Observations on the phylogeny of *Opisthadena* Linton, 1910 and related genera (Hemiuridae: Opisthadeninae) from Australian and French Polynesian waters

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Abstract. *Mitrostoma nototheniae* Manter, 1954 is redescribed from *Aplodactylus arctidens* Richardson, off northern Tasmania. *Opisthadena dimidia* Linton, 1910 is reported from *Kyphosus bigibbus* Lacepède, Ningaloo, Western Australia, *K. cinerascens* (Forsskål), off Heron Island and Ningaloo, Western Australia, *Kyphosus cornelii* (Whitley), off Kalbarri, Western Australia, *K. sydneyanus* Günther, off Fremantle, Western Australia, *K. sydneyanus* ?, Ningaloo, Western Australia and *K. vaigiensis* (Quoy et Gaimard), off Heron and Lizard Islands, Queensland and Moorea, French Polynesia: measurements and an illustration are given. *Neopisthadena habei* Machida, 1980 is reported from *K. sydneyanus* off Fremantle, Western Australia: measurements and an illustration are given. Data derived from these specimens are used to recode a data-matrix developed by León-Règagnon et al. (1996), and the resultant tree produced is almost congruent with that of these authors. Our data indicate that this group of parasites is associated mostly with herbivorous hosts and that *O. dimidia*, while geographically widespread, is stenoxenic to the genus *Kyphosus*.

The subfamily Opisthadeninae Yamaguti, 1970 was considered by Gibson and Bray (1979) to include the four genera *Opisthadena* Linton, 1910, *Genolinea* Manter, 1925, *Mitrostoma* Manter, 1954 and *Neotheletrum* Gibson et Bray, 1979, and to belong in the family Bunocotylidae Dollfus, 1950. Brooks et al. (1985) reverted to the earlier opinion that the taxon should be recognised as Bunocotylinae, a subfamily of the Hemiuridae Looss, 1899. The results of León-Règagnon et al. (1998) supported the clade formed by the constituent genera of the Opisthadeninae (now also including *Neopisthadena* Machida, 1980) and Gibson (2002) retained the taxon Opisthadeninae, but recognised it as a subfamily of the Hemiuridae. León-Règagnon et al. (1996) recently presented a cladistic analysis of *Opisthadena*, using as outgroups the other genera of the Opisthadeninae. Our collecting in the waters around Australia and in French Polynesia has produced members of three of these genera from new hosts and localities. We are reporting here these findings and using this new material to refine the evolutionary hypothesis proposed by León-Règagnon et al. (1996). In the case of *Mitrostoma nototheniae* Manter, 1954, reported here for only the second time, we present a full description. The other species are better known and, therefore, we are giving only illustrations and measurements.

MATERIALS AND METHODS

Digeneans collected from freshly killed fishes were fixed by being pipetted into nearly boiling saline and immediately preserved in 2% formaldehyde or 70% ethanol, or fixed in Berland's fluid and preserved in 80% ethanol. Whole-mounts were stained with Mayer's haematoxylin or Mayer's para-carmine, cleared in methyl salicylate or 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. 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. Fish synonymy is based on Froese and Pauly (2001).

The cladistic analyses were performed in PAUP* (Swofford 1998), using the exhaustive search option; 21 unordered characters of eight species were analysed, 1000 heuristic bootstrap replicates were performed.

RESULTS

Family: H e m i u r i d a e Looss, 1899
Subfamily: O p i s t h a d e n i n a e Yamaguti, 1970

Mitrostoma nototheniae Manter, 1954 Fig. 1

Description. Based on two whole-mounts. Measurements in Table 1. Body narrows anteriorly, truncate

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posteriorly (Fig. 1). Tegument unarmed, with fold around ventral sucker and transverse fold in anterior hindbody. Pre-somatic pit in posterior forebody, opens on surface as transverse slit. Pre-oral lobe forms hood-like fold, bears row of about 5 small papillae. Oral sucker subglobular, subterminal. Ventral sucker transversely oval, in anterior third of body; aperture surrounded by distinct sphincter. Pharynx subglobular. Oesophagus short or practically absent. Intestinal bifurcation in mid-forebody. Caeca blind, extend close to posterior extremity.

Testes 2, oval, entire, tandem, separated by uterus, in anterior half of hindbody, pre-ovarian. Seminal vesicle tubular, coiled, reaches into posterior half of distance between anterior testis and ventral sucker, fairly thin-walled. Pars prostatica long, almost rectilinear, reaching from distinctly within hindbody to almost sinus-sac in forebody, ensheathed in gland-cells. Ejaculatory duct not detectable. Sinus-sac small, thin-walled, oval, in mid-forebody. Hermaphroditic duct convoluted in sinus-sac. Sinus-organ not detected. Genital atrium absent. Genital pore median, bifurcal.

Ovary oval, post-testicular, separated from posterior testis by uterus. Seminal receptacle blind, antero-dorsal to ovary. Mehlis' gland dorsal to ovary. Uterus passes posteriorly to vitellarium, then forward sinistrally to ovary, between ovary and posterior testis, sinistrally to posterior testis, between testes, dextral to anterior testis, then sinistrally to seminal vesicle and pars prostatica, narrows dorsally to ventral sucker and passes towards sinus-sac; short distinct metraterm joins male duct in small chamber at base of sinus-sac. Eggs numerous, small, tanned, operculate. Vitellarium with two irregularly globular masses, immediately post-ovarian, oblique.

Excretory pore dorsally subterminal. Vesicle passes sinistrally to ovary and posterior testis, between testes, dextral to anterior testis, bifurcates immediately pre-testicular; arms unite dorsally to pharynx.

Type-host and locality: '*Notothenia macrocephala*', Wellington, New Zealand.

New records:

ex *Aplodactylus arctidens* Richardson (Perciformes: Aplodactylidae). Stomach. Stanley, Tasmania (40°46'S, 145°20'E, Jan. 2000). QM G217862, BMNH 2002.4.18.20.

Records:

1. Manter (1954); 2. Present study.

Descriptions: 1, 2.

Definitive host: Perciformes: Aplodactylidae: *Aplodactylus arctidens* ['*Notothenia macrocephala*', probably an error, see below] (1, 2).

