Helminth parasites of Madeiran rockpool fishes, with a redescription of *Schikhobalotrema longivesiculatum* Orecchia & Paggi, 1975 (Digenea: Haplosplanchnidae), and some comments on their zoogeographical relationships

David I. Gibson¹ and Graca Costa²

¹Department of Zoology, The Natural History Museum, Cromwell Road, London SW7 5BD, UK ²Departamento de Biologia, Universidade da Madeira, Lg. do Colégio, 9000 Funchal, Madeira, Portugal

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Abstract

Seven species of Madeiran rockpool fishes were examined for their helminth parasites. Only two of these harboured helminth parasites. The most frequently encountered parasite was the digenean *Schikhobalotrema longivesiculatum* Orecchia & Paggi, 1975 from *Parablennius parvicornis*; this species is redescribed and discussed. The paucity of the parasite fauna of Madeiran rockpool fishes and the zoogeographical relationships of the digenean fauna of Madeiran marine fishes are commented upon.

Introduction

Madeira comprises an isolated group of two (plus four very small) islands occurring at 32°30' N and 16°20' W, c.600 km off the Atlantic coast of NW Africa. There have been few studies on the helminth parasites of Madeiran marine fishes. Existing records have been limited to individual records, such as the occurrence of the opecoelid digenean Genitocotyle sp. (see Bartoli, Gibson & Ruitort, 1994) in a specimen of a Madeiran fish, Apogon imberbis, which died at London Zoo, and the presence of larvae of three species of trypanorhynch cestodes, a nematode Anisakis sp. and an acanthocephalan Bolbosoma sp. [B. vasculosum (Rud., 1819)] (see Costa et al., 1996a,b) in the scabbard fish Aphanopus carbo. The helminth fauna of marine fishes of the other "Macaronesian Islands", the Canaries and the Azores, is also little known, although the work of Gijón-Botella & López-Román (1989; and in several conference abstracts, e.g. 1996) has shed some light upon the digenean fauna of the Canaries and Gaevskaja & Kovaleva (1985) have studied the parasites of horse-mackerel from off the Azores. There have, therefore, been no previous studies on the helminths of Madeiran intertidal rockpool fishes. The present work attempts to redress this by examining the parasites of rockpool fishes and assessing their zoogeographical relationships. Rockpool fishes were chosen as the parasites of the major groups, i.e. blennies and gobies, have been well studied in other parts of the Mediterranean zoogeographical region (e.g. Naidenova, 1974).

Materials and methods

Thirty-three rockpool fishes were examined for helminths during July, 1996. These came from two sites at or close to Funchal, Madeira: Clube Naval (within the city limits) and Reis Magos (c. 10 km east of Funchal). The following species were studied: *Parablennius parvicornis* (Val.), *Lipophrys trigloides* (Val.) [Blennidae], *Mauligobius maderensis* (Val) [Gobiidae], *Lepadogaster lepadogaster* (Bonn.), *L. candollei* Risso [Gobiesocidae], *Thalassoma pavo* (L.) [Labridae] and *Scorpaena maderensis* (Val.) [Scorpaenidae].

The fishes were collected live at the two sites studied, kept in aquaria and examined within two days of collection. Worms were fixed unflattened in Berland's fluid for one minute and then stored in 70% alcohol. Platyhelminths were prepared as whole-mounts, stained in Mayer's paracarmine and mounted in Canada balsam. Serial sections were cut at 7–8 μ m, stained in Mayer's haemalum and eosin, and mounted in thin Canada balsam (see Cooper, 1988). The nematode was examined in creosote as a temporary mount.

Measurements are given in micrometres, except where stated.

Survey

The following helminths were recorded:

ex Parablennius parvicornis [n = 11] Eight fishes had no helminths. Schikhobalotrema longivesiculatum Orecchia & Paggi, 1975 [1, 8 and 5 specimens in 3/11 fishes]

ex *Mauligobius maderensis* [n = 9] Six fishes had no helminths. Tetraphyllidean larvae (Cestoda) [5 and 2 worms in 2/9 fishes] *Nybelinia* sp. larva (Cestoda) [1 worm] *Spirocamallanus* sp. (Nematoda) [1 female]

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ex Lipophrys trigloides [n = 1]
ex Lepadogaster lepadogaster [n = 4]
ex Lepadogaster candollei [n = 2]
ex Thalassoma pavo [n = 3]
ex Scorpaena maderensis [n = 3]
No helminths were found.
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Schikhobalotrema longivesiculatum Orecchia & Paggi, 1975

Description (Figure 1)

Based on 11 whole-mounts and 2 imperfect sets of serial sections from intestine (mainly posterior intestine) of *Parablennius parvicornis*.

