs (21°53'S, 152°21'E, Feb. 2001).

Prevalence and intensity: *G. bilineatus*, Lizard Island 75% (3 of 4), 6-10; *G. bicarinatus*, Lizard Island, 39% (9 of 23), 1-13; Swain Reefs, 100% (1 of 1), 5.

Deposition of specimens: *G. bilineatus*, Lizard Island, holotype QM G223080, paratypes QM G223081-223092, BMNH 2007.11.14.17-22; *G. bicarinatus*, Lizard Island, paratypes QM G223093-223101, BMNH 2007.11.14.3-16; Swain Reefs, paratypes QM G223102-223104, BMNH 2007.11.14.1-2.

Etymology: the species is named after Dr. Rafael Lamothe Argumedo, the laureate of this volume in recognition of his great contribution to fish parasitology.

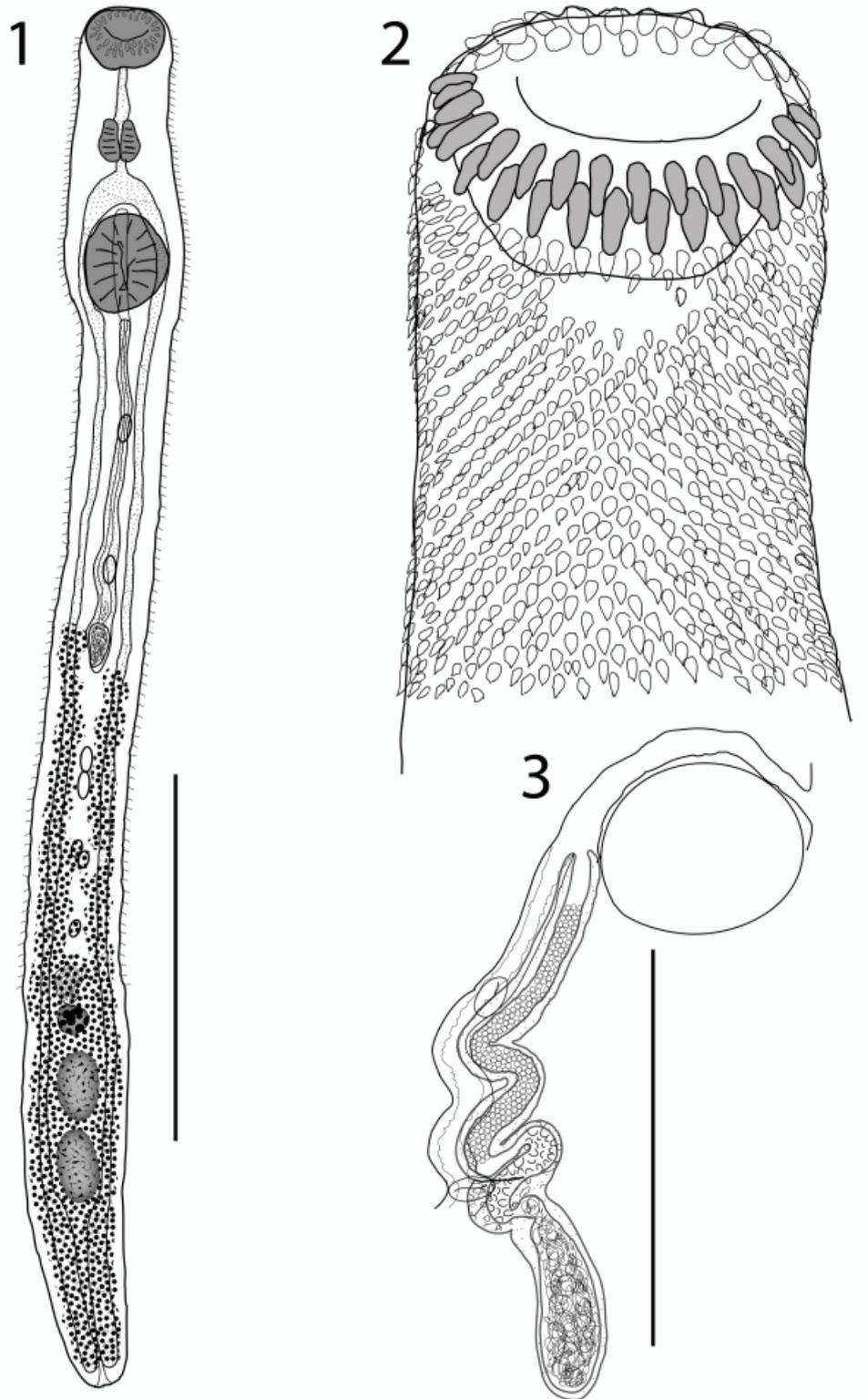
Remarks

According to the list of species of *Stephanostomum* in Bray and Cribb (2003), only 2 species have the vitellarium separated from the ventral sucker by an extent greater than 10% of the hindbody length and about 50 to 52 circum-oral spines. A further 1 has been added since. *S. lamothei* is distinguished from these species as follows.

