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Helminth ectoparasites of sillaginid fishes (Perciformes: Percoidei) have low species richness

Craig J. Hayward

Department of Zoology, University of New England, Armidale NSW 2351 Australia

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Abstract. Just nineteen species of ectoparasitic helminths were found in a survey of over 1,500 individuals of 26 species of sillaginid fishes in the Indo-west Pacific. A twentieth worm is known only from the literature; a twenty-first, also known only from the literature, is considered a doubtful record. Fifteen of the twenty worms are branchial monogeneans, one is a monogenean of the pharyngeal plates, one is an ectoparasitic digenean living under the scales, and three are leeches of the mouth cavity and fins. The most common monogeneans were diplectanids (*Diplectanum* spp. and *Monoplectanum* spp.) and microcotylids (*Polylabris* spp.), each with five recently described or redescribed species. Of the remaining monogeneans, three were extremely rare, and two were uncommon. *Pseudobivagina* sp. and *Polynemicola* sp. (Microcotylidae) and *Pseudempleurosoma* sp. (Ancyrocephalidae) were represented by only a single worm each from three different hosts (*Sillago robusta*, *S. sihama*, and *S. ingenuua*, respectively). The gyrodactylid *Gyrodactylus* sp. is widespread and was recorded from four species of sillaginids (*S. ciliata*, *S. japonica*, *S. schomburgkii* and *S. sihama*). *Encotyllabe chironemi* Robinson (Capsalidae) is recorded for the first time from sillaginids, but only on *S. aeolus*. Two additional monogeneans are known from sillaginids only in the literature: *Dactylogyrus* sp. (Dactylogyridae) is known only from cultured *S. sihama*; the single specimen of *Microcotyle* sp. (Microcotylidae) recorded from *Sillaginodes punctata* is probably a contaminant, since the haptor was missing. The generalist trematode *Transversotrema licinum* Manter (Transversotrematidae) was found for the first time in samples of four species of sillaginids (*Sillago analis*, *S. ingenuua*, *S. lutea* and *S. sihama*). Three species of piscicolid leeches were encountered: *Austrobdella translucens* Badham was common on the fins of three large inshore sillaginids (*S. ciliata*, *S. schomburgkii* and *S. analis*); a single specimen of the generalist species *Zeylanicobdella arugamensis* De Silva was recovered from *S. soringa*; and specimens of *Z. stellata* (Moore) infected *S. schomburgkii* and *S. analis*. The diversity of host-specific worms in Sillaginidae is low compared with those of some other Indo-west Pacific fishes.

Sillaginidae, also known as Indo-Pacific whitings, are schooling benthic fishes of mostly shallow marine waters and estuaries. This host family is comprised of just three genera: two of these are monotypic, and the third genus currently contains 25 probable species (see McKay 1992). Most species of sillaginids have relatively limited regional distributions, but one species, *Sillago sihama* (Forsskål) is sympatric with all the other tropical species over most of their ranges, except in the more temperate waters (the islands of Japan and southern regions of Australia).

Eleven species of ectoparasitic helminths have now been described from sillaginid fishes. Five of these are microcotylid monogeneans of the genus *Polylabris* Euzet et Cauwet, and these were described or redescribed by Hayward (1996a) primarily from Australian samples of these fishes. Five other monogeneans, of family Diplectanidae (*Diplectanum* Diesing and *Monoplectanum* Young), were also described or redescribed by Hayward (1996b) from tropical and subtropical waters of the Indo-west Pacific. The only other description of an ectoparasitic helminth from sillaginids is of the piscicolid leech *Austrobdella translucens* Badham, from *Sillago ciliata* Cuvier in south-eastern Australia. Two unidentified monogeneans have also been reported from sillaginid fish: *Microcotyle* sp. from *Sillaginodes punctata* (Cuvier) in south-western Australia (Williams 1991), and *Dactylogyrus* sp. from cultured *Sillago sihama* in Taiwan (Chen and Yu 1982). Given the large numbers of sillaginids examined, further species of helminths in addition to those already reported were expected to be found. This paper presents the taxonomy of these various helminths. An additional aim was to determine how the richness of helminth ectoparasites from Sillaginidae compares with those in other marine hosts in which it has been examined.

MATERIALS AND METHODS

Samples of Sillaginidae were fixed either immediately on capture, or were preserved after being obtained from markets, in 10% formalin. The gills were removed and examined for ectoparasites with a dissecting microscope in the laboratory.

Address for correspondence: C.J. Hayward, Department of Zoology, University of New England, Armidale NSW 2351 Australia;
Phone: (61) 67 732887; Fax: (61) 67 733814; E-mail: chayward@metz.une.edu.au

The external surfaces (fins, skin and mouth) and the sediments resulting from dissection were also examined for helminths. Several specimens of sillaginids from representative localities outside Australia and southeast Asia were sent as gifts of various institutions; and a number of specimens loaned from museums were dissected by removing only the right side of the gills then returning them to the gill chamber, in accordance with the Fish Parasite Dissection Policy of the Australian Museum. Specimens of rare sillaginids in the Queensland Museum were examined without dissection, after gently opening gill covers. Specimens of 26 of the 27 currently recognized species of Sillaginidae were examined (exclusive of four likely synonyms); many samples contained up to 40 fish. A total of 1,502 fish were examined.

Worms were mounted unstained in Euparal after clearing in glacial acetic acid, or were stained in Ehrlich's haematoxylin or Grenacher's carmine alum, then dehydrated in an alcohol series and mounted in Canada balsam. Some gyrodactylids were also mounted in ammonium picrate glycerine (Malmberg's mountant). One voucher specimen from a previous study was borrowed from the Natural History Museum, London (NHML), and micrographs of another species were borrowed from the Taiwan Fisheries Research Institute in Lu-Kang. Dr. Eugene Burreson (Virginia Institute of Marine Science, USA) very kindly identified leeches and these were retained in his collection. Worms were drawn with the aid of a drawing tube and body parts measured with a calibrated eyepiece graticule. Measurements are presented in micrometers. Gyrodactylids were examined with differential interference contrast settings. Voucher specimens from the present study were deposited in the Queensland Museum collection.

RESULTS

Class MONOGENEA Carus, 1863
Family Microcotylidae Taschenberg, 1879

Genus *Pseudobivagina* Mamaev, 1986

1. *Pseudobivagina* sp. Figs. 1–3

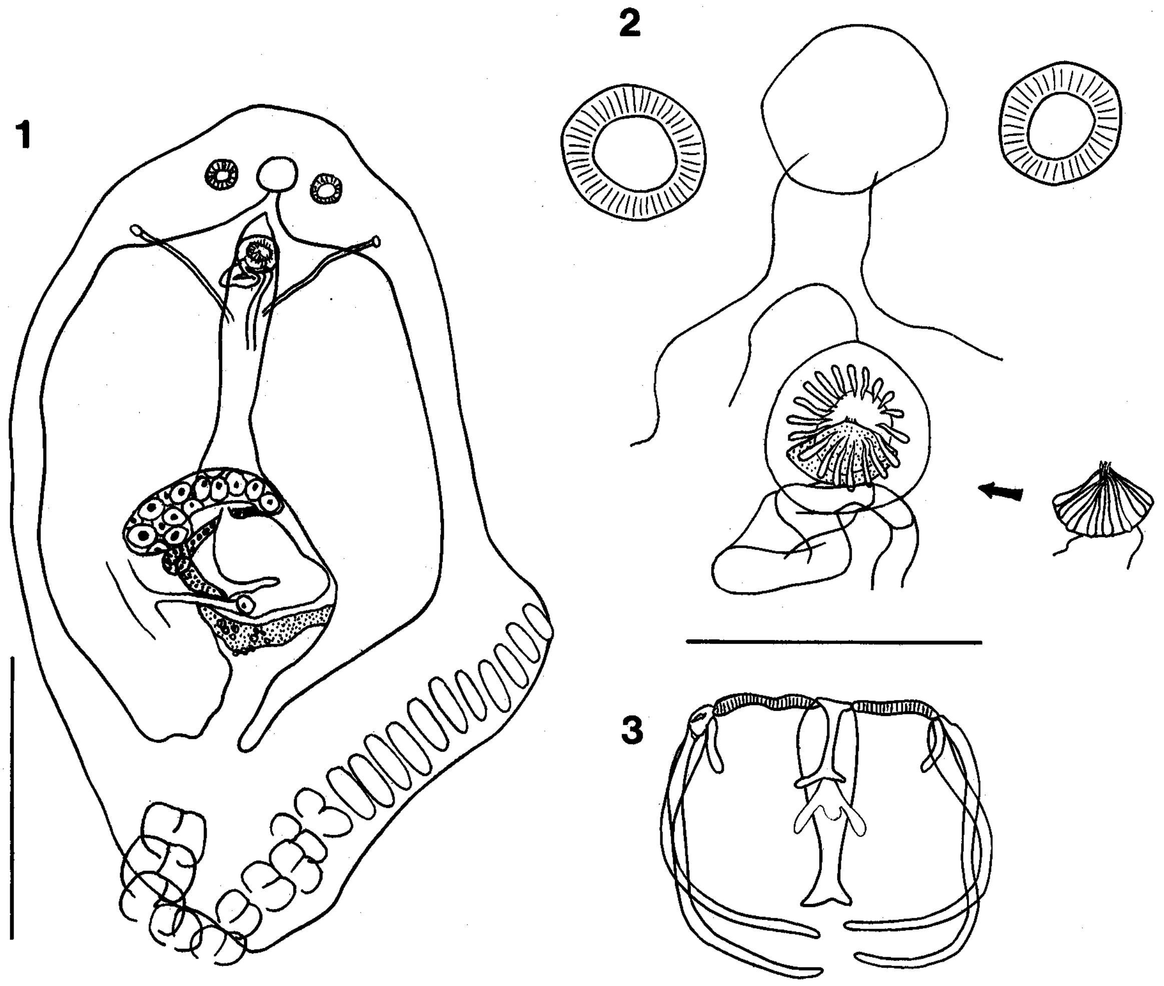
Host: *Sillago robusta* Stead, 1908, stout whiting.
Site of infection: gill filaments.
Material examined: 1 worm in 40 fish, Caloundra, Queensland, Australia, May 1993.
Deposition of specimen: voucher, QM G212258