Body small, 0.94–2.00 mm; elongate-fusiform, sometimes with slight dorsal or ventral flexure in hindbody of fixed specimens; widest point 245–513, at level of ventral sucker or just anterior or posterior. Forebody 262–638 (24–34% of body length); with fragments of material which might be residues of eye-spots lateral to pharynx, and gland-cells visible laterally anteriorly to vitelline field. Oral sucker well developed; ventro-terminal; 146–187 × 142–175, usually with slight eminence in centre of ventral margin. Ventral sucker 183–262 × 191–297, larger than oral sucker (width-ratio 1:1.30–1.75; usually c. 1:1.35–1.45); embedded; round to slightly transversely, occasionally longitudinally, oval. Many of the features of the internal anatomy are difficult to discern in whole-mounts.

Prepharynx short, 0-35; usually distinct. Pharynx well developed; $60-100 \times 71-106$; usually wider than long. Oesophagus (c. 150 long in sectioned specimen) with aglandular, muscular wall; wall contractile such that lumen can be completely closed at any point along its length. Intestine a single caecum; caecum tubular, extending back dorsally to ventral sucker and testis to end blindly opposite posterior half of testis or in post-testicular region.

Position of all parts of reproductive system somewhat variable dependent upon state of contraction and position of ventral sucker, e.g. uterus may be entirely in forebody or more usually equally dispersed between forebody and anterior hindbdy.

Testis single; longitudinally elongate-oval, often more tapered posteriorly; large, $187-597 \times 123-286$; in posterior half of body, 75-500 (usually <300) from posterior extremity. Cirrus-sac absent. Seminal vesicle long, narrow, thin-walled, often convoluted; extends from level of ovary (often close to seminal receptacle) passes ventral sucker dorso-dextrally, winds in posterior forebody and opens into short, tubular genital atrium. Pars prostatica very short, indistinct, with some external gland-cells visible in sections. Genital pore indistinct in whole-mounts, median or slightly submedian in forebody; situation variable, depending upon position of uterine field in relation to ventral sucker, usually at about level of anterior margin of vitelline field.

Ovary distinctly trilobed, ventro-dextral, between testis and ventral sucker, though may overlap either, depending upon state of contraction [anterior limit +131 to -105 in relation to hind margin of ventral sucker; posterior limit +120 to -445 in relation to anterior margin of testis]; $120-209 \times 80-187$; lobes of ovary oval, often horizontally triradiate, with oöcapt directed dorso-medially. Seminal receptacle well developed; $67-200 \times 56-112$; dorso-sinistral to ovary. Laurer's canal not seen. Mehlis' gland antero-ventral to seminal receptacle. Uterus relatively short; may form curved structure devoid of or greatly distended with eggs, sometimes winding; uterine field usually extends from anterior hindbody, passing dorsally to ventral sucker into posterior forebody; occasionally almost entirely restricted to forebody where it may reach level of posterior margin of pharynx; wall thin when extended, but thick and muscular with filamentous lining when contracted and devoid of eggs; uterus opens into base of

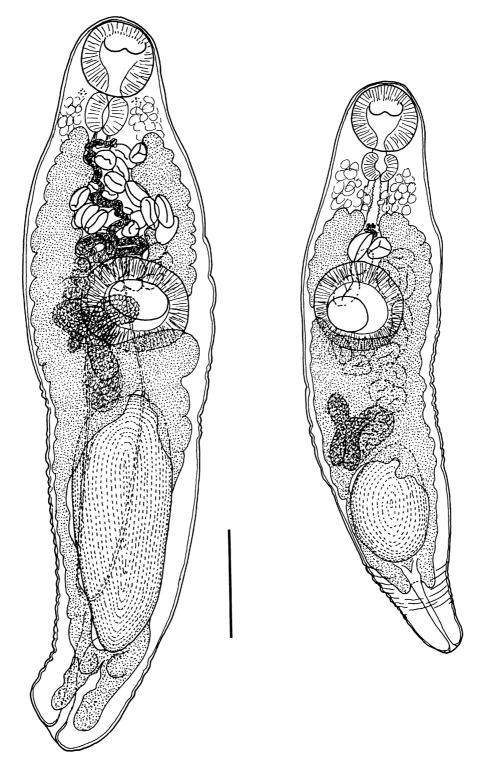


Figure 1. Two specimens of *Schikhobalotrema longivesiculatum* showing variations in the position of the uterine field and the ovary in relation to the ventral sucker and in the size and shape of the testis. *Scale-bar*: 250 μ m.