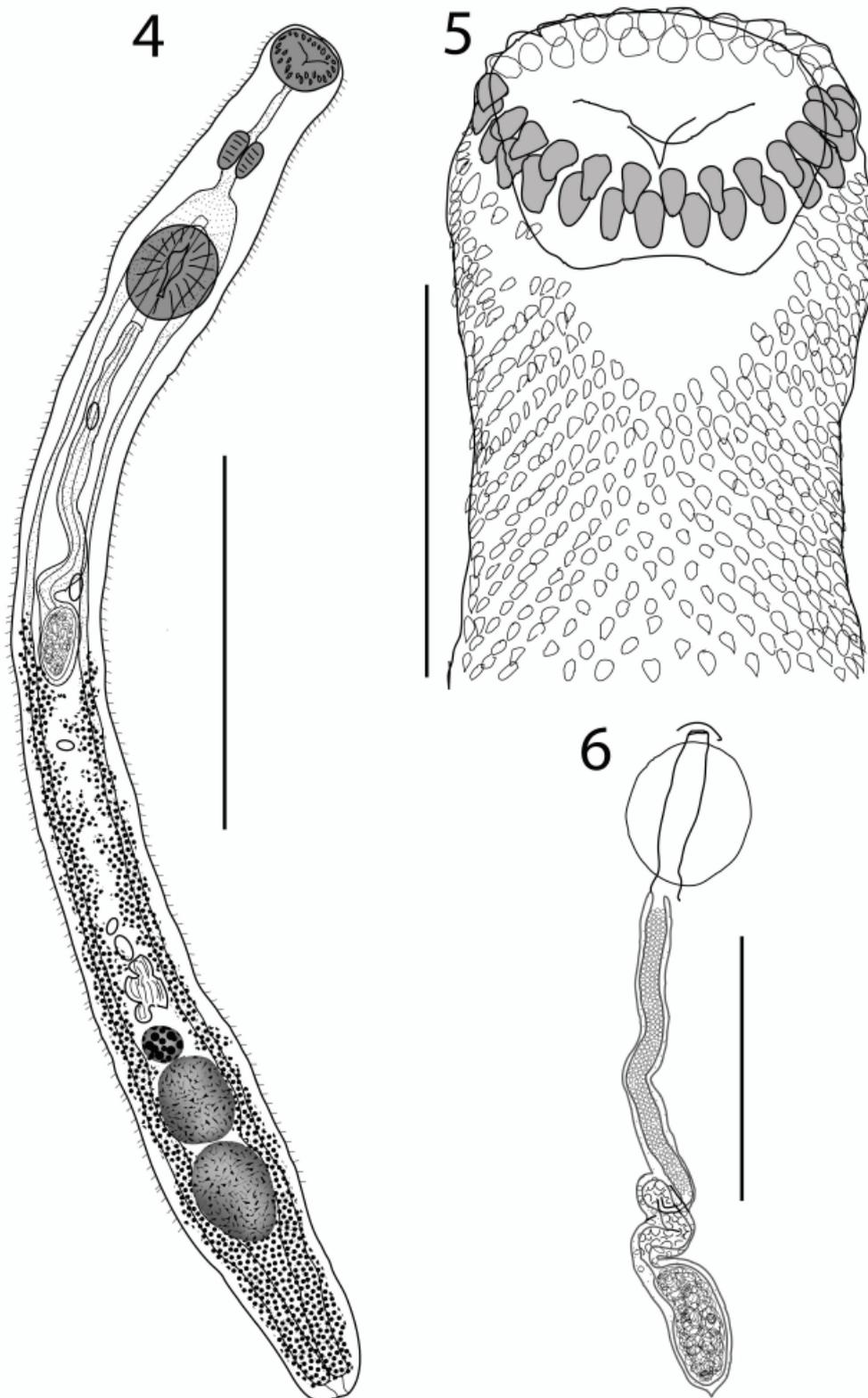
Stephanostomum caducum (Looss, 1901), mainly from gadids in the Mediterranean and the north-eastern Atlantic, has 48-50 circum-oral spines, widely spaced gonads with intervening vitelline follicles and gaps in the vitellarium lateral to the gonads (Looss, 1901; Nicoll, 1914; Srivastava, 1966; Kjøie, 1978).

Stephanostomum lineatum Manter, 1934 from gadids and morids off Florida and Argentina, has 50-52 circum-oral spines in 3 rows (rather than 2 as found in *S. lamothei*), widely spaced gonads with intervening vitelline follicles and gaps in the vitellarium lateral to the gonads (Manter, 1934; Szidat, 1961).

Stephanostomum euzeti Bartoli and Bray, 2004, found as an adult in the carangid *Seriola dumerili* (Risso) (Carangidae) and as a metacercaria in the bogue *Boops boops* (Linnaeus, 1758) (Sparidae) from the western Mediterranean, has 49-51 circum-oral spines, a wide funnel-shaped oral sucker, a relatively much longer forebody (20-35% of body length) and a relatively shorter



Figures 1-3. *Stephanostomum lamothei* n. sp. from *Grammatorcynus bilineatus*. 1, ventral view of holotype. 2, anterior extremity. 3, terminal genitalia. Scale bars: 1, 1mm; 2, 200 μ m; 3, 500 μ m.



Figures 4-6. *Stephanostomum lamothei* n. sp. from *Grammatorcynus bicarinatus*. 4, ventral view. 5, Anterior extremity. 6, terminal genitalia. Scale bars: 4, 1mm; 5, 200 μ m; 6, 500 μ m.

ovary to ventral sucker distance (about 31-42% of body-length) (Bartoli and Bray, 2004; Pérez-del Olmo et al., 2007).

Stephanostomum tupatupa n. sp. (Figs. 7-9)

Based on 5 whole-mount preparations. Measurements and ratios in Table 1. Body elongate, narrow, widest in region of ventral sucker or testes (Fig. 7). Tegument spinous, unarmed patch immediately posterior to oral sucker, spines acuminate with wide base, densely packed in forebody, smaller in hindbody, becoming sparse in hindbody, detectable only to well anterior to ovary. Oral sucker more or less terminal, antero-posteriorly narrow. Circum-oral spines in double ring, without ventral hiatus (Fig. 8). Ventral sucker rounded. Forebody long. Prepharynx long. Pharynx elongate oval. Oesophagus long. Intestinal bifurcation in posterior forebody. Caeca long, narrow, form uroproct.

Testes 2, oval, entire, tandem, contiguous. Post-testicular region short. Cirrus-sac relatively short (Fig. 9), anterior extremity dorsal to ventral sucker. Seminal vesicle saccular, oval, undivided. Pars prostatica separated from seminal receptacle by clear sphincter, relatively short, wider proximally, lined with anuclear cell-like bodies, surrounded by gland-cells; narrows distally to form relatively thick-walled duct. Ejaculatory duct relatively short, wide, lined with closely packed distinct cupolas, with round bases seen as circles on wall of duct, with distinct naked region distally. Genital atrium short, reaching dorsally to ventral sucker. Genital pore median, slit-like, immediately anterior to ventral sucker.

Ovary oval to round, entire, contiguous or very close to anterior testis. Mehlis' gland antero-dorsal to ovary. Laurer's canal opens dorsally to ovary. Uterine seminal receptacle in proximal uterus. Uterus narrow, intercaecal, pre-ovarian. Eggs large, tanned operculate. Metraterm of similar length to cirrus-sac, unarmed. Vitellarium follicular, just overlapping or reaching posterior end of cirrus-sac; fields confluent or nearly so ventrally and dorsally to uterus, lateral to and overlap gonads, no follicles between gonads, confluent dorsally and ventrally in post-testicular region.

Excretory pore terminal. Vesicle I-shaped, reaches to posterior testis.

Taxonomic summary

Type-host: *Caranx papuensis* Alleyne and Macleay, 1877, Carangidae, brassy trevally.