Description: Total length 610; body 335 wide; haptor 365 long (Fig. 1). Number of testes not discernible. Number of clamps 4 + 17. Maximum clamp width 59, height 46 (Fig. 3). Pharynx diameter 28; buccal organ diameter 20–23 (Fig. 2). Copulatory organ armed with a semicrown of 10 rib-like spines (12 long) and covered with a dome of 19 longer ribs (13 long, distally recurved) on walls of genital atrium (Fig. 2).

Comments: Species of *Pseudobivagina* are distinguished from other genera of Microcotylinae by the following characters: a muscular copulatory organ armed with a semicrown of rib-like spines and covered with a dome of longer ribs arranged on walls of genital atrium; a muscular ejaculatory duct differentiated into an expulsor anteriorly, and a thinner winding region posteriorly; the presence of two dorsolateral sucker-like vaginae; a well-developed rod-shaped supplementary process in clamps; and a subsymmetric haptor. The specimen in the present study has all of these characteristics, except that the paired vaginal pores lack conspicuous suckers. Even when the specimen was mounted dorsal side up and viewed under oil immersion, the vaginae were difficult to see; this probably owes at least partly to the slight contraction of the specimen. No species of *Pseudobivagina* have been reported from sillaginid fishes until now, and this single specimen seems to represent development in an accidental host.

The apparently slightly immature worm examined here does not belong to any of the three known species of the genus, which infect kyphosid fishes (*Kyphosus cinerascens* and *Kyphosus* sp. and a pomacentrid fish (*Chromis punctipinnis*) in the eastern Pacific Ocean (Hawaii, Mexico and California, respectively). These species of *Pseudobivagina* differ from each other primarily in the number of spines in the copulatory organ and in the number of clamps, and secondarily in the number of testes and shape of atrial spines. In the muscular copulatory organ, *P. aniversaria* Bravo-Hollis, 1979 has 2 spines, *P. kyphosi* Yamaguti, 1965 about 5, *P. punctipinnis* Crane, 1972 6–8, and *Pseudobivagina* sp. about 10 (Yamaguti 1965, Crane 1972, Bravo-Hollis 1979). *P. kyphosi* has (20–28) + (30–46) clamps, *P. punctipinnis* (40–60 in total), *P. aniversaria* (27–37) + (48–52), and *Pseudobivagina* sp. 4 + 17. *P. kyphosi* has 20–30 testes, *P. punctipinnis* 30–40, *P. aniversaria* 17–22, and the number of testes were not discernible in the single specimen of *Pseudobivagina* sp. The spines in the wall of the genital atrium in the present material also differ noticeably from those described in the three other species (Fig. 2): they are relatively stout and recurved in *Pseudobivagina* sp., but more slender and straighter in the other species.

Pseudobivagina sp. is also distinguished from the other species by the high ratio of asymmetry in clamp number. However, since it is apparently not fully mature, the number of clamps would be very likely to increase further with maturity. This species possesses only 4 clamps on the shortest side and 17 on the other (Fig. 1); this compares with between two to four times the total number of clamps in the other species. The ratio of clamp asymmetry is less than 20 : 80 in *Pseudobivagina* sp., whereas clamp ratios in *P. kyphosi* and *P. aniversaria* are about 40 : 60, and in *P. punctipinnis*, the illustration indicates an even more equal ratio.



Figs. 1–3. *Pseudobivagina* sp. from *Sillago robusta*, southern Queensland. **Fig. 1.** Whole mount. **Fig. 2.** Reproductive structures. **Fig. 3.** Clamp sclerotisation. Scale bars: 200 µm (Fig. 1) and 50 µm (Figs. 2 and 3).

Genus *Microcotyle* van Beneden et Hesse, 1863

2. ***Microcotyle*** sp. of Williams (1991)

Host: *Sillaginodes punctata* (Cuvier, 1929), King George whiting.

Site of infection: gills.

Material examined: 1 worm in 37 fish, Perth, Western Australia, date unknown, coll. Dr. A. Williams.

Specimen locality: voucher, NHML: 1987.9.9.71

Comments: Williams' (1991) report of this unidentified specimen of *Microcotyle* is, as with *Pseudobivagina* sp., perhaps an accidental infection, especially since the host specificity of some species of *Microcotyle* is low in comparison with other microcotylids (Mamaev 1986). However, since this single specimen was recovered from the gills of the host without the haptor, it may in fact be a contaminant, so Williams' record is considered doubtful here.

Genus *Polynemicola* Unnithan, 1971

3. ***Polynemicola*** sp. Figs. 4–7

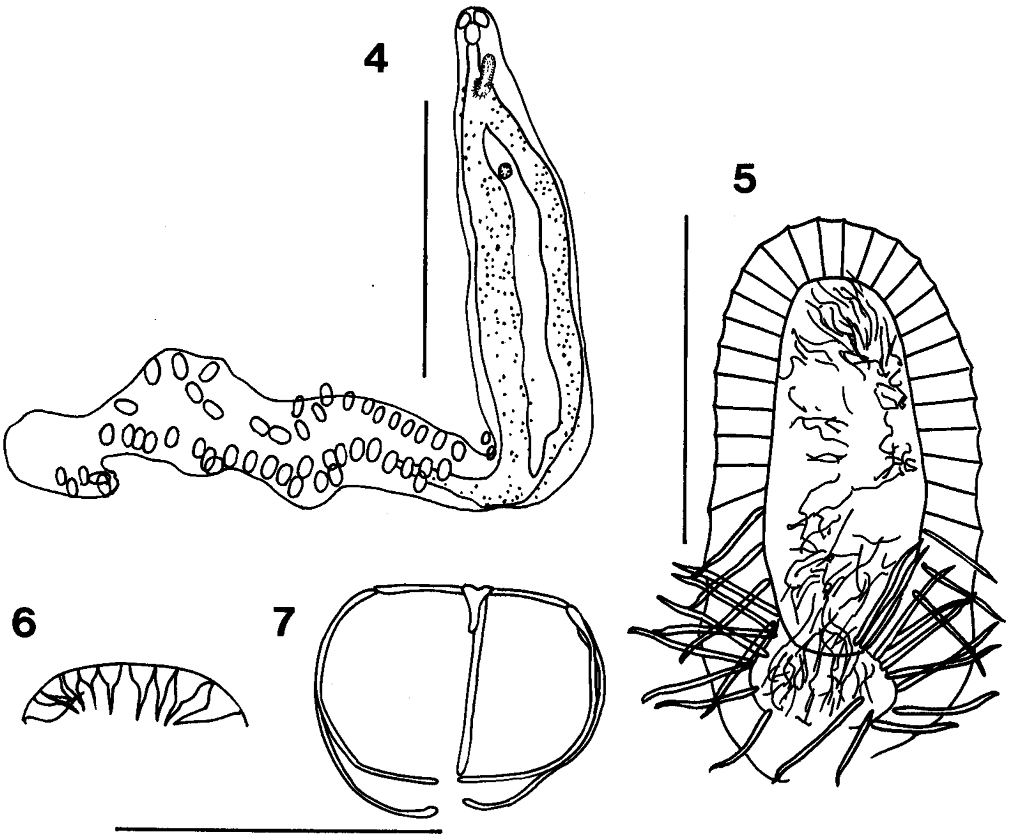
Host: *Sillago sihama* (Forsskål, 1775), silver whiting.