Distribution: **FAO Area 57** off Tasmania (2); **81** Off New Zealand (1).

Remarks. Manter (1954) described this species from the caeca and intestine of 'Maori chief *Notothenia macrocephala* Günther', off Wellington, New Zealand. According to Froese and Pauly (2001) *N. macrocephalus* is a junior synonym of *Paranotothenia magellanica* (Forster), and 'Maori chief' is an American common name for this species. Ours is only the second record of *Mitrostoma nototheniae* and the first from *Aplodactylus arctidens* and Tasmania. Evidence is accumulating that Manter's host identification may be erroneous. From Tasmanian *A. arctidens* we have also recovered specimens of the enenterids *Proenenterum isocotylum* Manter, 1954 and *P. ericotylum* Manter, 1954, and the fellodistomid *Choanomyzus tasmaniae* Manter et Crowcroft, 1950. The former two species were originally recorded from '*Notothenia macrocephala*' from New Zealand and Manter (1954) reported *C. tasmaniae* from '*Notothenia macrocephala*' from New Zealand. This latter species was originally described from Tasmania in *A. arctidens* (as *Dactylosargus arctidens*) (Manter and Crowcroft 1950). We suggest, therefore, that the evidence is strong that somehow Manter mistook the identity of the host-species in these cases and that none of these digeneans are to be found in *P. magellanica*.

We can detect no significant differences between our specimens and those described by Manter (1954). He figured a 'nipple-shaped protuberance' at the posterior extremity of the 'type' specimen, but considered that this was an 'abnormality'. Using this new material we have recoded this species in the matrix of León-Règagnon et al. (1996). Our coding differs in: Character (Ch.) 6, where oral papillae have been seen; Ch. 7, where we find the testes to be tandem; Ch. 8, where we find both character states; Ch. 9, where we find the vitellarium and ovary in the posterior third of the body; Ch. 12, where we find the pars prostatica to reach into the forebody; and Ch. 19, where we find that the excretory vesicle bifurcates immediately anterior to the testes. The eggs in *M. nototheniae* are 23-27 long (according to Manter 1954) and 22-31 long according to our measurements, so fit completely into neither states of character 2. They do, however, overlap into state 0, but not state 1, so the former coding is retained.

Opisthadena dimidia Linton, 1910 Fig. 2

Syns *O. cortesi* Bravo-Hollis, 1966; *O. kyphosi* Yamaguti, 1970; *Opisthadena* sp. of Cribb et al. (2001)

Type-host and locality: *Kyphosus sectatrix*, off Dry Tortugas, Florida.

New records:

ex *Kyphosus bigibbus* Lacepède, Kyphosidae. Stomach. Ningaloo, Western Australia (22°42'S, 113°40'E, April 2000). QM G217863-217865, BMNH 2002.4.18.1-2.

ex *Kyphosus cinerascens* (Forsskål), Kyphosidae. Stomach. Heron Island, Queensland (23°27'S, 151°55'E, Jan. 1998). QM G217866-217867, BMNH 2002.4.18.7.

ex *Kyphosus cinerascens* (Forsskål), Kyphosidae. Stomach. Ningaloo, Western Australia (22°42'S, 113°40'E, April 2000). QM G217868-217872, BMNH 2002.4.18.3-6.