genital atrium; no obvious metraterm present, although wall of terminal region of uterus is muscular. Large amounts of sperm observed in proximal uterus of specimen devoid of eggs. Eggs large, $76-95 \times 35-58$ (usually $80-86 \times 42-48$); <40 in number; thin-walled and readily collapse in whole-mounts (hence variable measurements). Vitellarium a large lobulate mass, apparently composed of interconnecting network of large follicles; extends from close to posterior extremity to level of pharynx or up to 75 posterior to pharynx; lateral fields usually confluent dorsally in short post-testicular region, dorsal to testis and in forebody (ventrally lateral fields tend to be separated by uterus) and ventrally in anterior hindbody; gaps may occur laterally to testis.

Excretory pore terminal; vesicle Y-shaped, narrow, tubular; stem short; bifurcation in post-testicular region; arms pass anteriorly lateral to testis and into forebody.

Discussion

Taxonomy

In possessing a single intestinal caecum and testis and lacking a cirrus-sac, this present material clearly fits into the family Haplosplanchnidae Poche, 1925. In both Skrjabin & Guschanskaja (1955) and Yamaguti (1971), the specimens key down to the genus Schikhobalotrema Skrjabin & Guschanskaja, 1955, but can be distinguished from the majority of its species by the fact that the ovary is lobed: in their generic definitions, Skrjabin & Guschanskaja (1955) indicated that the ovary was oval, rarely lobed, and Yamaguti (1971) that it was 'rarely lobed'. Skrjabin & Guschanskaja (1955) list only two species which possess a lobed ovary, S. kyphosi (Manter, 1947) from Kyphosus spp. off Florida and S. sparisomae (Manter, 1937) from Sparisoma spp. off Florida. Subsequently, three more species with a lobed ovary have been described: S. adbrachyura Siddiqi & Cable, 1960 from Sparisoma sp. off Puerto Rico; S. longivesiculatum Orecchia & Paggi, 1975 from Blennius sanguinolentus on the coast of Italy; and S. magnum Skinner, 1975 from Mugil cephalus off the coast of Florida. S. heterocotylum Nahhas & Cable, 1964 from Pseudoscarus guacamia off Curaçao also has an ovary which is 'entire to slightly lobed', but this species differs considerably in general body shape and other features, and it was transferred to Pseudoschikhobalotrema Yamaguti, 1971 by Yamaguti (1971).

S. kyphosi is readily distinguishable from the present material from Madeira in that the oral sucker is considerably larger than the ventral. S. adbrachyura differs in that the ventral sucker of these smaller worms is larger in relation to body-size and lies in the posterior half of the body: furthermore, the ovary is said (Siddiqi & Cable, 1960) to have 5-6 lobes and the caecum only extends to the level of the ovary [nevertheless, they may be young specimens of S. sparisomae]. In the case of S. magnum, according to Skinner (1975), the caecum is short, reaching only to the level of the ovary, the worms are larger and the eggs are smaller $(69-75 \times 47-59 \ \mu m)$. The two species most similar to the present material are S. sparisomae and S. longivesiculatum. However, S. sparisomae occurs mainly in scarid reef-fishes in the Gulf of Mexico (e.g. Manter, 1947; Nahhas & Carlson, 1994), and it can be most readily distinguished by the uterine field which extends well posterior to the anterior margin of the testis. Morphologically, the present material resembles S. longivesiculatum closely; when compared to the published description of this species, differences are few. In the Madeiran material: the ovary is more distinctly lobed; the intestinal caecum extends further posteriorly, into the posterior half of the testicular field in almost all specimens and sometimes into the posttesticular zone; and the uterus does not extend to the anterior margin of the testis, except in one case. We have confirmed the features of S. longivesiculatum in specimens kindly lent by Professors Orecchia and Paggi, although the ovary is more distinctly lobed than in the original figure; it should be mentioned, however, that these specimens are in rather poor condition and somewhat flattened. Hence, to some extent these differences may be artefacts caused by differences in treatment and condition. There is also some doubt concerning the use of the length of the intestinal caecum in relation to the testis as a diagnostic character, as Cribb et al. (1994) noted that this was quite a variable feature in S. pomacentri (Manter, 1937). Thus, there are no obvious features which can be used to distinguish the present material convincingly from S. longivesiculatum, and we, therefore, consider the Madeiran material conspecific with the latter species. This is supported by evidence from the host-species involved. Orecchia & Paggi (1975, 1978) reported S. longivesiculatum from four of 207 specimens of Blennius sanguinolentus on the western coast of Italy. Five other species of blenny (comprising >200 specimens) were also studied by these authors (Orecchia & Paggi, 1978), but none harboured the parasite. There are no other records of this