Site of infection: intestine.

Type-locality: Lizard Island (14°40'S, 145°28'E, June

2005).

Prevalence and intensity: 6.25% (1 of 16), 7.

Deposition of specimens: holotype QM G 223115, paratypes QM G 223116-23318, BMNH 2007.11.14.23-24.

Etymology: *Tupatupa* is a Papuan vernacular name for the host.

Remarks

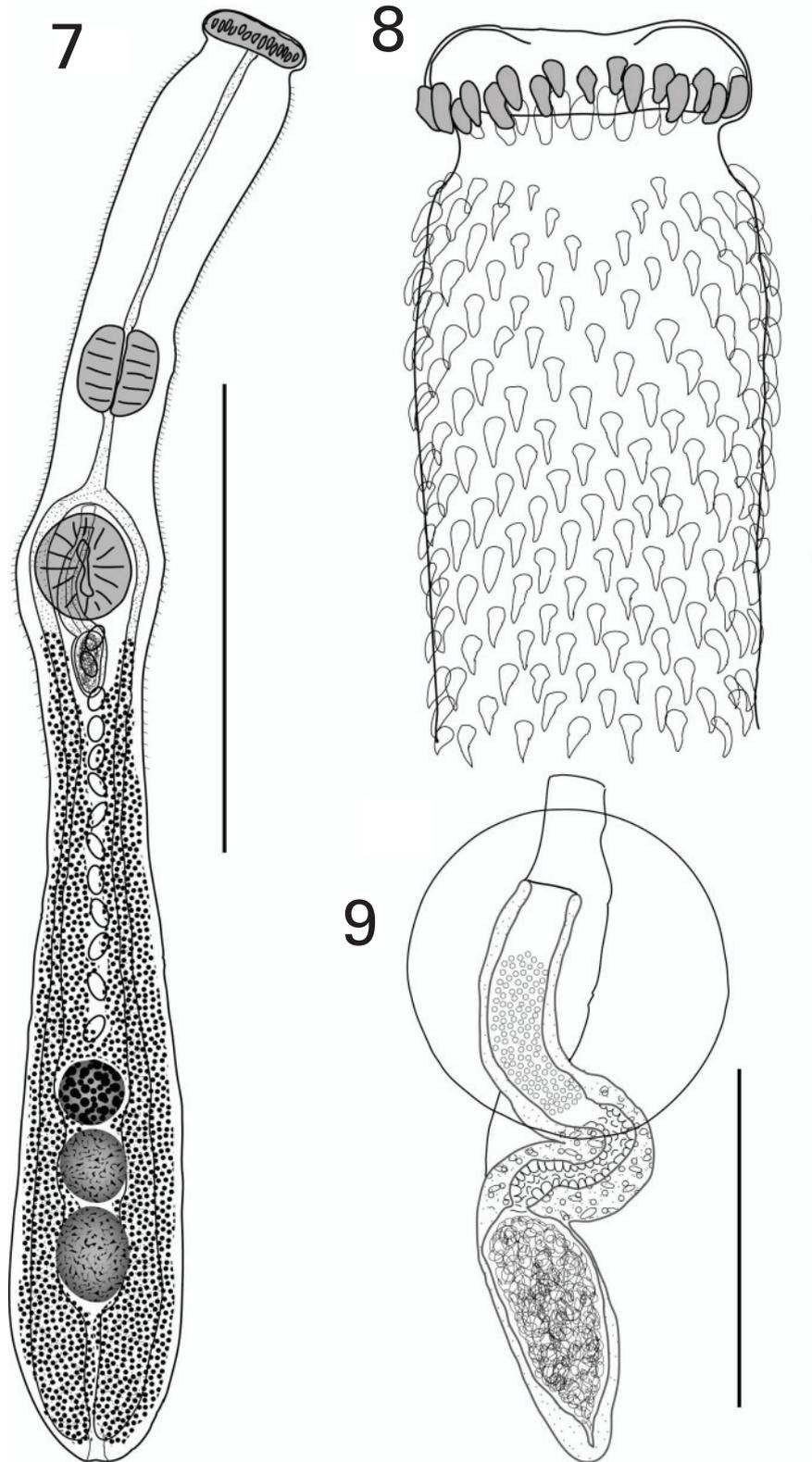
Stephanostomum tupatupa n. sp. fits comfortably into the Bray and Cribb's (2003) group one with the vitellarium distance from the ventral sucker less than 10% of the hindbody length. They list 5 species with circum-oral spines rows of about 36. *S. tupatupa* differs from these thus: *Stephanostomum cesticillum* (Molin, 1858), reported mainly from the angler *Lophius piscatorius* Linnaeus, 1758 (Lophiidae) from the Mediterranean and Atlantic Ocean, is the type-species of the genus, has separated testes with intervening vitelline follicles, a sucker ratio of 1:43-1.99, a ventral hiatus in the circum-oral suckers, blind-caeca, a long cirrus-sac, with a long ejaculatory duct armed with *occasional small spines*, not obvious in fixed specimens (Bartoli and Bray, 2001). Molecular results indicate that the records of this species from the John dory *Zeus faber* Linnaeus, 1758 (Zeidae) are valid (Bray et al., 2005), but records from other hosts need confirmation.

Stephanostomum carangi Liu, 1998 from the giant trevally *Caranx ignobilis* (Forsskål, 1775) (Carangidae) of Dongshan Island, China, is a broader worm (width about 18-23% of body-length), a funnel-shaped oral sucker, a relatively shorter forebody (about 24% of body-length) and ventral sucker to ovary distance (about 20% of body-length). The terminal genitalia are not well enough described for a meaningful comparison (Liu, 1998).

Stephanostomum coryphaenae Manter, 1947, reported mainly from the common dolphinfish *Coryphaena hippurus* Linnaeus, 1758 (Coryphaenidae) from the northern tropical Atlantic, is a broader worm (width about 13-22% of body-length), with a sucker ratio 1:1.4-1.8, a short forebody (about 15-18% of body-length) and longer post-testicular region (about 19% of body-length). The testes are said to be separated by *a few vitelline follicles* (Manter, 1947; Siddiqi and Cable, 1960; Travassos et al., 1967).

Stephanostomum simhai Gupta and Ahmad, 1979 from the goldlined seabream *Rhabdosargus sarba* (Forsskål, 1775) (Sparidae) in the Bay of Bengal, is said to have separate ani, and has a short forebody (about 24% of body-length) and long post-testicular region (about 20% of body-length). The terminal genitalia are not well enough described for a meaningful comparison (Gupta and Ahmad, 1979).