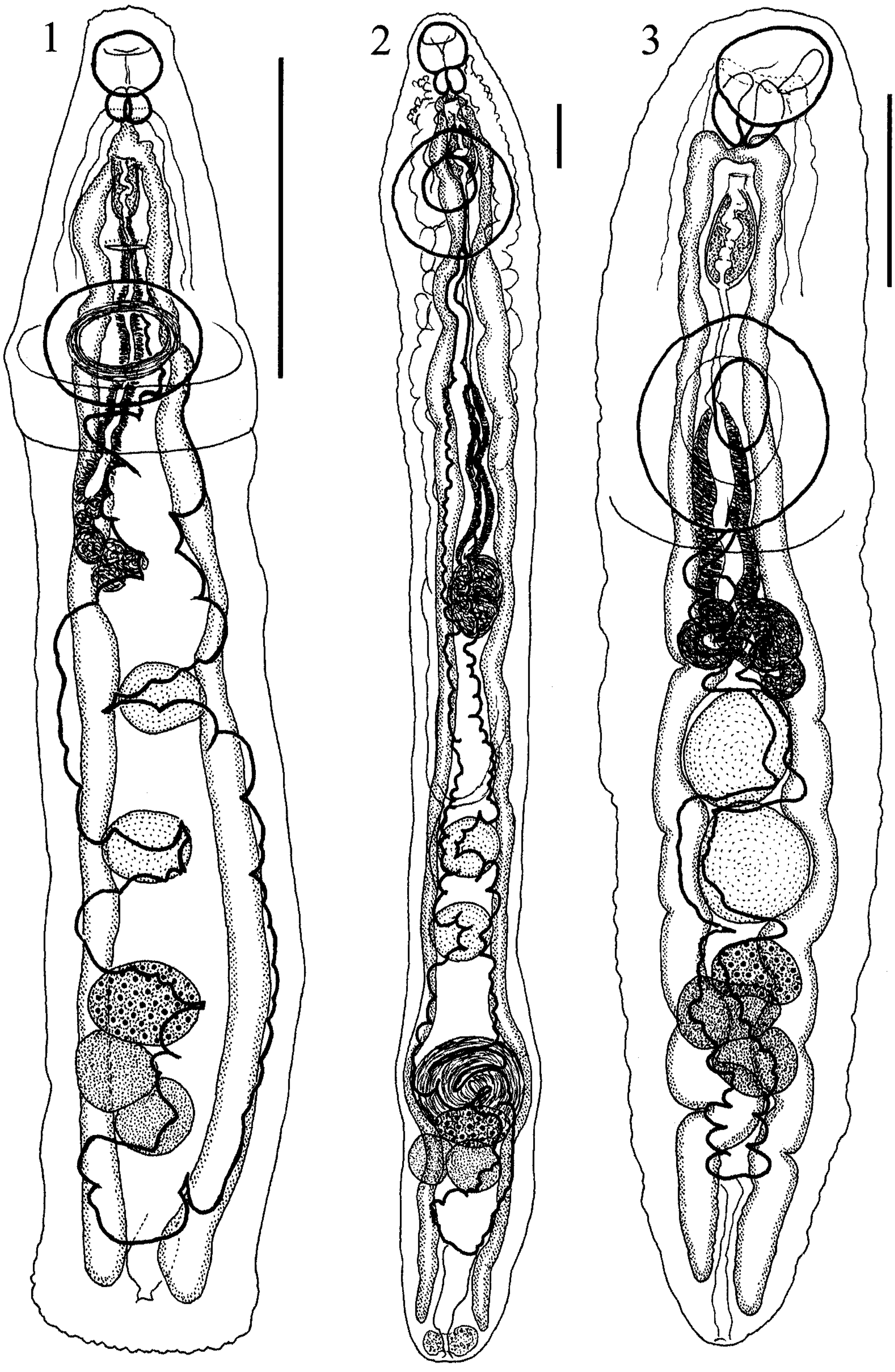

Fig. 1. *Mitrostoma nototheniae* Manter, 1954. Ventral view, suckers and uterus in bold outline, uterus passes ventrally to gonads but is treated as transparent, posterior and anterior extremities of excretory system only shown. **Fig. 2.** *Opisthadena dimidia* Linton, 1910 ex *Kyphosus vaigiensis*, Moorea, French Polynesia. Ventral view, suckers and uterus in bold outline, uterus passes ventrally to gonads but is treated as transparent, posterior and anterior extremities and bifurcation of excretory system only shown. **Fig. 3.** *Neopisthadena habei* Machida, 1980. Ventral view, suckers and uterus in bold outline, uterus passes ventrally to gonads but is treated as transparent, posterior and anterior extremities of excretory system only shown. Scale bars = 500 µm.

Table 1. Dimensions of *Opisthadena*, *Mitrostoma* and *Neopisthadena* spp.

Species Host Locality n	*Opisthadena dimidia* *Kyphosus vaigiensis* Heron Island 8	*Opisthadena dimidia* *Kyphosus vaigiensis* Lizard Island 2	*Opisthadena dimidia* *Kyphosus vaigiensis* Moorea 5
Length	4,254-8,623 (6,229)	1,464-5,492	4,049-8,571 (6,212)
Width	602-1,182 (885)	553-633	515-969 (709)
Forebody	490-875 (623)	424-492	439-774 (621)
Pre-oral lobe	16-51 (33)	28-45	22-85 (51)
Oral sucker	200-372 × 164-343 (255 × 233)	189-215 × 157-197	175-309 × 167-310 (229 × 228)
Pharynx	101-228 × 106-204 (143 × 154)	104-140 × 107-133	98-187 × 114-206 (138 × 151)
Oesophagus	47-90 (59)	5-12	50-90 (66)
IB to VS	92-280 (161)	133-184	112-252 (170)
Sinus sac	86-279 × 95-221 (170 × 155)	120-177 × 109-138	126-274 × 110-228 (193 × 156)
GP to VS	70-203 (126)	98-115	98-206 (165)
Ventral sucker	474-1,011 × 477-957 (694 × 682)	451-570 × 447-561	423-790 × 411-756 (575 × 568)
VS to SV	889-1,528 (1,238)	795-954	792-1,926 (1,336)
Seminal vesicle	210-532 × 163-354 (345 × 243)	201-340 × 142-203	202-508 × 154-313 (322 × 220)
SV to AT	511-1,457 (781)	807-1,034	548-1,199 (915)
Anterior testis	191-344 × 215-393 (259 × 306)	200-238 × 173-228	173-396 × 190-373 (264 × 268)
Distance between testes	41-339 (178)	63-176	58-210 (151)
Posterior testis	215-369 × 219-421 (279 × 325)	209-248 × 184-251	193-379 × 208-403 (267 × 291)
PT to Ov	158-697 (437)	299-307	292-936 (529)
Ovary	186-361 × 253-452 (262 × 341)	215-258 × 261-290	172-300 × 221-452 (231 × 315)
Vitelline masses	170-343 × 150-383 (252 × 258)	182-226 × 160-225	162-331 × 132-345 (237 × 219)
Post-vitelline region	514-1,009 (752)	506-687	478-1,092 (768)
Post-uterine region	331-542 (453)	380-447	339-709 (457)
Post-caecal region	82-228 (134)	82-182	49-259 (137)
Eggs	32-43 × 12-18 (36 × 14)	31-42 × 15-22	27-41 × 11-15 (33 × 13)
Width %*	13-16 (14)	12	11-13 (12)
Forebody %*	8.8-12 (10)	9.0-9.5	8.7-13 (10)
Sucker width ratio	1 : 2.7-3.2 (2.9)	1 : 2.8	1 : 2.4-2.6 (2.5)
OS to Pharynx ratio	1 : 1.4-1.7 (1.5)	1.5	1 : 1.5-1.6 (1.5)
VS to AT % *	30-44 (38)	40-42	38-43 (41)
Post-vitelline region %*	11-14 (12)	11-13	12-13 (12)
Post-uterine region %*	6.2-10 (7.5)	8.1-8.5	6.4-8.4 (7.4)
SV to AT %*	6.7-19 (13)	18-19	12-17 (15)
VS to SV %	16-25 (20)	17-18	19-24 (21)
SV to AT % of VS to SV	41-95 (63)	102-108	51-88 (69)

ex *Kyphosus cornelii* (Whitley), Kyphosidae. Stomach. Red Bluff, Kalbarri, Western Australia (27°42'S, 114°10'E, March 1988). QM G217873, BMNH 1988.6.28.43-52.

ex *Kyphosus sydneyanus* (Günther), Kyphosidae. Stomach. Off Fremantle, Western Australia (32°07'S, 115°44'E, March 1988). QM G217874, BMNH 1988.6.28.30-42.

ex *Kyphosus sydneyanus* ? (Günther), Kyphosidae. Stomach. Ningaloo, Western Australia (22°42'S, 113°40'E, April 2000). QM G217875-217881, BMNH 2002.4.18.8-12.

ex *Kyphosus vaigiensis* (Quoy et Gaimard) (Kyphosidae). Stomach. Heron Island, Queensland (23°27'S, 151°55'E, Jan. 1998, April 1999). QM G217882-217886, BMNH 2002.4.18.13-16.

ex *Kyphosus vaigiensis* (Quoy et Gaimard) (Kyphosidae). Stomach. Moorea, French Polynesia (17°30'S, 149°50'W, Dec. 1999). QM G217887-217889, BMNH 2002.4.18.18-19.

ex *Kyphosus vaigiensis* (Quoy et Gaimard) (Kyphosidae). Stomach. Lizard Island, Queensland (14°40'S, 154°28'E; Dec. 2000). QM G217890-217891, BMNH 2002.4.18.17.