Site of infection: gill filaments.

Locality and date: 1 worm in 40 fish, Jimbaran, Bali, Indonesia, Nov. 1995.

Deposition of specimen: voucher, QM G213055

Description: Total length 1490; body 180 wide; haptor 745 long. Number of testes not discernible. Clamps in two rows of at least 17 pairs (Fig. 4). Clamps small; maximum width 46, height 38 (Fig. 7). Pharynx 30 wide by 36 high; buccal organs small, 33 long by 24 wide. Vagina armed with triangular spines (Fig. 6); expanded vaginal chamber before vagina. Male copulatory organ 85 long by 54 wide at base. Three types of spines present in copulatory organ (Fig. 5): 25 stout spines (up

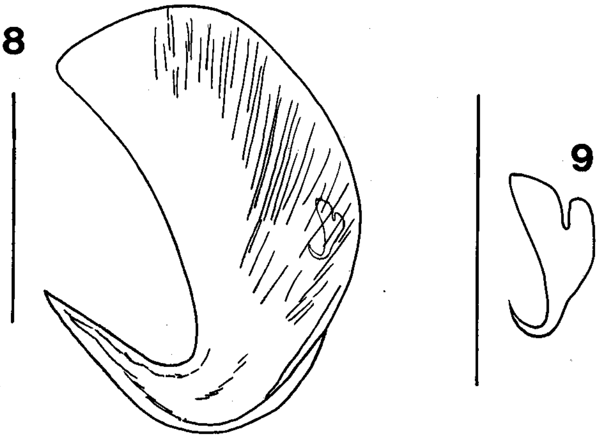


Figs. 4–7. *Polynemicola* sp. from *Sillago sihama*, Bali. **Fig. 4.** Whole mount. **Fig. 5.** Male copulatory organ. **Fig. 6.** Vaginal sclerotisation. **Fig. 7.** Clamp sclerotisation. Scale bars: 500 µm (Fig. 4) and 50 µm (Figs. 5–7).

to 19 long) posteriorly, in two rows on either side of muscular base of copulatory organ and slightly recurved distally; a semicircle of 26 thin straight spines (8 long) surround the anterior 'tongue' of copulatory organ; and numerous strandlike spines medially with irregular orientation.

Comments: This parasite belongs to the genus *Polynemicola* because of the shape of the spined, partially extruded copulatory organ (Fig. 5), and a single armed vagina (Fig. 6) with its distinctive vaginal chamber. Mamaev (1986) listed seven described species (and one *species inquirendum*) known from the Indo-west Pacific (Arabian Sea, India and North Vietnam). Six of these infect polynemid perciforms (Polynemidae): *P. ambigua* Mamaev, 1977, *P. polynemi* (MacCallum, 1917) Unnithan, 1971, *P. bulbovaginata* Unnithan, 1971, *P. aequispinosa* Mamaev, 1977, *P. tritestis* Unnithan, 1971 and *Polynemicola* sp. (= *Microcotyle* sp. of Gupta and Khullar 1968). The remaining two species (*P. sciaenae* Mamaev, 1977 and *P. heterocotyle* Mamaev, 1977) infect percoid perciforms (Sciaenidae) that are related to sillaginid fishes (Unnithan 1971, Mamaev 1977). Just prior to Mamaev's review, Bravo-Hollis (1985) described an additional species, *P. californica*, from a lutjanid fish (*Xenistius californiensis*) in the Eastern Pacific. Material of *Polynemicola* from *Sillago sihama* in the present study is not conspecific with any of the nine known species, because the copulatory organ has unique armature.

The armature of the copulatory organ of *Polynemicola* sp. from *S. sihama* appears to be most similar to that of *P. bulbovaginata* and *P. ambigua*. *Polynemicola* sp. differs from these two species most clearly in the presence of elongate and strandlike 'spines' medially. Furthermore, there is only one row of short peripheral spines in *Polynemicola* sp., whereas two were described in *P. ambigua*, and two were also illustrated in *P. bulbovaginata* (not described in the text). There are 25 basal spines in *Polynemicola* sp.; in contrast, Mamaev (1977) illustrated approximately 12 in *P. ambigua* (figure 1b) and in *P. bulbovaginata* Unnithan illustrated 12 (fig. 13) and 17 (fig. 14) (these counts were omitted in both descriptions). *Polynemicola* sp. also differs from these two species in the smaller dimensions of the buccal organs, pharynx and clamps, and in the fewer number of clamp pairs. However, this is likely to be due at least partly to the small body size (and therefore relative immaturity) of the worm in the present study.



Figs. 8, 9. *Encotyllabe chironemi* Robinson, 1961 from *Sillago aeolus*, Gulf of Thailand. **Fig. 8.** Large hamulus. **Fig. 9.** Small hamulus. Scale bars: 100 µm (Fig. 8) and 50 µm (Fig. 9).

As with *Pseudobivagina* sp., this single worm represents the only record of a species of *Polynemicola* in a sample of sillaginids – in this case, from Bali, Indonesia. It seems likely that this worm similarly developed in an 'accidental' host, since only one worm was collected from a total of 286 individual *S. sihama* examined fully (and a further 54 partially-dissected and/or inspected ones from museum collections).

Family Capsalidae Baird, 1853
Genus *Encotyllabe* Diesing, 1850

4. *Encotyllabe chironemi* Robinson, 1961 Figs. 8,9

Synonyms: *Encotyllabe chironemi* Robinson, 1961: Robinson (1961): 247, figs. 23, 24; Yamaguti (1963): 131; Khalil and Abdul-Salam (1988): 148; Williams and Beverley Burton (1989): 50, figs. 12–15.
Encotyllabe – Rohde et al. (1995): 950.

Records: 1. Robinson (1961); 2. Williams and Beverley Burton (1989); 3. Rohde et al. (1995); 4. this study.

Descriptions: 1. (1 specimen). 2. (29 specimens).

Hosts: *Cheilodactylus spectabilis* (Hutton, 1782) (= "*Chironemus spectabilis*"), banded morwong, *Nemadactylus macropterus* (Schneider, 1801), jackass morwong (Cheilodactylidae) (2, 3); *Sillago aeolus* Jordan et Evermann, 1902, oriental whiting (Sillaginidae) (4).

Site of infection: Epithelial surfaces between left and right pharyngeal tooth pads (most commonly in the upper pair, but also in the lower pair), along edges of pads, and rarely on pads.

Localities: Cook Strait, New Zealand (1); Coffs Harbour, Australia (2, 3); Gulf of Thailand (4).

Material examined: 33 worms in 40 fish, Samut Sakorn, Thailand, Oct 1994 (4).

Deposition of specimens: 2 vouchers from *Sillago aeolus*, QM G212256, G212257.

Comments: Khalil and Abdul-Salam (1988) list 18 species in this genus, but the identification of species remains difficult. This is because many of the descriptions were based on a small number of specimens, with only minor morphological differences. However, five species are now better-known, and have been adequately redescribed or described recently. Williams and Beverley-Burton (1989) redescribed *E. caballeroi*, *E. caranxi* and *E. chironemi* from eastern Australia, and Khalil and Abdul-Salam (1988) characterised *E. spari* and *E. kuwaitensis* from the Persian Gulf.