Stephanostomum trompeteri Zhukov, 1983, from



Figures 7-9. *Stephanostomum tupatupa* n. sp. from *Caranx papuensis*. 7, ventral view of holotype. 8, anterior extremity. 9, terminal genitalia. Scale bars: 10, 1mm; 11, 12, 200 μ m.

the cornet fish *Fistularia tabacaria* Linnaeus, 1758 (Fistulariidae) in the southern Gulf of Mexico (Zhukov, 1983). The illustration is of a twisted worm, but it appears that the forebody is short (about 20% of body-length) and that there is no significant oesophagus. The terminal genitalia are described perfunctorily in this Atlantic species.

Stephanostomum ditrematis (Yamaguti, 1939) Manter, 1947. (Figs. 10-12)

Syns. *Echinostephanus ditrematis* Yamaguti, 1939; *Stephanostomum seriola* Yamaguti, 1970.

Based on 9 whole-mount preparations. Measurements and ratios in Table 1. Body elongate, narrow, widest in region of ventral sucker or testes (Fig. 10). Tegument spinous, unarmed patch immediately posterior to oral sucker, spines acuminate with wide base, densely packed in forebody, smaller in hindbody, becoming sparse in hindbody, detectable to just anterior to ovary. Oral sucker more or less terminal, subglobular. Circum-oral spines in double ring, without ventral hiatus; posterior ventral spines smaller than remainder (Fig. 11). Ventral sucker rounded, in anterior fifth of body. Prepharynx long. Pharynx elongate. Oesophagus short. Intestinal bifurcation in posterior forebody or at about anterior margin of ventral sucker. Caeca long, narrow, form uroproct.

Testes 2, oval, entire, tandem, separated. Post-testicular region very short. Cirrus-sac elongate (Fig. 12), entirely within hindbody; anterior extremity well posterior to ventral sucker. Seminal vesicle saccular, oval, undivided. Pars prostatica separated from seminal receptacle by clear sphincter, elongate, wider proximally, lined with anuclear cell-like bodies, surrounded by gland-cells; narrows distally to form relatively thick-walled duct. Ejaculatory duct long, wide, lined with closely packed distinct deep cupolas, showing distally directed chevron-like effect, with round bases seen as circles on wall of duct, with distinct naked region distally. Genital atrium very long, reaching well into hindbody. Genital pore median, slit-like, immediately anterior to ventral sucker.

Ovary oval to round, entire, separated from anterior testis. Mehlis' gland antero-dorsal to ovary. Laurer's canal opens dorsally to ovary. Uterine seminal receptacle in proximal uterus. Uterus narrow, intercaecal, pre-ovarian. Eggs large, tanned operculate. Metraterm of similar length to cirrus-sac, lining irregular, but not armed. Vitellarium follicular, just overlapping or reaching posterior end of cirrus-sac; fields confluent or nearly so ventrally and dorsally to uterus, lateral to and overlap gonads, confluent ventrally and dorsally between ovary and anterior testis and between testes, confluent dorsally and ventrally in

post-testicular region.

Excretory pore terminal. Vesicle I-shaped, short, not traced past posterior testis.

Taxonomic summary

Host: *Gnathanodon speciosus* (Forsskål), Carangidae, golden trevally.

Site of infection: intestine.

Localities: Heron Island (23°27'S, 151°55'E, May, 2003); Lizard Island (14°40'S, 145°28'E, June 2005) (2 immature only).

Prevalence and intensity: Heron Island 25% (1 of 4), 7; Lizard Island 50% (2 of 4), 2-11.

Deposition of specimens: Heron Island, QM G223112-223114, BMNH 2007.11.14.25-29; Lizard Island, QM G223105-223111, BMNH 2007.11.14.30-33.

Remarks

Stephanostomum ditrematis (Yamaguti, 1939) is reported widely, mainly from carangids, and may constitute a composite species, but the type-specimens and the worms described by Bartoli and Bray (2004) from *Seriola dumerili* (Risso, 1810) (Carangidae) in the Mediterranean Sea off Corsica, are similar to those described here. It was reported from *Gnathanodon speciosus* by Parukhin (1970; 1976) from the Red Sea, Indian Ocean and the South China Sea. The cupolas lining the ejaculatory duct appear to be more prominent than those described by Bartoli and Bray (2004), where they were described as *weakly developed*, but the overall morphology is not sufficiently distinct to suggest that a separate species is present.