Records:

1. Linton (1910); 2. Manter (1947); 3. Sogandares-Bernal (1959); 4. Bravo-Hollis (1965); 5. Manter (1966) 6. Overstreet (1969); 7. Yamaguti (1970); 8. Machida (1980); 9. Hogans et al. (1983); 10. Dyer et al. (1985); 11. Kim et al. (1990); 12. Dyer et al. (1992); 13. León-Règagnon et al. (1996); 14. Lamothe-Argumedo et al. (1997); 15. León-Règagnon et al. (1997a); 16. León-Règagnon et al. (1997b); 17. Pérez-Ponce de León et al. (1999); 18. Hassanine (2000); 19. Cribb et al. (2001); 20. Present study.

Descriptions: 1, 2, 4, 7, 8, 18, 20.

Table 1. Continued.

Species Host Locality n	*Opisthadena dimidia* *Kyphosus cinerascens* Heron Island 2	*Opisthadena dimidia* *Kyphosus cinerascens* Ningaloo 9
Length	6,014-6,150	3,648-6,999 (5,267)
Width	814-861	474-957 (647)
Forebody	507-593	377-674 (494)
Pre-oral lobe	36-42	16-38 (27)
Oral sucker	224-240 × 200-206	147-258 × 131-232 (192 × 171)
Pharynx	131-134 × 142-143	86-150 × 90-170 (109 × 120)
Oesophagus	35-41	9-21 (14)
IB to VS	119-182	121-233 (168)
Sinus sac	126-134 × 126-149	84-150 × 72-128 (110 × 112)
GP to VS	58-129	84-194 (131)
Ventral sucker	629-641 × 617-634	398-748 × 399-706 (536 × 515)
VS to SV	1,434-1,535	764-1,429 (1,068)
Seminal vesicle	354-355 × 243-267	195-387 × 122-274 (282 × 179)
SV to AT	824-840	573-1,476 (1,060)
Anterior testis	226-237 × 295-336	187-239 × 178-302 (213 × 229)
Distance between testes	57-145	23-317 (153)
Posterior testis	245-253 × 307-329	194-237 × 195-278 (216 × 238)
PT to Ov	406-415	100-351 (228)
Ovary	252-260 × 329-355	150-270 × 184-313 (203 × 257)
Vitelline masses	231-264 × 187-274	157-326 × 127-365 (233 × 243)
Post-vitelline region	708-761	427-745 (564)
Post-uterine region	382-595	299-442 (358)
Post-caecal region	102-255	63-219 (124)
Eggs	41-43 × 11-14	29-40 × 10-15 (34 × 13)
Width %*	14	11-14 (12)
Forebody %*	8.2-10	7.8-11 (10)
Sucker width ratio	1 : 3.0-3.2	1 : 2.8-3.1 (3.0)
OS to Pharynx ratio	1 : 1.4-1.5	1 : 1.3-1.6 (1.4)
VS to AT % *	43-45	42-49 (45)
Post-vitelline region %*	12	10-12 (11)
Post-uterine region %*	6.3-10	5.5-8.5 (6.9)
SV to AT %*	14	16-23 (20)
VS to SV %	23-26	18-22 (20)
SV to AT % of VS to SV	54-59	75-112 (97)

* of body length
Abbreviations: AT – anterior testis, GP – genital pore, IB – intestinal bifurcation, Ov – ovary, OS – oral sucker, PT – posterior testis, SV – seminal vesicle, VS – ventral sucker.

Definitive hosts: Perciformes: Kyphosidae: *Kyphosus bigibbus* (20), *K. cinerascens* (7, 8, 13, 18, 19, 20), *K. cornelii* (20), *K. elegans* (3, 4, 13, 17), *K. incisor* (2, 13, 14, 15, 16), *K. sectatrix* [? = *sectarius*] (1, 2, 3, 6, 10, 11, 12, 13), *K. sydneyanus* (5, 20), *K. vaigiensis* (20), *Kyphosus* sp. (5); Perciformes: Xiphiidae: *Xiphias gladius* (9).

Distribution: **FAO Area 21** NW Atlantic Ocean (9); **31** Off Florida (1, 2, 13), Bimini, British West Indies (3), Biscayne Bay, Florida (6), Puerto Rico (10, 12, 13); **34** Canary Islands (11); **51** Gulf of Aqaba, Red Sea (18); **57** South Australia (5), Western Australia (20); **61** Japan (8, 13); **71** Heron Island, Queensland (5, 19, 20), Lizard Island, Queensland (20); **77** Quintana Roo, Pacific coast Mexico (13, 14); Chamela Bay, Mexico (15, 16), Jalisco, Mexico (13), Baja California (4, 13, 17), Taboga Island, Pacific coast of Panama (3), Hawaii (7, 13), Moorea, French Polynesia (20).

Remarks. Measurements are given in Table 1. This species has been adequately described by Linton (1910), Manter (1947), Bravo-Hollis (1965), Yamaguti (1970) and Machida (1980), but we have included detailed measurements of our specimens for comparison (Table 1). We can detect no significant differences between our specimens and those described earlier, but we have recoded the matrix in León-Règagnon et al. (1996) in respect of: Character 4, in which we find the testes in either the middle or posterior third of the body-length or

Table 1. Continued.