species. In Madeira the present material was found in *Parablennius parvicornis*, and *Parablennius* is the genus to which *B. sanguinolentus* has now been transferred (Zander, 1986). Furthermore, Zander (1986), in a footnote, stated that *P. parvicornis* may be conspecific with *P. sanguinolentus*.

Other records of *Schikhobalotrema* spp. from the Mediterranean region have tended to be from mugilids, usually being referred to as *Schikhobalotrema* sp. (e.g. Orecchia, Paggi & Radujkovic, 1988) or also as *S. sparisomae* (e.g. Gaevskaja et al., 1975; Saad-Fares, 1985) and *S. acutum* (Linton, 1910) (see Fayek, Amer & Ahmed, 1990). These require confirmation: that described by Saad-Fares (1985), for example, differs considerably from the original description of *S. sparisomae*. Other species of the genus have been recorded from mugilids in other regions.

Fauna

The helminth fauna of the Madeiran rockpool fishes examined was extremely depauperate, with 27 of 33 fishes [81.8%] having no helminths and no fish having more than 8 worms [mean intensity 3.3; abundance 0.03]. There are several possible reasons for this, which are generally related to the fact that the Madeiran coast is volcanic in origin and extremely precipitous, dropping directly to a depth of 20m, with virtually no or very limited littoral and sublittoral regions (as defined by Lewis, 1977). Hence there are few areas of rockpools, and these are now diminishing due to the commercial development of the islands. As a consequence of this, littoral molluscs, prerequisites for the life-cycle of digeneans in the region, are few. Several specimens of the trochid snail Osilinis edulis (Lowe) were the only molluscs readily observed. Similarly, areas of sandy/muddy substratum, utilised by many littoral invertebrates which act as intermediate hosts of helminth species, are limited. An additional factor in the case of Parablennius parvicornis, the species of fish studied in the greatest number, is that it feeds almost exclusively on algae (Zander, 1986); this explains the finding of only a single species of helminth parasite in this particular fish.

Zoogeographical relationships

According to Wirtz (1994), the relationships between the fish faunas of three Macaronesian island groups is close; for example, 80% of blenny species are shared by Madeira and the Azores and 67% by Madeira and the Canaries. However, many coastal fishes are not able to cross the wide ocean between these islands and the mainland: Wirtz cites the sea-breams where there are 24 species in the Canaries only 100 km from the mainland, but only 15 species at Madeira and seven at the Azores, 610 and 1,450 km from the mainland, respectively. Nevertheless, according to Briggs (1974), the majority of coastal fishes present off Madeira are also found on the eastern Atlantic mainland or neighbouring islands. According to Ekman (1967), these islands are situated in the Mauretanean subregion of the Mediterranean-Atlantic fauna, which extends south from Gibraltar to Capo Blanco. Briggs stated that the relationship between the Madeiran coastal fauna and the Mediterranean is close, indicating that three-quarters of the Madeiran shore fauna is shared with the Mediterranean. Briggs claimed that 29 of the Madeiran shore fishes (almost a quarter, using Briggs' figures) might be considered as trans-Atlantic, as they are also recorded on the western side of this ocean, possibly arriving from the Caribbean region via the Gulf Stream. Briggs also indicated that Madeira has a low degree of endemism (3.2%), although one of the species dealt with in the current study, Mauligobius maderensis, appears to be endemic to the Macaronesian islands.