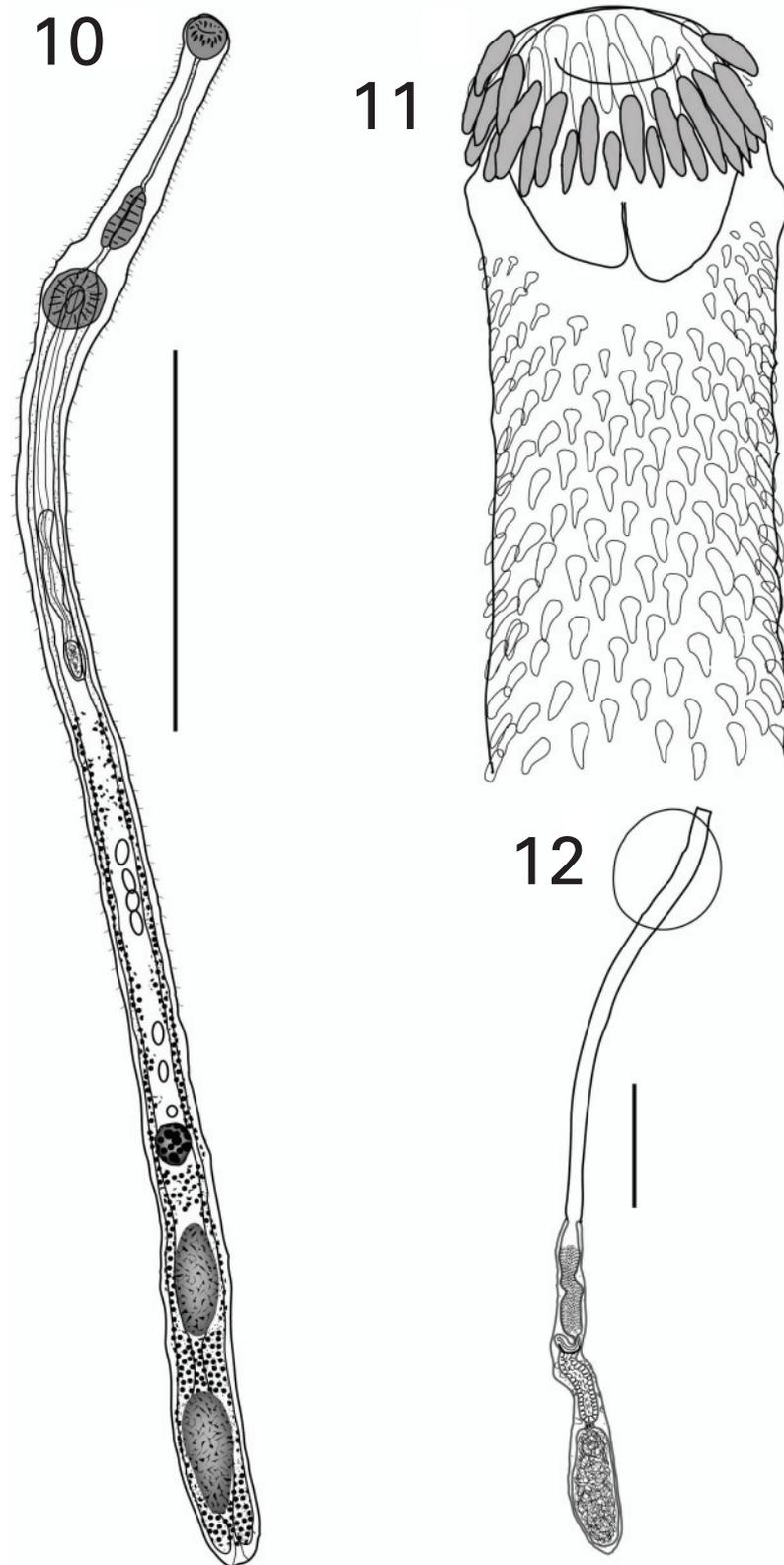
In all, 4 *Stephanostomum* species have been reported from *Gnathanodon speciosus* and the remaining 3 can readily be distinguished from *S. ditrematis*: *Stephanostomum lebedevi* Parukhin, 1974, which was reported by Parukhin (1976) from the Red Sea, has 46-48 circum-oral spines (Parukhin, 1974).

Stephanostomum megacephalum Manter, 1940, which was reported by Parukhin (1970; 1976) from the Red Sea and the Gulf of Mannar, is reported with 30-32 circum-oral spines, almost always 32 (Manter, 1940).

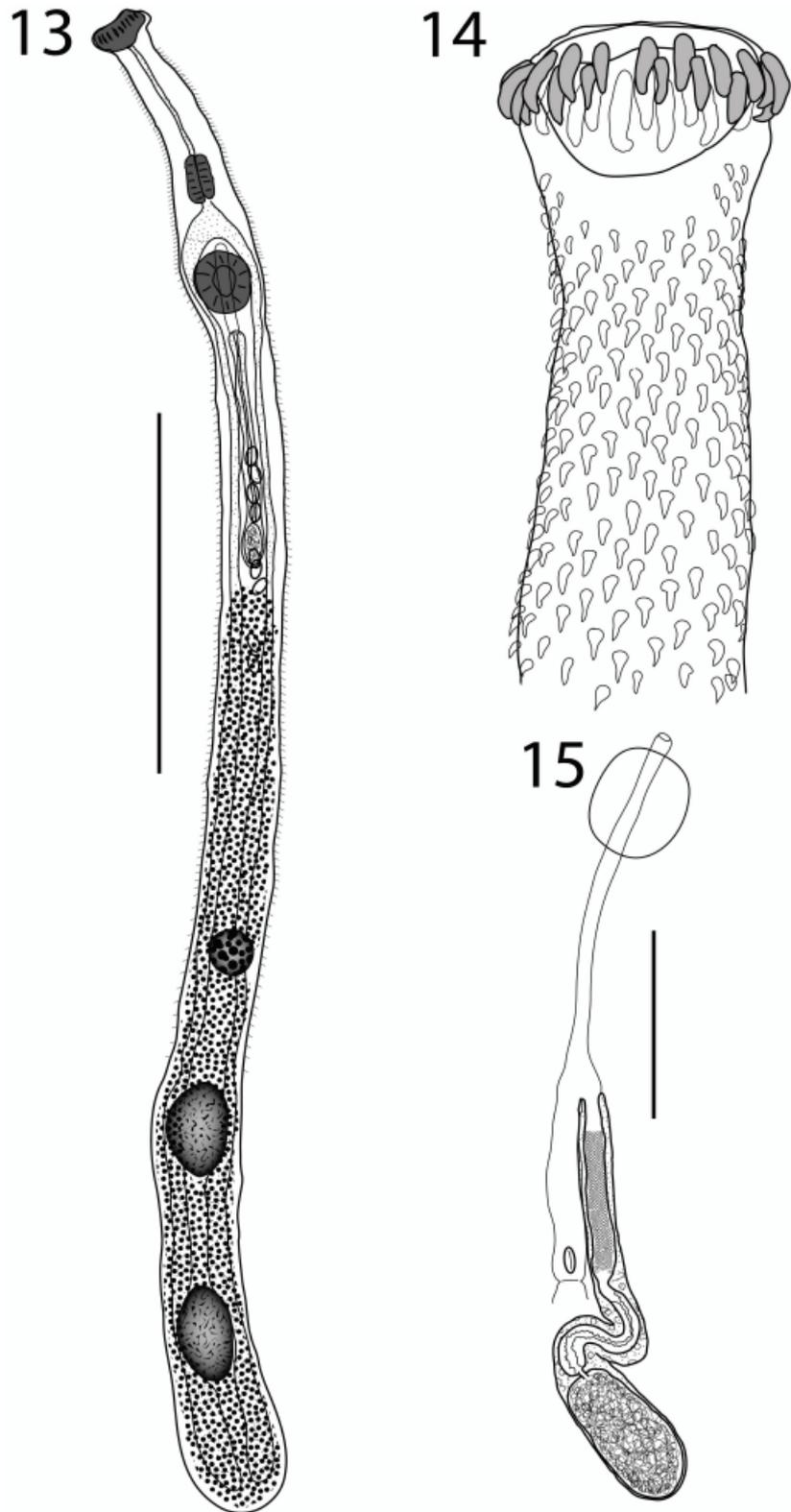
Stephanostomum talakitok Bray and Cribb, 2006, reported from Ningaloo Reef, Western Australia, has contiguous gonads with no intervening vitelline follicles, and a very short genital atrium (Bray and Cribb, 2006).

