Syst Parasitol (2011) 78:123–138
DOI 10.1007/s11230-010-9283-6

Two new species of ancyrocephalid monogeneans from *Lethrinus rubrioperculatus* Sato (Perciformes: Lethrinidae) off New Caledonia, with the proposal of *Lethrinitrema* n. g.

L. H. S. Lim · Jean-Lou Justine

Received: 1 September 2010 / Accepted: 22 October 2010

Abstract *Lethrinitrema gibbus* n. g., n. sp. and *L. dossenus* n. sp. are described from the fish *Lethrinus rubrioperculatus* Sato collected off New Caledonia, South Pacific. Members of *Lethrinitrema* n. g. (Ancyrocephalidae) are characterised by having two pyriform haptoral reservoirs and ventral anchors with lateral grooves. The elongate tubular distal end of each reservoir bifurcates, draining into a superficial lateral groove on each side of the ventral anchors. The haptoral reservoirs are postulated to store secretory products which assist in attachment to the host. *Lethrinitrema* spp. also possess tandem gonads, a male copulatory organ without an accessory piece or with thinly sclerotised accessory piece, and a dextrolateral, non-sclerotised vaginal bulb. The two new species have small, poorly demarcated haptors with small haptoral armament and a crown-like piece on the tip of the inner root of the ventral anchors. They differ from each other in the shape and size of the ventral bar and male copulatory organ (40–45 μm in length in *L. gibbus vs* 24–30 μm in *L. dossenus*). Three other species, previously included in *Haliotrema* Johnston & Tiegs, 1922, are transferred to *Lethrinitrema*, i.e. *L. chrysostomi* (Young, 1968) n. comb., *L. fleti* (Young, 1968) n. comb. (both briefly redescribed from paratypes) and *L. lethrini* (Yamaguti, 1937) n. comb. All species of *Lethrinitrema* parasitise *Lethrinus* spp. (Lethrinidae), and there is evidence for the existence of further *Lethrinitrema* spp. on *Lethrinus* spp. in the Indo-Pacific region.

L. H. S. Lim (✉)
Institute of Biological Sciences, University of Malaya,
50603 Kuala Lumpur, Malaysia
e-mail: susan@um.edu.my

J.-L. Justine
UMR 7138 Systématique, Adaptation, Évolution,
Muséum National d'Histoire Naturelle, 57 rue Cuvier,
75231 Paris Cedex 05, France
e-mail: justine@mnhn.fr

J.-L. Justine
Aquarium des Lagons, BP 8185, 98807 Nouméa,
New Caledonia

Introduction

There are about 40 species, belonging to six genera in two subfamilies, Lethrininae and Monotaxinae, within the Lethrinidae (see Carpenter & Allen, 1989). The most speciose genus is *Lethrinus* Cuvier, with 26–30 species (Froese & Pauly, 2010; Randall, 2005; Sato, 1978) in tropical waters of the Indo-Pacific region. Only *L. atlanticus* Valenciennes occurs in the Atlantic Ocean, off West Africa. Off New Caledonia, 13 species of *Lethrinus* have been recorded (Randall, 2005).

Lethrinid species, particularly those caught off New Caledonia, harbour a variety of monogeneans, including *Encotyllabe* sp. (Capsalidae) on the pharyngeal teeth, and various species of microcotylids,

diplectanids and ancyrocephalids on the gills (Justine, 2007, 2010). Microcotylid species are rare and usually immature. Diplectanids from lethrinids include species of *Calydiscoides* Young, 1969 on *Lethrinus* spp. (Lethrininae) and *Lamellodiscus* Johnston & Tiegs, 1922 on *Gymnocranius* spp. and *Gnathodentex* spp. (both Monotaxinae) (Justine, 2007; Justine & Briand, 2010; Rascalou & Justine, 2007). To date, there are only three *Haliotrema* spp. (Ancyrocephalidae) described from *Lethrinus* spp., i.e. *H. chrysostomi* Young, 1968 from *L. chrysostomus* (Richardson) [now *L. miniatus* (Forster)] and also from a haemulid, *Plectorhinchus pictus* (Thunberg) [now *Diagramma picta* (Thunberg)], off Australia; *H. fleti* Young, 1968 from *L. fletus* Whitley [now *L. laticaudis* Alleyne & Macleay], *L. laticaudis*, *L. miniatus* and *L. nebulosus* (Forsskål) off Australia (see Young, 1968); and *H. lethrini* (Yamaguti, 1937) Young, 1968 from *L. haematopterus* (Bleeker) off Japan and *L. miniatus* off Australia.