According to Khalil and Abdul-Salam (1988), the most important features in specific identification are the shape of the body, measurements of the various organs, the relative position of the two testes, the size and shape of the penis, the extent of the vitellarium, and the size and shape of the hamuli. The morphology of large hamuli of worms in the present study is identical to that figured by Williams and Beverley-Burton (1989) for *E. chironemi*, with the characteristically distinct ridge along the convex edge (Fig. 8). In eight specimens in this study, both large and small hamuli were slightly smaller than reported by Williams and Beverley-Burton (1989) (distance A 185–236 against 202–267; distance B 146 to 191 against 166–216 in large hamuli; in small hamuli, distance A 24 and 27 against 33). There was also a minor difference in the morphology of the small hamuli as depicted by Williams and Beverley-Burton (1989): the notch between the roots of the hamuli appeared deeper and narrower in this study (Fig. 9). These differences are probably due to growth. The shape of the body, the extent of the vitellarium and the position of the testes did not differ appreciably from that described by Williams and Beverley-Burton (1989) for *E. chironemi*. The penis differed only slightly in shape from that depicted by Williams and Beverley-Burton (1989) in their figure 13, in being usually more tapered distally.

Family Ancyrocephalidae Bychowski, 1937
Genus *Pseudempleurosoma* Yamaguti, 1965

5. *Pseudempleurosoma* sp. Figs. 10–12

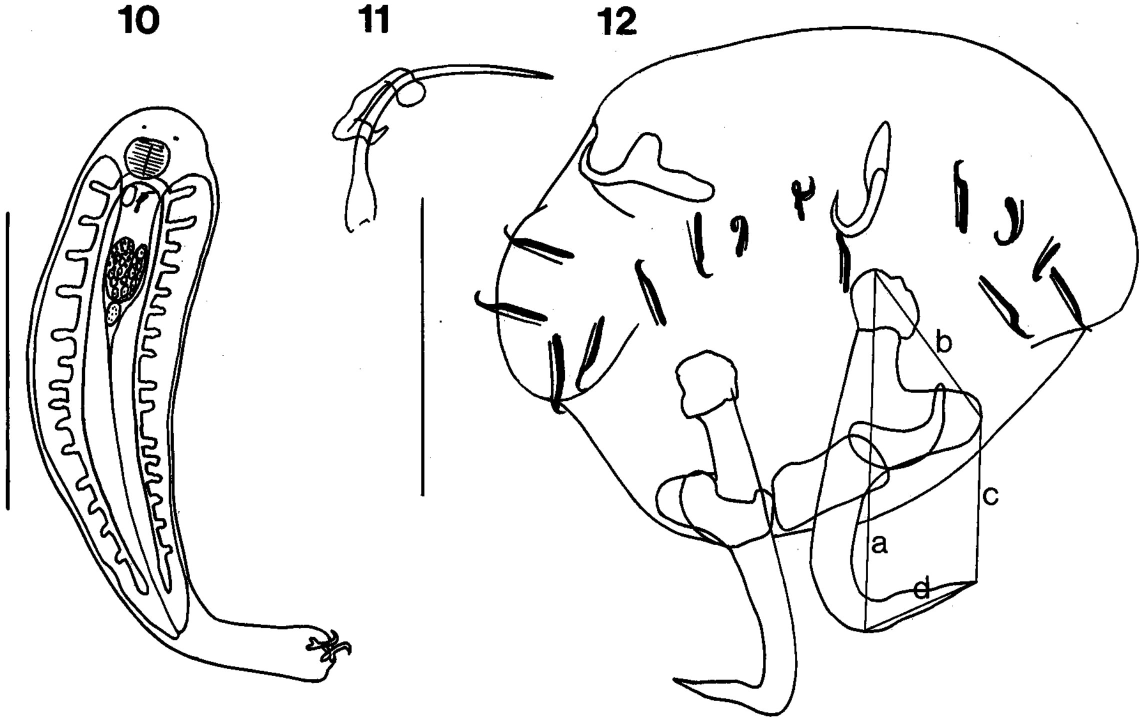
Host: *Sillago ingenuua* McKay, 1985, bay whiting.

Site of infection: gill filaments.

Material examined: 1 worm in 1 fish, Kuala Terengganu, peninsular Malaysia, Apr. 1994.

Deposition of specimen: voucher, QM G213056.

Description: Body 1180 by 256 (Fig. 10). Two pairs of eyespots, posterior pair larger. Intestinal caeca with numerous lateral diverticula, caeca not united posteriorly. Vitellarium divided into numerous transversely-elongate lobes and coextensive with intestine. Pharynx large, 80 in diameter. Male copulatory organ slender, 51



Figs. 10–12. *Pseudempleurosoma* sp. from *Sillago ingenuua*, peninsular Malaysia. **Fig. 10.** Whole mount. **Fig. 11.** Male copulatory organ. **Fig. 12.** Haptor. Lettering refers to distances measured. Scale bars: 500 µm (Fig. 10) and 50 µm (Figs. 11,12).

long, slightly swollen proximally; accessory piece present midway along the length (Fig. 11). Haptor 113 wide. Two pairs of hooks ventrally oriented (Fig. 12). Large hooks with long deep-root, swollen distally, and with long superficial root; total length (a) 61, (b) 30, (c) 28, (d) 20 (distances measured shown in Fig. 12). Small hooks almost similar in size to marginal hooks; total length (a) 24, (b) 15, (c) 9.5, (d) 5. Fourteen marginal hooks, 13 in length. Three bars between ventral hooks: median bar rectangular, 21 by 9; outer bars recurved at both ends, 16 long by 9 wide. Genital aperture slightly dextral, sucker-like, 27 by 25.

Comments: This species bears much similarity in form to that of *P. carangis* Yamaguti, 1965 in general morphology of the body and most aspects of its internal anatomy (Fig. 10), and large hooks (Fig. 12). Hence this worm is placed in the genus *Pseudempleurosoma*. However, Yamaguti's (1965) generic diagnosis appears to be too narrow to accommodate the present material from *Sillago ingenuua*. This is not surprising, because generic diagnoses based on only one species are often narrow. In contrast to *P. carangis*, the anterior pair of marginal hooks is not unusually large in the present species. Yamaguti (1965) also describes one bar between the large hooks and two between the small hooks; in the present material, there are instead three bars between the large hooks and none between the small hooks. Similarly, Yamaguti (1965) describes the male copulatory organ as being a slender tube that is enclosed by a sheath proximally. This is too specific to include *Pseudempleurosoma* sp., since the penis is slightly swollen proximally, and instead of a sheath there is an accessory piece present midway along the length (Fig. 11). This species differs from *P. carangis* in the morphology of the central haptoral bars. In *P. carangis*, the median bar is a shield-like arc, and the lateral ones are rodshaped; in *Pseudempleurosoma* sp., the median bar is rectangular, and the outer bars are recurved at both ends. This species also appears to differ from *P. carangis* in the elongation of the haptor into a 'stalk', but this may be simply a fixation artifact. Finally, the gut in *Pseudempleurosoma* sp. is not confluent posteriorly, whereas Yamaguti (1968) shows extensive confluence in *P. carangis*. In this respect, *Pseudempleurosoma* sp. is more similar to the genus *Diplectanotrema* Johnston et Tiegs, 1922 than to either *Empleurosoma* Johnston et Tiegs, 1922 or *Pseudempleurosoma* (see table in Yamaguti 1968). However, only *Pseudempleurosoma* shares the character of a confluent vitellarium with *Pseudempleurosoma* sp.

Pseudempleurosoma carangis was described from Hawaii from two species of perciform fishes (*Caranx lugubris* and *C. sexfasciatus*, Carangidae) and also a beryciform fish (*Myripristis berndti*, Holocentridae). As in *Pseudobivagina* sp. from *Sillago robusta*, *Pseudempleurosoma* sp. belongs to a genus that infects teleosts unrelated to sillaginids in the eastern Pacific, and is extremely rare in sillaginids.

According to Pariselle et al. (1991), another dactylogyrid is closely related to the genera *Diplectanotrema* and *Pseudempleurosoma*. This worm, tentatively placed in the genus *Enterogyrus* by Cone et al. (1987), infected a pomacentrid (*Pomacanthus paru*) from the Caribbean. If more material becomes available, it would prove worthwhile to reexamine the original specimens and review the generic status of each of *Pseudempleurosoma* sp. reported here and *P. carangis*, both species of *Diplectanotrema* (*D. balistes* (MacCallum, 1915) Johnston et Tiegs, 1922 and *D. trachuri* Kovaleva, 1970), the sole species of *Empleurosoma* (*E. pyriforme* Johnston et Tiegs, 1922, since transferred to the genus *Protogyrodactylus* by Gussev 1973), and '*Enterogyrus* sp.' of Cone et al. (1987).