Stephanostomum hawaiiense Yamaguti, 1970. (Figs. 13-15)

Based on 5 whole-mount preparations. Measurements and ratios in Table 1. Body elongate, narrow, widest in



Figures 10-12. *Stephanostomum ditrematis* (Yamaguti, 1939) from *Gnathanodon speciosus*. 10, ventral view. 11, anterior extremity. 12, terminal genitalia. Scale bars: 7, 1mm; 8, 9, 200 μ m.



Figures 13-15. *Stephanostomum hawaiiense* Yamaguti, 1970 from *Carangoides fulvoguttatus*. 13, ventral view. 14, anterior extremity. 15, terminal genitalia. Scale bars: 13, 1mm; 14, 15, 200 μ m.

region of ventral sucker or testes (Fig. 13). Tegument spinous, unarmed patch immediately posterior to oral sucker, spines acuminate with wide base, densely packed in forebody, smaller in hindbody, becoming sparse in hindbody, detectable to anterior testis. Oral sucker more or less terminal, weakly infundibuliform. Circum-oral spines in double ring, ventral hiatus (Fig. 14). Ventral sucker rounded. Forebody short. Prepharynx long. Pharynx elongate oval. Oesophagus short. Intestinal bifurcation in posterior forebody. Caeca long, form uroproct.

Testes 2, oval, entire, tandem, well separated. Post-testicular region short. Cirrus-sac relatively short (Fig. 15), anterior extremity well into hindbody. Seminal vesicle saccular, oval, undivided. Pars prostatica separated from seminal receptacle by clear sphincter, fairly long, slightly wider proximally, lined with anuclear cell-like bodies, surrounded by gland-cells, narrows distally. Ejaculatory duct of similar length to pars prostatica when withdrawn, wide, lined with closely packed distinct cupolas, with round bases seen as circles on wall of duct, with distinct naked region distally; in 1 specimen the ejaculatory duct is extruded through the genital pore as a cirrus; in another the ejaculatory duct is extruded within the genital atrium. Genital atrium long, reaching well into hindbody. Genital pore median, slit-like, immediately anterior to ventral sucker.

Ovary oval to round, entire, well separated from anterior testis. Mehlis' gland antero-dorsal to ovary. Laurer's canal opens dorsally to ovary. Uterine seminal receptacle in proximal uterus. Uterus narrow, intercaecal, pre-ovarian. Eggs large, tanned operculate. Metraterm of similar length to ejaculatory duct, unarmed. Vitellarium follicular, not quite reaching posterior end of cirrus-sac; fields confluent ventrally and dorsally to uterus, lateral to gonads, confluent between gonads, confluent dorsally and ventrally in post-testicular region.

Excretory pore terminal. Vesicle I-shaped, reaches to posterior testis.

Taxonomic summary

Host: *Carangoides fulvoguttatus* (Forsskål, 1775), Carangidae, yellowspotted trevally.

Site: intestine.

Locality: off Coconut beach and east of Lizard Island (14°40'S, 145°28'E, April 2006).

Prevalence and intensity: 14% (2 of 14), 2-3.

Deposition of specimens: QM G223119-223122, BMNH 2007.11.14.34-37.

Remarks

This species belongs to the group with >10% of the hindbody devoid of vitelline follicles as listed by Bray and

Cribb (2003). Within that group it can be differentiated by the circum-oral spine number centred on 36 and a ventral hiatus in the spine rows. Three species exhibit this combination of characters, *Stephanostomum hawaiiense* Yamaguti, 1970, *S. lateolabracis* Liu, 1998 and *S. manteri* Vigueras, 1955.

We consider the present material practically indistinguishable from *S. hawaiiense* from the bigeye trevally *Caranx sexfasciatus* (Carangidae) from off Hawaii as described by Yamaguti (1970). The original description differs slightly from our interpretation in that we observe a uroproct, whereas Yamaguti did not. The uroproct is often obscured by vitelline follicles in this genus and we do not consider this point strong enough to consider the forms different. The armament of the ejaculatory duct was described as *basally rounded spines*, which we interpret to be the circular cupolas we observed.