Species Host Locality n	*Opisthadena dimidia* *Kyphosus sydneyanus* off Fremantle 5	*Opisthadena dimidia* *Kyphosus sydneyanus*? Ningaloo 12	*Opisthadena dimidia* *Kyphosus cornelii* Kalbarri 2
Length	4,264-8,328 (6,320)	4,573-7,682 (6,129)	2,812-3,706
Width	553-1,014 (787)	516-898 (747)	589-599
Forebody	386-545 (437)	432-623 (563)	387-474
Pre-oral lobe	26-42 (35)	22-47 (35)	37-45
Oral sucker	175-267 × 173-289 (216 × 235)	153-246 × 140-237 (215 × 199)	175-190 × 178-207
Pharynx	113-207 × 113-196 (165 × 151)	92-159 × 94-165 (129 × 138)	117-136 × 117-121
Oesophagus	0-10 (2)	7-47 (18)	0-13
IB to VS	122-215 (165)	138-222 (179)	113-210
Sinus sac	133-226 × 97-150 (177 × 117)	94-181 × 88-163 (142 × 138)	133-146 × 78-82
GP to VS	52-97 (78)	122-188 (149)	65-143
Ventral sucker	513-876 × 468-880 (681 × 670)	438-735 × 410-703 (586 × 572)	448-487 × 471-481
VS to SV	1,040-1,668 (1,289)	786-1,883 (1,237)	400-624
Seminal vesicle	189-447 × 112-234 (353 × 191)	141-400 × 118-270 (276 × 203)	174-254 × 83-116
SV to AT	454-1,197 (827)	884-1,653 (1,280)	167-333
Anterior testis	247-337 × 186-285 (300 × 238)	171-259 × 200-279 (211 × 247)	224-261 × 148-206
Distance between testes	0-526 (187)	38-385 (158)	0-12
Posterior testis	272-351 × 197-328 (313 × 277)	203-282 × 215-298 (233 × 263)	195-245 × 219-229
PT to Ov	108-479 (366)	252-644 (375)	0-113
Ovary	180-323 × 179-354 (266 × 294)	179-272 × 234-366 (232-299)	147-210 × 220-235
Vitelline masses	192-353 × 180-304 (297 × 244)	164-208 × 301-340 (236-263)	203-232 × 158-186
Post-vitelline region	547-1,260 (957)	565-902 (724)	380-607
Post-uterine region	430-734 (596)	314-585 (459)	363-443
Post-caecal region	76-261 (140)	95-218 (159)	135-231
Eggs	36-55 × 15-19 (43 × 17)	32-40 × 10-17 (36 × 13)	32 × 12
Width %*	11-13 (13)	11-13 (12)	16
Forebody %*	6.3-9.1 (7.1)	7.7-10 (9.3)	10-14
Sucker width ratio	1 : 2.7-3.0 (2.8)	1 : 2.71-3.06 (2.88)	1 : 2.3-2.7
OS to Pharynx ratio	1 : 1.5-1.7 (1.6)	1 : 1.38-1.51 (1.45)	1 : 1.5-1.7
VS to AT %*	36-41 (39)	40-49 (45)	26-33
Post-vitelline region %*	13-16 (15)	10-14 (12)	14-16
Post-uterine region %*	8.8-11 (10)	6.1-9.2 (7.5)	12-13
SV to AT %*	11-14 (13)	18-24 (21)	5.9-9.0
VS to SV %	18-24 (21)	15-25 (20)	14-17
SV to AT % of VS to SV	44-76 (63)	71-157 (107)	42-53

extending into both regions; Ch. 7, where we find the testes to be tandem; Ch. 8, where we find that the posterior testis lies more than its own length from the ovary; Ch. 13, where we find papillae around the aperture of the ventral sucker (not used in analysis); and Ch. 20, where we find the vitelline masses to be symmetrical. We follow Overstreet (1969) and Machida (1980) in considering *O. cortesi* and *O. kyphosi*, respectively, synonyms of *O. dimidia.* This also means that we do not agree with León-Règagnon et al. (1996) in considering *O. kyphosi* valid, and prefer Machida's (1980) interpretation, feeling that the papillae are so small and easily obscured by some fixation methods that it is inadvisable to rely on this character to distinguish species.

Opisthadena dimidia is now known to have an extremely wide distribution in *Kyphosus* spp. in the Atlantic, Indian and Pacific Oceans (León-Règagnon et al. 1996). It might well be argued that it is unlikely that this is a single species, as the hosts are not wide-spread pelagic fishes. This could well be the case, but we are unable to detect any morphological features on which a specific separation could be made. This species has been reported in Australian waters before, by Manter (1966), including a mention of it occurring in three species of *Kyphosus* off Heron Island. All records but one are from *Kyphosus* spp. and this record from *Xiphias gladius* in the NW Atlantic (Hogans et al. 1983) is likely to either accidental (Gibson 1996) or erroneous, as only two specimens were recovered from 300 fishes.

Table 1. Continued.