The single worm of *Pseudempleurosoma* sp. was recovered from the gills of one *S. ingenuua* examined from Malaysia, but was absent from larger samples of this host species from the west, south and northeast (Madras, India, n = 32; Mackay, Australia, n = 40; Torres Strait, Australia, n = 21; Kaohsiung, Taiwan, n = 9). Since related species of worms infect the foregut of their hosts, the present material may also occur in the foregut as well as the single occurrence on the gills. (This habitat was not considered in the present study.)

Family Dactylogyridae Bychowski, 1937
Genus *Dactylogyrus* Diesing, 1850

6. ***Dactylogyrus*** sp. of Chen and Yu (1982)

Comments: This unidentified worm has been reported only from a cultured population of *Sillago sihama* (misidentified as *S. japonica*) in Taiwan by Chen and Yu (1982), and was not found in the present study. A micrograph of a specimen borrowed from Dr. Yu (Taiwan Fisheries Research Institute, Taiwan) has the general appearance of a dactylogyrid, with one large pair of hamuli and a transverse bar. No further details were visible.

Family Gyrodactylidae Cobbold, 1864
Genus *Gyrodactylus* Nordmann, 1832

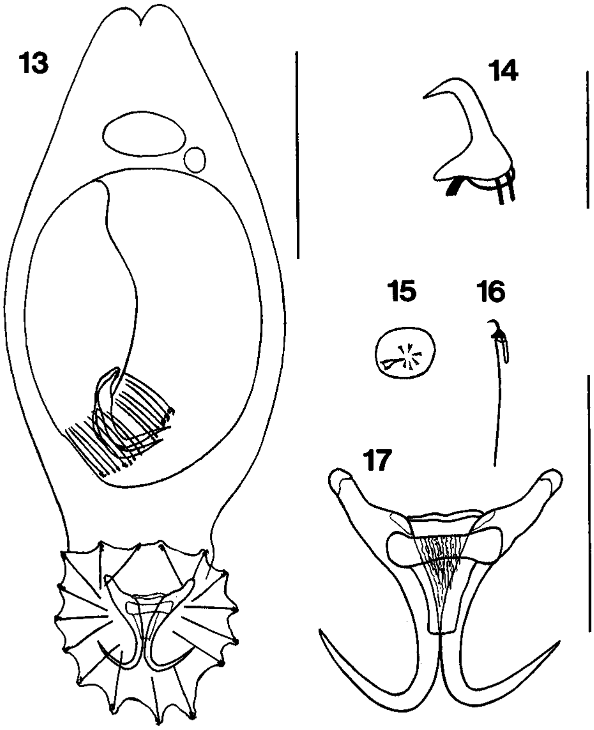
7. ***Gyrodactylus*** sp. Figs. 13–17

Synonyms: Gyrodactylidae of Rohde et al. (1995): 951.

Records: 1. Rohde et al. (1995): 951 ("Gyrodactylidae"); 2. this study

Hosts: *Sillago ciliata* Cuvier, 1829, sand whiting (1, 2); *S. japonica* Temminck et Schlegel, 1843, Japanese whiting (2); *S. schomburgkii* Peters, 1865, yellowfin whiting (2); *S. sihama*, silver whiting (Sillaginidae) (2).

Site of infection: gill filaments.



Figs. 13–17. *Gyrodactylus* sp. from *Sillago japonica*, South Korea. **Fig. 13.** Whole mount. **Fig. 14.** Marginal hook sickle. **Fig. 15.** Penis. **Fig. 16.** Marginal hook. **Fig. 17.** Haptoral sclerotisations. Scale bars: 100 µm (Fig. 13), 5 µm (Fig. 14) and 50 µm (Figs. 15–17).

Localities: Australia: Adelaide (2), Shoalhaven River (2), Coffs Harbour (1), Burdekin River (2), Darwin (2). Malaysia: Cendering (2). South Korea: Kwangyang Bay (2).

Material examined: *Sillago ciliata*: 2 of 40 hosts ex Burdekin River, Australia, June-August 1993: 333 worms; 1 of 40 hosts ex Shoalhaven River, Australia, July 1993: 64 worms; *S. japonica* (type host): 45 worms in 2 of 6 fish, Kwangyang Bay, South Korea, December 1994; *S. schomburgkii*: 1 of 40 hosts ex Adelaide, Australia, December 1993: 2007 worms; *S. sihama*: 2 of 40 hosts ex Darwin, Australia, August 1994: 38 worms; 1 of 38 hosts ex Cendering, Malaysia, April 1994: 2 worms.

Deposition of specimens: two vouchers from *Sillago japonica*, QM G213057, 213058; 2 voucher specimens from *S. sihama*, Darwin, QM G213059, 213060; 2 voucher specimens from *S. schomburgkii*, QM G213061, 213062.

Description (from 2 voucher specimens from *S. japonica*): Body 330 long by 125–132 wide. Cephalic lobes well developed (Fig. 13). Pharynx 33 wide by 21 long; processes short. Haptor subcircular, 81 wide. Total length of hamuli 47; roots of moderate length (Fig. 17), 16, 17; shaft 36, 38; point 21. Dorsal bar simple; transverse width 13, 14. Ventral bar with slightly enlarged ends, 18, 22 long; membrane 14, 16 long. Marginal hooks (Fig. 16) 27, 28 long; sickles very small (Fig. 14), 3.9 long, 2.9 wide proximally; filament loop 6, 7. Penis with one large spine and six small spines (Fig. 15), diameter 11.

Comments: Formalin-fixed material is not optimal for examining gyrodactylids, although in most cases it can be used for taxonomic studies of the hard body parts (Malmberg 1970). In the present study, two such specimens mounted in ammonium picrate glycerine soon after fixation were rendered sufficiently flat for description of the sclerotised parts of the haptor. The excretory system was not examined, since live material was not available.

Haptoral anatomy varies little among species of *Gyrodactylus*, even in those species colonising branchial habitats (Kearn 1994); this may make identification difficult. The material in the present study could not be placed in a subgenus with certainty because the excretory system is unknown. Nevertheless, the anchors and ventral bar (Fig. 17) appear to have their greatest affinity with subgenus C1, *Gyrodactylus* (*Metanephrotus*) Malmberg, 1964. Within this subgenus, the marginal hook sickles of the present material are most similar in their shape and relatively very small size (Fig. 14) to those in the *G. harengi* species-group (Malmberg 1970). This group contains just *G. harengi* Malmberg, 1957 from *Clupea harengus* (Clupeiformes) in Scandinavia, and perhaps also a second species, *G. harengi* Malmberg, 1957 *sensu* Zhukov, 1960, from northeastern Siberia in the same host but different subspecies. *Gyrodactylus* sp. is distinct from both in the longer anchor roots and anchor points (Fig. 17), and in the slight constriction of the haptor from the body. Additionally, the arrangement of the marginal hooks around the haptor of *Gyrodactylus* sp. (Fig. 13) appears to be unique. Examination of the excretory system in live material would confirm whether the present species deserves be placed in a separate species-group (or perhaps a different subgenus) on its own.

To date almost all gyrodactylids of the skin and gills of marine fishes have been reported from cold waters. In the present study, however, *Gyrodactylus* sp. was found to have wide latitudinal distribution encompassing the tropics, from approximately 35°N in South Korea to about 35°S in southern Australia. Gyrodactylids spread to new hosts primarily by direct contact, hence they are especially likely to flourish in sillaginids because they are schooling fishes. However, *Gyrodactylus* sp. was never prevalent in the samples examined. Both juvenile and mature fishes were infected with this worm. This worm is reported here in four different species of *Sillago* (*S. japonica* in Korea, *S. sihama* in peninsular Malaysia and northern Australia, *S. ciliata* in northeastern and southeastern Australia, and *S. schomburgkii* in southern Australia), although others may be infected in nature, and were perhaps not detected in such species simply because of their small sample sizes. However, because specimens from only one host and locality in the present study were sufficiently flattened for characterisation, it cannot be ruled out that the specimens from other sillaginids assigned here to *Gyrodactylus* sp. are actually very closely related but allopatric species with separate identities.