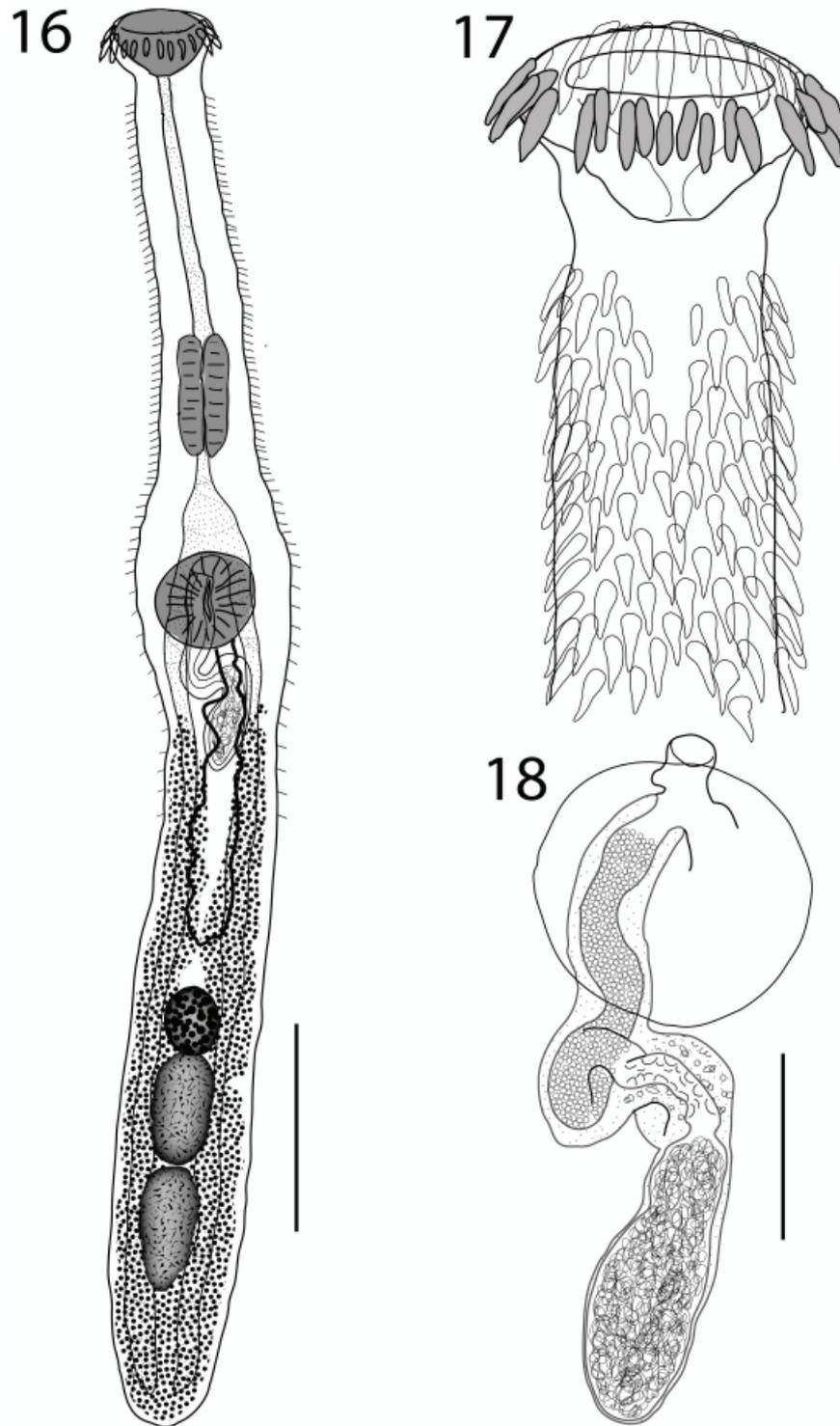
It appears that *S. lateolabracis* from the Japanese seaperch *Lateolabrax japonicus* (Cuvier, 1828) (Lateolabracidae) off Dongshan Island, China, was incorrectly placed in this group (Group 2) of species by Bray and Cribb (2003) as it has <10% of the hindbody devoid of vitelline follicles; in fact the vitellarium reaches close to the ventral sucker (Liu, 1998). It should have been listed in Group 1. A ventral hiatus in the circum-oral spine rings is described, but is not clear in the illustration.

Stephanostomum manteri from the barjack *Carangoides ruber* (Bloch, 1793) (Carangidae) off Cuba (Vigueras, 1955) has 36 circum-oral spines in the illustration, and a ventral hiatus is described. It apparently has a short genital atrium, not reaching into the hindbody.

Stephanostomum carangi Liu, 1998. (Figs. 16-18)

Based on 5 whole-mount preparations. Measurements and ratios in Table 1. Body elongate, narrow, widest in region of ventral sucker or testes (Fig. 16). Tegument spinous, unarmed patch immediately posterior to oral sucker, spines acuminate, densely packed in forebody, smaller in hindbody, becoming sparse in hindbody, detectable to level of ovary. Oral sucker more or less terminal, shallow infundibuliform. Circum-oral spines in double ring, without ventral hiatus (Fig. 17). Ventral sucker rounded. Forebody relatively long. Prepharynx long. Pharynx elongate oval. Oesophagus short. Intestinal bifurcation in posterior forebody. Caeca long, narrow, probably forms uroproct.

Testes 2, oval, entire, tandem, contiguous. Post-testicular region short. Cirrus-sac relative short (Fig. 18), anterior extremity dorsal to ventral sucker. Seminal vesicle saccular, oval, undivided. Pars prostatica separated from



Figures 16-18. *Stephanostomum carangi* Liu, 1998 from *Carangoides fulvoguttatus*. 16, ventral view. 17, anterior extremity. 18, terminal genitalia. Scale bars: 16, 1mm; 17, 18, 200 μ m.

seminal receptacle by clear sphincter, short, lined with anuclear cell-like bodies, surrounded by gland-cells; narrows distally. Ejaculatory duct relatively long, wide, lined with closely packed distinct cupolas, with round bases seen as circles on wall of duct, with distinct naked region distally. Genital atrium very short, reaching dorsally to anterior part of ventral sucker. Genital pore median, slit-like, immediately anterior to ventral sucker.

Ovary oval to round, entire, contiguous or very close to anterior testis. Mehlis' gland antero-dorsal to ovary. Laurer's canal opens dorsally to ovary. Uterine seminal receptacle in proximal uterus. Uterus narrow, intercaecal, pre-ovarian. Eggs large, tanned operculate. Metraterm unarmed, usually distended with eggs. Vitellarium follicular, overlapping cirrus-sac reaching close to ventral sucker; fields confluent or nearly so ventrally and dorsally to uterus, lateral to and overlap gonads, no follicles between gonads, confluent dorsally and ventrally in post-testicular region.

Excretory pore terminal. Vesicle I-shaped, reaches to posterior testis.

Taxonomic summary

Host: *Carangoides fulvoguttatus* (Forsskål, 1775), Carangidae, yellowspotted trevally.

Site of infection: intestine.

Locality: Lizard Island (14°40'S, 145°28'E, August 2002).

Prevalence and intensity: 14% (2 of 14), 1-2.

Deposition of specimens: QM G223123-223124, BMNH 2007.11.14.43.

Remarks

Four species of *Stephanostomum* were listed by Bray and Cribb (2003) as having less than 10% of the hindbody devoid of vitelline follicles, with a circum-oral spine number centred on 36 and without a ventral hiatus: *S. carangi* Liu, 1998, *S. coryphaena* Manter, 1947, *S. simhai* Gupta and Ahmad, 1979 and *S. trumpeteri* Zhukov, 1983.

The present worms are practically indistinguishable from *S. carangi* from *Caranx ignobilis* (Carangidae) from off Dongshan Island, China (Liu, 1998) despite the fact that the original description, based on 2 specimens, appears to be based on flattened and distorted worms, as is indicated by the twisted appearance of the prepharynx and pharynx. This has also meant that the width ratio (about 18-23% of body-length) is much greater than found in our, unflattened specimens. The terminal genitalia are not described in detail, but the relatively short pars prostatica and long ejaculatory duct appear to be indicated.