Species Host Locality n	*Opisthadena dimidia* *Kyphosus bigibbus* Ningaloo 5	*Mitrostoma nototheniae* *Aplodactylus arctidens* Tasmania 2	*Neopisthadena habei* *Kyphosus sydneyanus* off Fremantle 1
Length	3,959-6,895 (5,092)	1,383-2,240	3,535
Width	479-701 (572)	264-404	737
Forebody	407-574 (474)	350-452	825
Pre-oral lobe	13-31 (21)	13-47	44
Oral sucker	148-209 × 127-185 (173 × 152)	85-105 × 76-113	259 × 318
Pharynx	87-125 × 89-128 (99 × 106)	48-63 × 53-74	199 × 194
Oesophagus	8-22 (16)	0-24	0
IB to VS	147-255 (186)	231-245	507
Sinus sac	93-148 × 78-136 (115 × 104)	72-100 × 39-47	297 × 137
GP to VS	98-180 (130)	149-204	403
Ventral sucker	392-588 × 387-581 (470 × 461)	132-207 × 162-254	560 × 502
VS to SV	928-1,491 (1,149)	76-152	148
Seminal vesicle	126-331 × 86-239 (204 × 138)	80-161 × 39-121	1,255 × 75
SV to AT	746-1,510 (1,061)	69-117	0
Anterior testis	204-253 × 169-255 (218 × 204)	103-112 × 84-145	282 × 309
Distance between testes	21-313 (112)	38-117	0
Posterior testis	205-265 × 181-267 (224 × 216)	106-133 × 97-133	307 × 299
PT to Ov	155-450 (259)	44-141	45
Ovary	151-245 × 174-307 (200 × 235)	106-134 × 110-134	145 × 245
Vitelline masses	143-299 × 106-273 (221 × 183)	81-134 × 75-140	194-204 × 225-284
Post-vitelline region	382-704 (515)	172-320	652
Post-uterine region	259-429 (329)	131-167	375
Post-caecal region	56-238 (117)	66-85	89-153
Eggs	27-40 × 9-15 (31 × 11)	22-31 × 9-14 (26 × 12)	28 × 14
Width %*	10-13 (11)	18-19	21
Forebody %*	7.9-10 (10)	20-25	23
Sucker width ratio	1 : 2.9-3.1 (3.0)	1 : 2.1-2.3	1 : 1.6
OS to Pharynx ratio	1 : 1.4-1.5 (1.4)	1 : 1.4-1.5	1 : 1.6
VS to AT %*	45-50 (47)	16-19	12
Post-vitelline region %*	9.2-11 (10)	12-14	18
Post-uterine region %*	5.6-7.9 (6.6)	7.5-9.4	11
SV to AT %*	17-24 (20)	5.0-5.2	0
VS to SV %	22-24 (23)	5.5-6.8	4.2
SV to AT % of VS to SV	74-110 (90)	77-90	0

* of body length
Abbreviations: AT – anterior testis, GP – genital pore, IB – intestinal bifurcation, Ov – ovary, OS – oral sucker, PT – posterior testis, SV – seminal vesicle, VS – ventral sucker.

Neopisthadena habei **Machida, 1980** Fig. 3

Type-host and locality: *Kyphosus cinerascens*, Kii Peninsula, Japan.

New record:
Ex *Kyphosus sydneyanus* (Günther), Kyphosidae. Stomach. Off Fremantle, Western Australia (32°07'S, 115°44'E, March 1988). BMNH 1988.6.28.29.

Records:
1. Machida (1980); 2, Hafeezullah (1990); 3. León-Règagnon et al. (1996); 4. Present study.

Descriptions: 1, 2, 4.

Definitive hosts: Kyphosidae: *Kyphosus cinerascens* (1, 2, 3), *K. sydneyanus* (4).

Distribution: **FAO Area 51** Gulf of Mannar (2); **57** off Western Australia (4); **61** off Japan (1, 3).

Remarks. Measurements are given in Table 1. This is the fourth record of this species (see above). Machida (1980) and Hafeezullah (1990) presented good descriptions from which the single specimen we have available does not differ significantly, apart from being considerably smaller. This may be a juvenile form as the relatively few eggs appear to be poorly formed and there are many small globules of egg-shell-like material in the uterus.

Hassanine (2000) described *Opisthadena dimidia* from *Kyphosus cinerascens* from the Red Sea and stated that the variation found encompassed the features of *Neopisthadena*. We doubt this finding, as none of the 54 specimens we have seen, from a wide geographical range, shows this type of variation and we consider it possible that Hassanine (2000) had a mixed sample.

Checking the matrix in León-Règagnon et al. (1996) against our observations and the description of Hafeezullah (1990) has suggested the following changes: Character 7, we found the testes tandem; Ch. 8, the distance between the posterior testis and the ovary varies between both character states.

PHYLOGENETIC RELATIONSHIPS

We have based our cladistic study on the matrix presented by León-Règagnon et al. (1996), but have included four new characters. We have also recoded some characters of the species (see below). The matrix is shown as Table 2. The parsimony searches in PAUP* were exhaustive, with *Genolinea* and *Neotheletrum* as outgroups and all characters were unordered. A single most parsimonious tree of length 26 was recovered (Fig. 4).

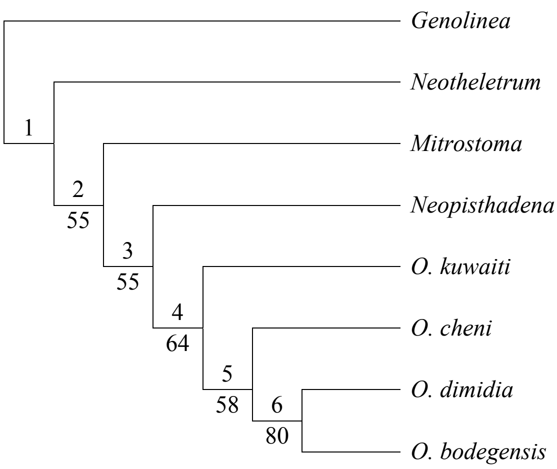

Fig. 4. Phylogeny of *Opisthadena* and related forms. The single most parsimonious tree based on 21 characters, with *Genolinea* and *Neotheletrum* as outgroups. Characters unordered. Tree length 26. CI = 0.769, CI excluding uninformative characters = 0.549, RI = 0.714, HI = 0.231. Internode numbers are given above the internodes and Bootstrap support figures (1000 replicates) below. Character support for each internode and terminal taxon is defined below (numbered characters) and includes apomorphy (A), homoplasy (H) or reversal (R): 1: (none); 2: (A: 7^2, 9^1); 3: (A: 16^1); 4: (A: $?1^2$, 12^1, 21^0, 23^0); 5: (A: 3^1); 6: (A: 5^1, 14^1); *Neotheletrum*: (A: 7^0, 15^0; H: 9^0, 24^1); *Mitrostoma*: (A: 18^1; H: 10^1); *Neopisthadena*: (A: 12^0; H: 9^0, 22^1); *Opisthadena kuwaiti*: (A: 2^1, 11^1; H: 9^0, 22^1, 24^1); *O. cheni*: (H: 10^1, 22^1); *O. dimidia*: (A: $?4^1$; R: 3^0); *O. bodegensis*: (none).