Malmberg (1970) noted that ecological characters are also very significant in discriminating species, since the majority of species are host specific. There are no described species of gyrodactylids from sillaginid fishes, providing further evidence that the present material belongs to at least one distinct species.

Class DIGENEA van Beneden, 1898
Family Transversotrematidae Witenberg, 1944
Genus *Transversotrema* Witenberg, 1944

8. *Transversotrema licinum* Manter, 1970

Transversotrema licinum Manter, 1970: Manter (1970): 486, figs. 1–5; Yamaguti (1971): 28; Beumer et al. (1983): 11; AbdulSalam et al. (1988); Cribb et al. (1992): 915, figs. 2, 6, 7; Grutter (1994): 22; Grutter (1995): 898.

Records: 1. Manter (1970). 2. AbdulSalam et al (1988). 3. Cribb et al. (1992). 4. Grutter (1994, 1995). 5. This study.

Types: Holotype, USNPC 70521 ex *Scorpius* sp., Dunwich, Stradbroke Island, Queensland; paratypes, Harold Manter Laboratory (Nebraska), No. 638–639 ex *Microcanthus strigatus*, Dunwich, Stradbroke Island, Queensland.

Descriptions: 1 (number of specimens unknown), 3 (8 specimens).

Hosts: *Scorpius* sp., scorpion-fish (Scorpaenidae) (1, type host); 'several species of fishes' (2); *Microcanthus strigatus* (Cuvier, 1831), stripey (Scorpididae) (1); *Upeneus tragula* Richardson, 1846, darkband goatfish (Mullidae) (3); *Scolopsis monogramma* (Cuvier, 1830), monocle bream (Nemipteridae) (3); *Lutjanus adetii* (Castelnau, 1873), hussar (3), *L. bohar* (Forsskål, 1775), twospot red snapper (3), *L. carponotatus* (Richardson, 1842), Spanish flag (3), *L. quinquelineatus* (Bloch, 1790), five-lined seaperch (Lutjanidae) (3); *Chaetodon mertensii* Cuvier, 1831, Merten's butterflyfish (Chaetodontidae) (3); *Mugil cephalus* Linnaeus, 1758 (= "*M. georgii*"), sea mullet (3), *Liza vaigensis* (Quoy et Gaimard, 1824), diamond-scaled grey mullet (3), *L. subviridis* (Valenciennes, 1836), greenback grey mullet (3), *Valamugil cunnesius* (Valenciennes, 1836), longfin grey mullet (Mugilidae) (3); *Siganus doliatus* Cuvier, 1830, barred rabbitfish (4), *S. lineatus* (Valenciennes, 1835) (= "*S. bilineatus*"), golden-lined rabbitfish (Siganidae) (4); *Thalassoma lunare* Linnaeus, 1758, crescenttail wrasse (Labridae) (4); *Sillago sihama*, silver whiting (5), *S. analis* Whitley, 1943, golden-lined whiting (5), *S. ingenuua*, bay whiting (5), *S. lutea* McKay, 1985, mud whiting (Sillaginidae) (5).

Site of infection: under scales, but in present study all found detached in fixative.

Localities: Australia: Queensland: Moreton Bay (1, 3, type locality), Heron Island (3, 4), Mackay (5), Burdekin River (5), Lizard Island (4), central and northern Queensland coast (3), Duyfken Point (5). Northern Territory: Charles Point, near Darwin (5). Western Australia: Point Samson (5). Persian Gulf (2).

Material examined: *Sillago sihama*: 40 hosts, Darwin, Northern Territory, August 1994: 7 worms; 40 hosts, Duyfken Point, Gulf of Carpentaria, Queensland, December 1993: 12 worms; ex 40 hosts, Burdekin River, Queensland, May–August 1993: 28 worms; *S. analis*, 40 hosts, Burdekin River, May–July 1993: 13 worms; *S. ingenuua*, 40 hosts, Mackay, Queensland, October 1994: 8 worms; *S. lutea*, 40 hosts, Point Samson, Australia, June 1995: 74 worms.

Deposition of specimens: 2 vouchers from *Sillago sihama*, Burdekin River, QM G213063, 213064; 2 vouchers from *S. ingenuua*, QM G213065, 213066.

Comments: This worm belongs to a small family of digeneans that as adults live under the scales of marine and freshwater fishes in warm-tropical waters of the Indo-west Pacific. This family was recently reviewed by Cribb et al. (1992). *Transversotrema licinum* is easily identified in Cribb et al.'s key (1992) by the following features: mouth position midventral, seminal vesicle bipartite (both characters of the genus *Transversotrema*); absence of vitelline follicles near eyespots, and a ratio of body width to length greater than 3 (characters of *T. licinum*). The life cycle includes a molluscan intermediate host, and as such, this is one of only two known ectoparasites of sillaginid fishes without a direct life cycle (the other is a generalist pennellid copepod).

In sillaginid fishes, *T. licinum* occurs in northern regions of Australia (Burdekin River near Townsville; Mackay; Darwin; Point Samson), but not in any southern regions of the continent. Since all parasites were recovered from the fixative the hosts were preserved in, it is possible that samples of sillaginids collected from warm waters outside Australia (but without their sediments) would have also harboured these parasites, especially since *T. licinum* is known to occur in one of these localities (Persian Gulf), and is likely to occur in intermediate localities as well.

Class HIRUDINEA Lamarck, 1809
Family Piscicolidae Johnston, 1865
Genus *Austrobdella* Badham, 1916

9. ***Austrobdella translucens*** Badham, 1916

Synonyms: *Austrobdella translucens* Badham, 1916: Badham (1916): 3, figs. 1–6, pl. 1–12; Ingram (1957): 198; Soós (1965): 428; Richardson (1967): 228; Beumer et al. (1983): 30; Sawyer (1986): 662; *non sensu* Moore (1957): 101; Burreson (1995): 602. *Austrobdella* sp. – Beumer et al. (1983): 30.

Records: 1. Badham (1916). 2. This study.

Descriptions: 1 ("large" number of specimens).

Type: Australian Museum, W403 ex *Sillago ciliata*, Port Hacking, NSW Australia, Aug. 1912.

Hosts: *Sillago analis*, goldenlined whiting (2), *S. ciliata*, sand whiting (1, 2, type host), *S. schomburgkii*, yellowfin whiting (Sillaginidae) (2).

Site of infection: fins (especially caudal); detaching into fixative upon preservation.

Localities: Australia. New South Wales: Port Hacking (1, type locality); Clarence River (2), Urunga (2), Shoalhaven River (2), Callala Bay (2). Queensland: Burdekin River (2), Moreton Bay (2). Western Australia: Shark Bay (2).

Material examined: ex *Sillago analis*: 40 hosts ex Burdekin River, Australia, May–July 1993: 1 worm; 40 hosts ex Shark Bay, Australia, November 1993: 20 worms; ex *S. ciliata*: 40 hosts ex Burdekin River, Australia, July–August 1993: 1 worm; 4 hosts ex Moreton Bay, Australia, April 1993: 2 worms; 32 hosts ex Clarence River, Australia, April 1993: 10 worms; 15 hosts ex Urunga, Australia, January 1994: 5 worms; 40 hosts ex Shoalhaven River, Australia, July 1993: 73 worms; 1 host ex Callala Bay, Australia, May 1993: 1 worm; ex *S. schomburgkii:* 40 hosts ex Shark Bay, Australia, November 1993: 4 worms.

Deposition of specimens: 28 in Dr. Eugene Burreson's collection.

Comments: Apart from its affinity for the fins of certain sillaginid hosts in Australia, this species is distinctive in the combination of the following features: marked division of the body into trachelosome and urosome; transparency of the body; red-brown, stellate pigment cells; a single pair of eyes; and lack of pulsative vesicles (Badham 1916). The identity of representative specimens was confirmed by Dr. Eugene Burreson.

Moore's (1957) record of *A. translucens* from two species of notothenioid fishes in Antarctic waters is considered here to be most doubtful, firstly because of the apparently otherwise strong specificity of this worm for only large in shore species of the genus *Sillago* in Australia (Badham 1916; present study), and secondly because Moore's material is larger and pigmentation appears to differ despite the fact that Badham examined a wide range of developmental stages. Burreson (pers. comm.) considers Moore's *Austrobdella translucens* to be synonymous with *Notobdella nototheniae* Benham, 1909. Beumer et al. (1983) list '*Austrobdella* sp.' as being recorded from *Sillago ciliata* by Crowcroft (1951), but this listing appears to be erroneous.