Stephanostomum coryphaena reported mainly from

Coryphaena hippurus (Coryphaenidae) from the northern tropical Atlantic, has distinct gaps between the gonads, a short forebody (about 15-18% of body-length), a longer post-testicular region (about 19% of body-length) and a longer ovary to ventral sucker distance (about 35%). The testes are said to be separated by a few vitelline follicles (Manter, 1947; Siddiqi and Cable, 1960; Travassos et al., 1967).

Stephanostomum simhai Gupta and Ahmad, 1979 from the goldlined seabream *Rhabdosargus sarba* (Forsskål, 1775) (Sparidae) in the Bay of Bengal, is said to have separate ani, and has distinct gaps between the gonads, a short forebody (about 24% of body-length) and long post-testicular region (about 20% of body-length). The terminal genitalia are not well enough described for a meaningful comparison (Gupta and Ahmad, 1979).

Stephanostomum trompeteri Zhukov, 1983 is from the cornet fish *Fistularia tabacaria* Linnaeus, 1758 (Fistulariidae) in the southern Gulf of Mexico (Zhukov, 1983). The illustration is of a twisted worm, but it appears that the forebody is short (about 20% of body-length) and the ovary is slightly separated from the anterior testis. The terminal genitalia are described perfunctorily in this Atlantic species, but it appears that the genital atrium reaches to the posterior part of the ventral sucker.

Stephanostomum nyoomwa Bray and Cribb, 2003. (Figs. 19-21)

Taxonomic summary

Host: *Caranx sexfasciatus* Quoy and Gaimard, 1825, Carangidae, bigeye trevally.

Site of infection: intestine.

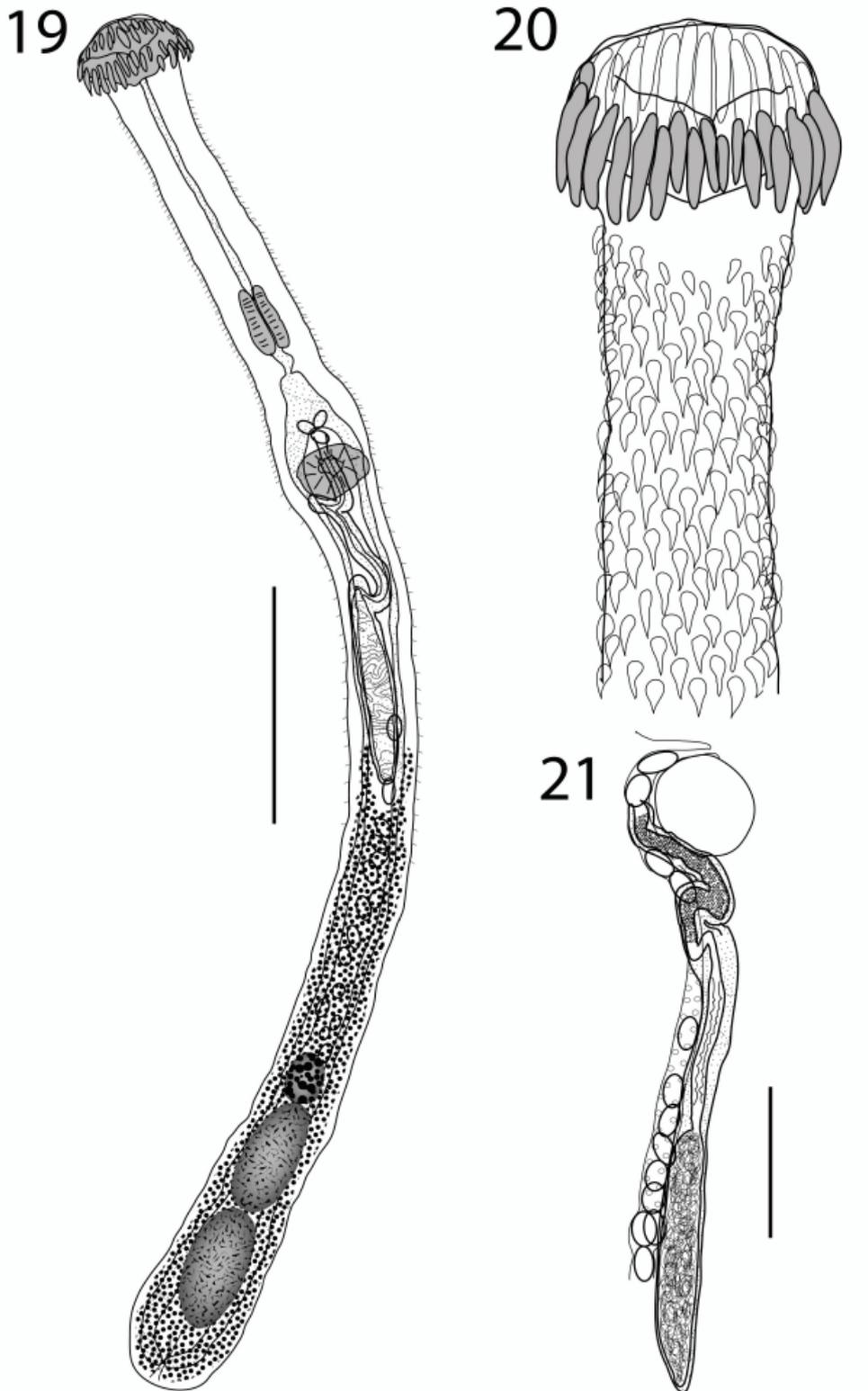
Locality: off Casuarina Beach, Lizard Island (14°40'S, 145°28'E, April 2006).

Prevalence and intensity: 50% (1 of 2), 10.

Deposition of specimens: QM G223125-G223129, BMNH 2007.11.14.38-42.

Remarks

The measurements are given in Table 1. This species was originally reported from *Caranx sexfasciatus* from Heron Island, in the southern Great Barrier Reef. The specimens from Lizard Island are indistinguishable from those described by Bray and Cribb (2003), apart from the sucker-width ratio (the ventral sucker is relatively smaller in the Lizard Island specimens) and the scattering of cupolas in the metraterm in some specimens.



Figures 19-21. *Stephanostomum nyoomwa* Bray and Cribb, 2003 from *Caranx sexfasciatus*. 19, ventral view. 20, anterior extremity. 21, terminal genitalia. Scale bars: 19, 500 μ m; 20, 21, 200 μ m.

Acknowledgements

We are grateful to Rob Adlard, Matt Nolan and Terry Miller for assistance with the collection. This study has been supported by the Australian Research Council, Australian Biological Resources Study and the Lizard and Heron Island Research Stations.

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