Table 2. Matrix of *Opisthadena* and outgroup species, recoded states in bold.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Genolinea	1	0	0	0	0	**0**	1	**0,1**	1	0	0	2	0	0	**1**	0	1	0	**1**	1	**1,2**	0,1	1	0	0
Neotheletrum	1	0	0	0	0	0	**0**	**0,1**	0	0	0	2	0	0	0	0	1	0	1	1	**?**	0,1	1	1	1
Mitrostoma	1	0	0	0	0	1	2	**0,1**	**1**	1	0	**2**	0	0	1	0	1	1	**1**	1	1	0	1	0	0
Neopisthadena	1	0	0	0	0	1	2	**0,1**	0	0	0	0	0	0	1	1	1	0	1	1	1	1	1	0	0
O. dimidia	2	0	0	**0,1**	1	1	2	**0**	1	0	0	1	**1**	1	1	1	1	0	1	1	**0**	0	0	0	0
O. cheni	2	**0**	1	0	0	1	2	0	1	1	0	1	1	0	1	1	1	0	?	1	**0**	1	0	0	0
O. kuwaiti	?	1	0	0	0	0	2	0	0	0	1	1	0	0	?	1	1	0	?	1	**0**	1	0	1	0
O. bodegensis	2	0	1	0	1	1	2	0	1	0	0	1	0	1	1	1	1	0	**1**	1	**0,1**	0	0	0	0
O. setipinnae	?	1	1	0	?	?	1	1	0,1	0	0	0	?	?	?	0	1	0	?	1	0	0	0	0	0

Character argumentation

Characters 1-21 are from León-Règagnon et al. (1996), 22-25 are new. Four characters listed by León-Règagnon et al. (1996) are not used in the analysis, but are retained in this list and matrix to allow the numbering of the characters to be retained. These characters are numbers 6 and 13, where we believe that the observation of these papillae is unreliable (see above) and characters 17 and 20, which are invariant in the species analysed.

(1) Seminal vesicle: 0, saccate; 1, tubular; 2, seminal sac. (2) Egg size: 0, >25 µm; 1, 13-18 µm. (3) Pharynx size: 0, pharynx smaller than the oral sucker; 1, pharynx and oral sucker of similar size. (4) Testes location: 0, in middle third of body; 1, in posterior third of body. (5) Excretory ducts: 0, not branched anteriorly to the ventral sucker; 1, branched anteriorly. (6) Oral papillae: 0, absent; 1, present. (7) Testes position: 0, symmetrical; 1, oblique; 2, tandem. (8) Distance between posterior testis and ovary: 0, posterior testis lies more than its own length from the ovary; 1, posterior testis lies less than its own length from the ovary. (9) Location of vitellarium and ovary: 0, in third quarter of body; 1, in fourth quarter of body. (10) Muscular sphincter around ventral sucker: 0, absent; 1, present. (11) Seminal vesicle wall: 0, thin; 1, thick. (12) Anterior extremity of pars prostatica: 0, at level of ventral sucker; 1, in hind-body; 2, in forebody. (13) Papillae around aperture of ventral sucker: 0, absent; 1, present. (14) Extension of excretory ducts: 0, running anteriorly of ventral sucker; 1, anterior to ventral sucker, but with branches running posteriorly to testes level. (15) Transverse fold in anterior hindbody: 0, absent; 1, present. (16) Distinct ejaculatory duct: 0, absent; 1, present. (17) Blind seminal receptacle: 0, absent; 1, present. (18) Presomatic pit: 0, absent; 1, present. (19) Excretory vesicle bifurcation: 0, near posterior margin of ventral sucker; 1, at level of testes. (20) Uterine seminal receptacle: 0, present; 1, absent. (21) Vitelline masses configuration: 0, symmetrical; 1, oblique; 2, tandem. (22) Sucker-width ratio: 0, >1:2; 1, <1:2. (23) Forebody as proportion of body length: 0, <18%; 1, >19%. (24) Uterus: 0, pre-dominantly pre-ovarian, 1, about equally pre- and post-ovarian, 2, predominantly post-ovarian. (25) Vitelline masses: 0, 2; 1, 3.

Observations on other species

Opisthadena cheni Martin, 1978. According to our interpretation of Martin (1978) we have recoded the following characters: Character 2, the eggs are quoted as being 28-44 long; Ch. 7, the testes appear more or less tandem in the figure; Ch. 21, the vitelline masses appear to be symmetrical and are described as transverse.

Opisthadena kuwaiti Al-Yamani et Nahhas, 1981. We have recoded a few characters on the basis of our interpretation of Al-Yamani and Nahhas (1981): Character 1, we query the status of the seminal vesicle, although it seems likely that the original coding is correct; Ch. 7 the testes are described and figured as tandem; Ch. 21, the vitelline masses are described as 'side by side' and illustrated as symmetrical (in the specialised meaning associated with digenean description).

Opisthadena bodegensis Johnson et Copsey, 1953. We have recoded a few characters based on our reading of Johnson and Copsey (1953) and observations of the type-specimen by Patricia Pilitt and Eric Hoberg (pers. comm.): Character 7, the testes are described as slightly tandem, but appear oblique in the specimen and have been coded as such; Ch. 19, the excretory vesicle is described and figured as bifurcating between the testes; Ch. 21, the vitelline masses are described as 'side by side' and are symmetrical in the type-specimen.

Opisthadena setipinnae Qiu et Liang in Shen and Qiu, 1995. This species is reported in the engraulid *Setipinna taty* from Tianjin Tanggu, China (Shen and Qiu 1995). It is coded for the matrix, but as several character states are not available in the description, it was not included in the final analysis. On the other hand, the species *O. fujianensis* Tang, Shi, Cao, Guan et Pan, 1983 and *O. marina* Tang, Shi, Cao, Guan et Pan, 1983 are not included because, following León-Règagnon et al. (1996), we consider these forms *species inquirendae*.

Our observations on *Neotheletrum* Gibson et Bray, 1979 come from the descriptions of the type-species *N. lissosomum* (Manter, 1940) and *N. gravidum* (Manter, 1940), *N. magnasaccum* (Sogandares-Bernal et Sogandares, 1961) and *N. pomacentri* (Nahhas et Cable, 1964) (Bray and Cribb 2000, Manter 1940, Nahhas and Cable 1964, Sogandares-Bernal and Sogandares 1961), plus the observations of León-Règagnon et al. (1996). We have recoded: Character 7, as all descriptions indicate that the testes are 'oblique' or 'diagonal'; Ch. 8, where it appears that both character states apply; and Ch. 21, which is considered inapplicable to this genus, as it has three vitelline masses.