The larval helminths recorded in this study and previously, although they are sometimes not identified at the specific level, tend to be those not unusual in North Atlantic teleosts. When we look at the zoogeographical relationships of digenean parasites of Madeiran marine fishes based in previous records, we can determine little; for, as indicated above, there only appears to be one, that of Genitocotyle sp. reported by Bartoli et al. (1994); but this exhibits a clear link to the western Mediterranean, as its closest relative appears to be G. mediterranea Bartoli, Gibson & Ruitort, 1994 from Symphodus ocellatus off Corsica. However, other *Genitocotyle* spp. are from the Gulf of Mexico and the Pacific coast of North America. When records of the digenean parasite of marine fishes of the Canaries are examined, as outlined by Gibson & Køie (1991), there is more evidence. Here there are distinct links with the Mediterranean and even the Black Sea, e.g. Gijón-Botella & López-Román's (1989) records of Arnola microcirrus (Vlassenko, 1931) and "Opecoeloides furcatum Odhner" [whether it be O. furcatus (Bremser in Rudolphi, 1819) or Poracanthium furcatum Dollfus, 1948: see Bartoli & Gibson, 1991] and Gijón-Botella & López-Román's (1996) record of Wardula sarguicola Bartoli & Gibson, 1989. Links with the Gulf of Mexico are not obviously apparent, but these authors (Gijón-Botella & López-Román, 1989) indicate links with the Pacific coast of North America in the form of Stephanostomum longisomum Manter, 1940 and Metadena caballeroi Nahhas & Krupin, 1977 [very likely the Black Sea/Mediterranean species M. pauli (Vlassenko, 1931), according to Bartoli & Gibson (1995)]. They (Kim et al., 1990) have also indicated links with Hawaii in the form of records of five species of Hawaiian digenean originally described by Yamaguti (1970); however, these would all require confirmation. The apparent conspecificity of the Madeiran material of Schikhobalotrema and S. longivesiculatum from the Mediterranean plus its similarity with S. sparisomae from the Gulf of Mexico, and the links suggested by the distribution of Genitocotyle spp. (as indicated above), imply close ties with the Mediterranean/Black Sea digenean fauna and a weaker link with the Gulf of Mexico and perhaps the Western coast of North America. Such links make sense in terms of ocean currents and the known zoogeographical relationships associated with the ancient Tethys Sea.

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References

- Bartoli, P. & Gibson, D.I. (1991) On Podocotyle scorpaenae, Poracanthium furcatum and Derogenes latus, three poorly known digenean parasites of eastern Mediterranean teleosts. Systematic Parasitology, 20, 29–46.
- Bartoli, P. & Gibson, D.I. (1995) Three rare and little known cryptogonimid digeneans from the sciaenid fish *Sciaena umbra* (L.) in the western Mediterranean. *Systematic Parasitology*, **30**, 121– 139.
- Bartoli, P., Gibson, D.I. & Ruitort, J.-J. (1994) Genitocotyle mediterranea n. sp (Digenea, Opecoelidae) from Symphodus ocellatus (Teleostei, Labridae) in the Western Mediterranean. Parasite, 1, 365–370.
- Briggs, J.C. (1974) Marine zoogeography. New York: McGraw-Hill, 475 pp.