This leech is specific to the large inshore species of *Sillago* (*S. analis*, *S. ciliata* and *S. schomburgkii*). Its single occurrence in the sediments of the sample of *S.*

burrus from Shark Bay is probably a result of contamination from congeneric hosts at this locality, and so this is not considered here to be a true host record. *A. translucens* commonly occurred in northwestern, and southeastern waters of Australia where these fishes were examined, but was absent from a large sample of *S. schomburgkii* from southern Australia (Adelaide). This absence could be due to low temperatures in this region. It is possible that *A. translucens* occurs outside Australia, since one host (*S. analis*) is likely to occur in southern New Guinea, but the remaining two hosts are probably endemic to Australian waters.

Genus *Zeylanicobdella* De Silva, 1963

10. ***Zeylanicobdella arugamensis*** De Silva, 1963

Zeylanicobdella arugamensis De Silva, 1963: De Silva (1963): 47, figs. 1–3; De Silva and Fernando (1965): 228, fig. 1; Sanjeeva Raj et al. (1977): 36, figs. 1a–c.

Type: Colombo National Museum, Sri Lanka (deposition number not given).

Records: 1. De Silva (1963). 2. De Silva and Fernando (1965). 3. Sanjeeva Raj et al. (1977). 4. Gosper (1995). 5. This study.

Descriptions: 1. (number of specimens unknown), 2. (7 specimens), 3. (42 specimens).

Site of infection: Surface of body, fins and head, and mouth cavity.

Localities: Sri Lanka: Arugam (1, type locality), Kathaluwa (1), Puttalam lagoon (2); Singapore (2); India: Pulicat Lake (3); Australia: Coffs Harbour (4); Thailand: Bang Saen (5).

Hosts: *Arius maculatus* (Thunberg, 1792) (= *Tachysurus m.*), spotted catfish (Ariidae) (1, type host?); *Macrones gulio* (Hamilton-Buchanan, 1822), long-whiskers catfish (Bagridae) (1, type host?); *Oreochromis mossambicus* (Peters, 1852) (= *Tilapia m.*), Mozambique tilapia (Cichlidae) (1, type host?), *Glossogobius giuris* (Hamilton-Buchanan, 1822), tank goby (Gobiidae) (1), *Drepane punctata* (Linnaeus, 1758), concertina-fish (Drepanidae) (2), *Hippocampus kuda* Bleeker, 1852, yellow seahorse (Syngnathidae) (2); "marine eel" (2); *Plotosus canius* (Hamilton-Buchanan, 1822), canine eel-catfish (Plotosidae) (3); *Anguilla reinhardtii* Steindachner, 1867, long-finned eel (Anguillidae) (4); *Sillago soringa* Dutt et Sujatha, 1983, soringa whiting (Sillaginidae) (5).

Material examined: ex *Sillago soringa*: 8 hosts ex Bang Saen, Gulf of Thailand, November 1994: 1 worm.

Deposition of specimen: in Dr. Eugene Burreson's collection.

Comments: The single specimen in the present study was identified by Dr. Burreson. Although in poor condition, the external morphology of the specimen appears the same as that in *Zeylanicobdella arugamensis*. The pigmentation pattern is variable (Sanjeeva Raj et al. 1977), and so is less useful in identification. This is a rather widespread and generalist leech, known from southeastern Australia north to Malaysia and the Gulf of Thailand, and west to India and Sri Lanka; it is probably more widespread. It is apparently a euryhaline species, yet specimens from brackish water reportedly die rapidly if placed in seawater *in vitro* (D. Gosper, pers. comm.).

11. ***Zeylanicobdella stellata*** (Moore, 1958)

Synonyms: *Ottoniobdella stellata* Moore, 1958: Moore (1958): 307, fig. 2, pl. VII fig. 3; *Malmiana stellata* (Moore, 1958) Soós, 1965: (Soós, 965): 440.

Records: 1. Moore (1958). 2. This study.

Descriptions: 1 (from 1 specimen).

Type: Natal Museum, lot 38 ex "toby fish", Richards Bay, Natal, South Africa, July 1953.

Localities: South Africa: Richards Bay, Natal (1, type locality). Australia: Shark Bay, Western Australia (2).

Hosts: "toby fish" (1, type host); *Sillago schomburgkii*, yellowfin whiting (2), *S. analis*, golden-lined whiting (Sillaginidae) (2).

Site of infection: Mouth cavity, detaching from preserved hosts into fixative.

Material examined: ex *S. schomburgkii*: 40 hosts ex Shark Bay, Australia, Nov. 1993: 7 worms; ex *S. analis*: 40 hosts ex Shark Bay, Australia, Nov. 1993: 1 worm.

Deposition of specimens: 6 in Dr. Eugene Burreson's collection.

Comments: E. Burreson (pers. comm.) notes that *Ottoniobdella* is not a valid genus, and believes that the only two specimens of this leech belong to the genus *Zeylanicobdella*. The material in the present study is also thought by Burreson to be conspecific with Moore's holotype. This species is distinct from *Z. arugamensis* in its robustness and in the pigmentation pattern (E. Burreson, pers. comm.). As with *Z. arugamensis*, *Z. stellata* appears to be a widespread and generalist leech, and was very uncommon in sillaginid fishes.

DISCUSSION

The sillaginid lineage has been colonized by monogeneans on at least four independent occasions – twice by *Polylabris*, once by diplectanids, and once by a gyrodactylid. One of the species of microcotylids of the genus *Polylabris* is not closely related to the other four from sillaginids. (These four are bivaginate instead of univaginate, and the two groups are geographically remote.) This implies that two colonisation events were involved, one the result of host-switching and/or host-parasite cospeciation over a relatively long period

Table 1. Ectoparasitic helminths of Sillaginidae

Helminth	Known sillaginid hosts	Region(s) where sillaginids known to be infected (no. localities)
Class Monogenea		
Family Microcotylidae		
Polylabris sillaginae	*Sillaginodes punctata, Sillago aeolus, S. bassensis, S. burrus, S. ciliata, S. flindersi, S. ingenuua, S. maculata, S. robusta, S. schomburgkii, S. sihama*	circum-Australia (25); New Caledonia (1); Gulf of Thailand (1)
P. australiensis	*S. analis, S. schomburgkii*	south and southwestern Australia (4)
P. queenslandensis	*S. analis, S. ciliata, S. maculata, S. sihama*	mid- to northeastern Australia (3)
P. williamsi	*S. analis, S. schomburgkii*	mid-western Western Australia (1)
P. madagascarensis	*S. sihama*	southeastern Africa (2)
Pseudobivagina sp.	*S. robusta*	mideastern Australia (1)
Polynemicola sp.	*S. sihama*	midsouthern Indonesia (1)
Family Diplectanidae		
Diplectanum sillagonum	*S. attenuata, S. sihama, S. vincenti*	tropical Australia n. to southern China, w. to Persian Gulf (18)
D. blairense	*S. indica, S. sihama*	midsouthern Indonesia n. to south China, w. to Persian Gulf (9)
D. puriense	*S. chondropus, Sillaginopsis panijus*	Bay of Bengal/Andaman Sea (2)
Monoplectanum australe	*Sillago burrus, S. maculata*	midwestern, northern and mideastern Australia (5)
M. youngi	*S. analis, S. attenuata, S. ciliata, S. lutea, S. parvisquamis, S. sihama*	northern Australia n. to southern China, w. to Persian Gulf (15)
Family Dactylogyridae		
Dactylogyrus sp.	*S. sihama*	culture facilities in Taiwan (1)
Family Ancyrocephalidae		
Pseudempleurosoma sp.	*S. sihama*	peninsular Malaysia (1)
Family Capsalidae		
Encotyllabe chironemi	*S. aeolus*	Gulf of Thailand (1)
Family Gyrodactylidae		
Gyrodactylus sp.	*S. ciliata, S. japonica, S. schomburgkii, S. sihama*	southern Australia n. to South Korea (6)
Class Digenea		
Family Transversotrematidae		
Transversotrema licinum	*S. analis, S. ingenuua, S. lutea, S. sihama*	northern Australia (5)
Class Hirudinea		
Family Piscicolidae		
Austrobdella translucens	*S. analis, S. ciliata, S. schomburgkii*	midwestern and eastern Australia (8)
Zeylanicobdella stellata	*S. analis, S. schomburgkii*	midwestern Australia (1)
Z. arugamensis	*S. soringa*	Gulf of Thailand (1)

of time, and the other a result of a more recent host switch (Hayward 1996a). The five known diplectanids are evidently related, and so each probably arose as a result of host isolation (and/or host switching events) after a single common ancestor became established in the host lineage (Hayward, 1996b). On present evidence, *Gyrodactylus* sp. is assumed to be a single species that is widespread in sillaginids.