Our observations on *Genolinea* Manter, 1925 are based on examination of numerous specimens of the type-species, *G. laticauda* Manter, 1925, from the northern Atlantic Ocean[1] (northern Pacific forms may belong to a distinct species, *G. anura* (Layman, 1930) according to Gibson 1996). We have recoded the following: Character 6, we have been unable to detect oral papillae, the oral sucker is invested with a hood-like fold, something like that found in *Mitrostoma* (this character was not used in the analysis); Ch. 8, the posterior testis in fully-gravid specimens of *G. laticauda* may be more than its own length from the ovary, although in most specimens they are adjacent or contiguous; Ch. 15, a transverse tegumental fold is present closely posterior to the ventral sucker; Ch. 19, in several whole-mounts the bifurcation of the excretory vesicle can be seen at the level of the anterior part of the

[1] See p. 288

anterior testis or just anterior to it, and in one set of serial sections it appears to be about halfway between the anterior testis and the ventral sucker, rather than close to the ventral sucker; and Ch. 21, in these specimens the vitelline masses range from virtually symmetrical to tandem, many are diagonally oblique.

Relationships

The single most parsimonious tree derived from our analysis is shown as Fig. 4. In the legend we summarise the apomorphies, homoplasies and reversal which can be deduced from this tree. This analysis has highlighted problems with several of the characters. The distinct sphincter around the ventral sucker aperture is a case in point. It is most distinctive in *Mitrostoma* and is coded as present in *O. cheni* due to the original description. All of these species do, however, have concentric muscles around the aperture, but in most cases these are not well enough developed for them to be considered a distinct sphincter, but it is very much a case of individual interpretation. Similarly the presence of an ejaculatory duct is a matter of some interpretation. Even if the pars prostatica reaches close to the sinus-sac it may have a short, gland-less duct between, which might be interpreted as an ejaculatory duct.

Our tree (Fig. 4) is mostly congruent with the single most parsimonious tree of León-Règagnon et al. (1996), with *Neopisthadena*, the sister-group to the monophyletic *Opisthadena*. *O. setipinnae*, not included by León-Règagnon et al. (1996) and not included in our final analysis, was resolved in a preliminary analysis (not shown) as the sister taxon to *O. bodegensis* but is dissimilar in its host, an engraulid clupeiform rather than a stichaeid perciform, and its distribution off China rather than California. León-Règagnon et al. (1996) pointed out that *O. dimidia* was very widespread, but that unlike other widespread digeneans such as *Derogenes varicus* (Müller, 1780), it was restricted to one genus of hosts. Substantially, this remains the case and our evidence merely emphasises the widespread nature of the species, suggesting perhaps that the distribution is likely to be more or less continuous, and that of the scenarios suggested by León-Règagnon et al. (1996) the idea that its occurrence in the Caribbean Sea is anthropogenic is unlikely to be true. We believe that the records of *Mitrostoma* in the omnivore *Paranotothenia magellanica* are likely to be erroneous, and that the major (perhaps sole) host is the largely herbivorous fish *Aplodactylus arctidens*. This indicates that the species under study here are mostly parasites of herbivorous fishes, although these fishes are not all closely related. The hosts of *Neopisthadena* and *O. dimidia* (syn. *O. kyphosi*) are herbivorous *Kyphosus* spp., and that of *O. cheni*, the related herbivore *Girella nigricans*. The host of *O. kuwaiti* is the herbivorous and detritivorous mugilid *Valamugil seheli. O. setipinnae* is anomalous, in that its engraulid host, *Setipinna taty*, is a schooling omnivore. As León-Règagnon et al. (1996) pointed out, the data we have at present leave many questions as to the evolutionary associations in this group of parasites unresolved.

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[1]The details of the *Genolinea laticauda* specimens examined are as follows:
ex *Glyptocephalus cynoglossus* (L.), Pleuronectidae, stomach, Hamilton Inlet Bank, Canada (54°07'N, 54°26'W, depth 192m, July 1975) (2 specimens); ex *Hemitripterus americanus* Cuvier, Hemitripteridae, stomach, Passamaquoddy Bay, New Brunswick, Canada (45°05'N, 67°00'W, Aug. 1982) (1 specimen); ex *Lycodes vahlii* Reinhardt, Zoarcidae, stomach, Funk Island Bank, Canada (51°12'N, 51°38'W, July 1975) (1 specimen); ex *Macrourus berglax* Lacepède, Macrouridae, stomach, off Rona, NW Scotland (60°22'N, 04°26'W, depth 700-720m, April 1973); Anton Dohrn Bank (65°30'N, 30°04'W, depth 370-440m, May 1974); Funk Island Bank, Canada (51°20'N, 51°32'W, depth 232m, July 1975); Grand Bank of Newfoundland (45°38'N, 48°16'W, depth 715-720m, May 1981). (21 specimens, including 1 set of serial sections); ex *Microstomus kitt* (Walbaum), Pleuronectidae, stomach, off Faeroes (62°N, 07'W). (4 specimens); ex *Myoxocephalus octodecemspinosus* (Mitchill), Cottidae, stomach, Passamaquoddy Bay, New Brunswick, Canada, (45°05'N, 67°00'W, Aug. 1982) (7 specimens); ex *Pseudopleuronectes americanus* (Walbaum), Pleuronectidae, stomach, Passamaquoddy Bay, New Brunswick, Canada, (45°05'N, 67°00'W, Aug. 1982) (3 specimens); ex *Trachyrincus scabrus* (Rafinesque), Macrouridae, stomach, Bay of Biscay (47°02'N, 05°37'W, depth 330-610m, Jan. 1971) (2 specimens); ex *Urophycis chuss* (Walbaum), Phycidae, stomach, Passamaquoddy Bay, New Brunswick, Canada (45°05'N, 67°00'W, Aug. 1982) (4 specimens); ex *Urophycis tenuis* (Mitchill), Phycidae, Scotian Shelf, Canada (1 specimen).

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