- Cooper, D.W. (1988) The preparation of serial sections of platyhelminth parasites, with details of the materials and facilities required. *Systematic Parasitology*, **12**, 211–229.
- Costa, G., Eiras, J.C., Chubb, J., MacKenzie, K. & Berland, B. (1996a) Parasites of the black scabbard fish, *Aphanopus carbo* Lowe, 1839 from Madeira. *Bulletin of the European Association* of Fish Pathologists, **16**, 13–16.
- Costa, G., Hemmingsen, W. & MacKenzie, K. (1996b) Prevalence and intensity of some parasites of the black scabbard-fish, *Aphanopus carbo* from Madeira. [EMOP VII Abstracts] *Parassitologia*, **38**(1–2), 30.
- Cribb, T.H., Bray, R.A. & Barker, S.C. (1994) Bivesiculidae and Haplosplanchnidae (Digenea) of fishes of the southern Great Barrier Reef, Australia. *Sysematic Parasitology*, 28, 81–97.
- Ekman, S. (1967) Zoogeography and the sea. London: Sidgwick & Jackson, 417 pp.
- Fayek, S.A., Amer, O.H. & Ahmed, N.E. (1990) Some fish trematodes from the Mediterranean Sea. *Veterinary Medical Journal*. *Giza*, 38, 429–438.
- Gaevskaja, A.V. & Kovaleva, A.A. (1985) Parasitofauna of *Trachurus picturatus picturatus* and ecological and geographical peculiarities of its formation. *Ekologiya Morya, Kiev*, **20**, 80-84 (in Russian).
- Gaevskaja, A.V. et al. (Eds) (1975) [Identification key to parasites of vertebrates from the Black and Azov Seas.] Kiev: Naukova Dumka, 551 pp (In Russian).
- Gibson, D.I. & Køie, M. (1991) Magnibursatus caudofilamentosa (Reimer, 1971) n. comb. (Digenea: Derogenidae) from the stickleback Gasterosteus aculeatus L. in Danish waters: a zoogeographical anomaly? Systematic Parasitology, 20, 221–228.
- Gijón-Botella, H. & López-Román, R. (1989) Aportación al catálogo de Digenea de peces marinos del Archipélago de Canarias. *Revista Ibérica de Parasitologia*, **49**, 137–138.
- Gijón-Botella, H. & López-Román, R. (1996) Parasitising by Wardula sarguicola Bartoli & Gibson, 1989 in Diplodus sargus cadenati de la Paz, Banchot and Daget capturated [sic] in the Atlantic (Archipelago in the Canary Islands). [EMOP VII Abstracts] Parassitologia, 38(1–2), 35.
- Kim, M., Gijón-Botella, H. & López-Román, R. (1990) The Bunocotylidae, Derogenidae, Hemiuridae and Azygiidae of marine fishes. (ICOPA VII Abstracts). *Bulletin de la Société Française de Parasitologie*, 8 (Suppl. 2), 733.
- Lewis, W.H. (1977) Ecology field glossary. A naturalist's vocabulary. Westport, Conn.: Greenwood Press, 152 pp.
- Manter, H.W. (1937) The status of the trematode genus Deradena Linton with a description of six species of Haplosplanchnus Looss (Trematoda). Skrjabin Jubilee Volume. Moscow: pp. 381– 387.
- Manter, H.W. (1947) The digenetic trematodes of marine fishes of Tortugas, Florida. American Midland Naturalist, 38, 257–416.
- Nahhas, F.M. & Carlson, K. (1994) Digenetic trematodes of marine fishes of Jamaica, West Indies. *The Hofstra University Marine Laboratory. Ecological Survey of Jamaica*. Publication No. 2, 60 pp.
- Naidenova, N.N. (1974) [Parasitic fauna of the fishes of the family Gobiidae of the Black and Azov Seas.] Kiev: Naukova Dumka, 182 pp (In Russian).
- Orecchia, P. & Paggi, L. (1975) Nuovo reperto parassitologico in Blennius sanguinolentus Pallas, 1811: Schikhobalotrema longivesiculatum sp.n. (Haplosplanchnidae Poche, 1925). Parassitologia, 17, 69–74.
- Orecchia, P. & Paggi, L. (1978) Aspetti di sistematica e di ecologia degli elminti parassiti di pesci marini studiati presso l'Istituto

di Parassitologia dell'Universitita di Roma. *Parassitologia*, **20**, 73–89.

- Orecchia, P., Paggi, L. & Radujkovic, B.M. (1988) Digeneans of fishes from the Adriatic Sea with a description of *Lecithaster atherinae* n. sp. from *Atherina (Hepsetia) boyeri. Parassitologia*, **30**, 225–229.
- Saad-Fares, A. (1985) Trématodes de poissons des côtes du Liban. Thèse, Université des Sciences et Techniques du Languedoc, Montpellier, 434 pp.
- Skinner, R. (1975) Parasites of the striped mullet, *Mugil cephalus*, from Biscayne Bay, Florida, with descriptions of a new genus and three new species of trematodes. *Bulletin of Marine Science*, 25, 318–345.
- Siddiqi, A.H. & Cable, R.M. (1960) Digenetic trematodes of marine fishes of Puerto Rico. *Scientific Survey of Porto Rico and the Virgin Islands*, 17, 257–369.

- Skrjabin & Guschanskaja (1955) [Suborder Hemiurata (Markevitsch, 1951) Skrjabin & Guschanskaja, 1955]. In: Skrjabin, K.I. (Ed.). [Trematodes of animals and man.] Osnovy Trematodologii, 10, 339–643 (In Russian).
- Wirtz, P. (1994) Underwater guide. Fish. Stuttgart: Verlag Stephanie Naglschmid, 160 pp (In English and German).
- Yamaguti, S. (1970) *Digenetic trematodes of Hawaiian fishes*. Tokyo: Keigaku Publishing Company, 436 pp.
- Yamaguti, S. (1971) Synopsis of the digenetic trematodes of vertebrates. Tokyo: Keigaku Publishing Company, Vol. 1, 1,074 pp.
- Zander, C.D. (1986) Blenniidae. In: Whitehead, J.P., et al. (Eds) Fishes of the North-eastern Atlantic and the Mediterranean. Paris: UNESCO, Vol. III, pp. 1,096–1,112.