If it is assumed that the rare monogeneans considered in the present study are specific to Sillaginidae (except for *Encotyllabe chironemi*), it could be argued that sillaginids have been colonized by monogeneans on at least eight occasions. However, the rarity of four monogeneans in sillaginids (two unrelated microcotylids, *Pseudobivagina* sp. and *Polynemicola* sp., an ancyrocephalid, *Pseudempleurosoma* sp., and a dactylogyrid, *Dactylogyrus* sp.) probably indicates that they are accidental infections – in other words, the oncomiracidia settled on incorrect hosts. On the other hand, some monogeneans in other host groups are considered host specific despite their rarity – for example, species of *Grubea* on scombrid fishes of the genus *Scomber* – see Rohde (1987).

At least four ectoparasitic helminths infect Sillaginidae but are primarily parasites of other fishes. These are the capsalid monogenean, *Encotyllabe chironemi*; the trematode, *Transversotrema licinum*; and two of the three leeches found (both in the genus *Zeylanicobdella*). The third leech, *Austrobdella translucens*, in contrast, was relatively common, but only in the three large inshore species of sillaginids known from Australia.

Despite the large sample sizes, the ectoparasite fauna of sillaginids is depauperate (Table 1) in comparison with those groups for which there has been some study of helminth diversity, especially those occurring in tropical latitudes. For example, Byrnes and Rohde (1992) considered the ectoparasitic helminths of just four species of sparid fishes (genus *Acanthopagrus*) from around Australia; in this region alone these four host species harboured almost the same number of monogeneans as 26 species of sillaginids (14 as compared with 16), and also a single unidentified species of leech (*Austrobdella* sp.) compared with three leeches in sillaginids. Although the genera differed, sillaginids and sparids shared a common pattern of diversity among gill monogeneans: in each host group there was a group of congeneric diplectanids (3 *Diplectanum* spp. and 2 *Monoplectanum* spp.; and 6 *Lamellodiscus* spp., respectively), as well as a group of congeneric microcotylids (5 *Polylabris* spp.; and 4 *Polylabroides* spp., respectively). Both groups also harboured a single capsalid (*Encotyllabe* and *Benedenia*, respectively). Additionally, both groups are infected with ancyrocephalids: sillaginids hosted one (*Pseudempleurosoma*), whereas sparids hosted two in Australia (*Haliotrema* and *Allomurraytrema*). The remaining monogeneans of sillaginids did not have counterparts in the four sparids: two additional microcotylids (*Pseudobivagina* and *Polynemicola*), the dactylogyrid (*Dactylogyrus*), and the gyrodactylid (*Gyrodactylus*). Conversely, only sparids were infected with an anoplodiscid (*Anoplodiscus*).

The difference in ectoparasite diversity between sillaginid and sparid fishes is likely to be shown to be even more pronounced when more samples of sparids in the Indo-west Pacific are examined quantitatively. The reason may be that Sparidae is a much more widespread family with greater overall diversity than Sillaginidae. Hence any parasites acquired outside the Indo-west Pacific that have been transmitted to sparids inside this area would inflate their regional ectoparasite diversity. On a smaller scale, within the Indo-west Pacific itself, it is not surprising that the most widespread and undoubtedly most abundant sillaginid (*Sillago sihama*) is infected with the highest number of ectoparasitic helminths, with 11 of the 20 known species. This proportion of the total infecting *S. sihama* is even higher when parasites that infect other host groups are excluded, with 10 out of 16 worms. Three sillaginids harbour the next most highest number of worms, with 5 (of 16) helminths each – the large Australian inshore species, *S. analis*, *S. ciliata* and *S. schomburgkii*.

Preliminary evidence indicates that the relative diversity of ectoparasitic helminths in reef and reef-associated fishes is higher than in sillaginids, but similar to that in Australian sparids. Rohde et al. (1994) found that the relative diversity of ectoparasitic worms in a single reef-associated lethrinid (*Lethrinus miniatus*) was higher than in three of the four sparids examined extensively from around Australia. Despite the fact that only 41 fishes from just three localities in eastern Australia were examined, 12 species of monogeneans were recorded in *L. miniatus*, as well as one generalist leech (*Trachelobdella lubrica*). This compares with 7, 8, 10 and 13 species of helminths in almost 1,000 Australian sparids from all around Australia. As in the sparid and sillaginid hosts, the common monogeneans formed natural groupings at generic or familial levels: three species of ancyrocephalids (*Haliotrema* spp.) were present, as well as four diplectanids (3 *Calydiscoides* and 1 *Protolamellodiscus*), and five capsalids (4 Benedeniinae and 1 *Encotyllabe*).

Perhaps the main type of speciation that accounts for different numbers of ectoparasite taxa among different host lineages occurs after host-switching, at least for marine monogeneans. The diversity of congeneric species of ectoparasites *within* host lineages can also be attributed to host-switching, but only to a certain extent (since congeners of parasites may also arise within a given host lineage by host-parasite cospeciation.) Host switching requires chance genetic changes that lead oncomiracidia to settle and reproduce on new hosts. Because chance is involved, the number of groups parasitising a given host lineage cannot be predicted with certainty, but the number of taxa should be highest in host lineages that have had the greatest exposure to potential new colonists. Host switching is therefore most likely to occur wherever the highest diversity of ectoparasites already exists: shallow marine waters of the tropics (see Rohde et al. 1995). Host lineages that have the most ectoparasite taxa should therefore include shallow-water tropical ones (and perhaps those having some species in the tropics), but also old host lineages, and those of shallow waters that have intermediate dispersal ability and/or wide distribution such as Sparidae and Sciaenidae.

A second type of speciation - allopatric (including parapatric) - acts on a different scale to host-switching, and increases the number of congeneric monogeneans (and other host-specific worms) within a *single* host species. If isolation leading to this form of speciation is of sufficient duration, the hosts themselves may speciate along with their parasites. (As mentioned, the result of this form of parasite speciation within a group of related hosts is difficult to distinguish from that of host-switching.) In theory, allopatric parasite speciation should be no less common at high latitudes than at low ones, but this remains to be verified. This type of speciation is most likely to be responsible for the occurrence of multiple congeners of host-specific helminths within a given host, as found for example in *Lethrinus miniatus* by Rohde et al. (1994). Kennedy and Bush (1992) concluded that multiple congeners generally contributed little to the richness of monogeneans in freshwater fishes and even less in marine fishes. However, this conclusion was based on data sets that appear to underrepresent the high numbers of congeneric monogeneans found in some tropical fishes, both freshwater and marine.

Among marine fishes, multiple congeners are likely to be most common among fishes belonging to groups inhabiting the shallow inshore, including reef and reef-associated groups (such as in many fishes from Hawaii – see Yamaguti's checklist of 1968), but not necessarily in marine fishes inhabiting deeper waters of the continental shelf, nor in pelagic fishes. This is because deeper-water and pelagic fishes can disperse into new habitats along two dimensions, whereas shallow-water inshore fishes tend to disperse along just one axis – the shoreline. According to Keenan (1994), this principle is probably responsible for the higher degree of genetic differentiation among subpopulations of coastal and freshwater fishes than of other marine fishes. Hence among coastal fishes, there should be greater opportunities for isolation of host populations leading to allopatric speciation of their parasites, followed by parasite exchange, than would be expected among other marine fishes. (This would be especially true if past changes in seawater levels isolated populations of coastal fishes more than deeper-water and pelagic ones.) Some shallow-water fishes do indeed have remarkable numbers of parasite congeners – for example, sciaenid, sparid and serranid fishes in the Mediterranean (see checklist of Euzet et al. 1993). Gussev (1995) similarly emphasized the importance of isolation of populations of freshwater fishes leading their monogeneans to speciate allopatrically, and noted that in this environment it was also associated with glacioeustatic changes in combination with the topography of continental shelves.

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