Ancyrocephalid species were collected from nine species of *Lethrinus* off New Caledonia, namely *L. harak* (Forsskål), *L. lentjan* (Lacépède), *L. miniatus*, *L. nebulosus*, *L. obsoletus* (Forsskål), *L. ravus* Carpenter & Randall, *L. rubrioperculatus* Sato, *L. variegatus* Valenciennes and *L. xanthochilus* Klunzinger. However, only sufficient numbers of specimens were collected from *L. rubrioperculatus* for descriptions. Thus far, no ancyrocephalid species have been recovered from members of the Monotaxinae (Table 1).

In this paper, we describe two new monogenean species from *L. rubrioperculatus* and propose a new genus to accommodate them. We have also re-examined the type-specimens of *H. chrysostomi* and *H. fleti* from *Lethrinus* spp., *H. australe* Johnston & Tiegs, 1922 (type-species) from *Upeneus signatus* (Günther) [now *Parupeneus signatus* (Günther)] (Mullidae) (type-host) and voucher specimens of several *Haliotrema* spp. from lethrinids and mullids for comparative purposes (see below).

Materials and methods

Specimens of *Lethrinus rubrioperculatus*, ("spot-cheek emperor"; local name "bossu rond") were caught with hand lines on board the R/V "Coris" in the waters (depth of 10–40 m) off New Caledonia, in both the lagoon and along the barrier reef 20 km off Nouméa. Live fish were kept in an icebox with refrigerated seawater and immediately brought back to the laboratory. All fish were measured, weighed and photographed. A unique number (JNC) was assigned to each fish. The parasite material was then assigned a corresponding JNC linked to the respective fish host.

Gills were extracted and examined in seawater with a dissecting microscope. Live monogeneans were individually picked off the gills with fine needles and immediately prepared for staining with carmine by an initial flattening between a slide and a coverslip in 70% ethanol (Justine, 2005). Some specimens were fixed in modified ammonium picrate-glycerine (Malmberg, 1957; Lim, 1991), examined unstained using phase contrast microscopy, and later washed and stained in Gomori's trichrome stain. A few specimens were also examined live in seawater.

Monogeneans were drawn with an Olympus BH2 microscope and a Leitz DM2500 microscope, both equipped with a camera lucida. Drawings were scanned and redrawn on a computer with Adobe Illustrator. Alternatively, microscope images of the hard and soft body parts were captured, using a Leica digital camera (3.3MP) (on a DM2500) and QWin Plus image analysis software, and drawn on a digitising tablet (WACOM) using Adobe Illustrator

Table 1 Ancyrocephalid and diplectanid monogeneans found on the gills of members of the Lethrinidae (Lethrininae and Monotaxinae) off New Caledonia

Host genus and subfamily	Diplectanid genus	Ancyrocephalid genus
Lethrinus spp. (Lethrininae)	*Calydiscoides* Young, 1969	*Lethrinitrema* n. g.
Gnathodentex spp. (Monotaxinae)	*Lamellodiscus* Johnston & Tiegs, 1922	None
Gymnocranius spp. (Monotaxinae)	*Lamellodiscus* Johnston & Tiegs, 1922	None

software. In this paper only one species is fully illustrated, since both are similar in their non-sclerotised anatomical structures.

Measurements of the haptoral and reproductive hard-parts (parameters measured indicated in Fig. 2) were made on flattened, stained or unstained specimens cleared in ammonium picrate glycerine using the measuring option in QWin software. The measurements are given as the mean and range (within parentheses) in micrometres, with the length first followed by the width. The terms 'posterior glandular mass' and 'opisthaptoral reservoirs' were used by Young (1968) to refer to the peduncular glands and the haptoral reservoirs, respectively.

The type- and voucher specimens of *Haliotrema* spp. (see list below) re-examined in this study were obtained from: MNHN (Muséum National d'Histoire Naturelle, Paris); BMNH (Natural History Museum, London), USNPC (United States National Parasite Collection, Beltsville); UMZP (University of Malaya, Kuala Lumpur); and AMS (Australian Museum, Sydney).

Museum specimens examined in this study

Haliotrema australe Johnston & Tiegs, 1922, holotype and paratype on slide AMS W883.

Haliotrema chrysostomi Young, 1968, 2 paratypes, USNPC 61283: 1 slide marked 'paratype 1' from *Lethrinus chrysostomus*; 1 slide marked 'paratype 4' from *Plectorhinchus pictus*.

Haliotrema fleti Young, 1968, 2 paratypes, USNPC 61285, from *L. fletus*: 3 slides, marked as 'paratype 2', 'paratype 1 anterior end', and 'paratype 1 posterior end'.

Haliotrema sp., 3 vouchers, BMNH 1994.8.10.98-100 (1 slide) (leg. I. Al-Mathal), from *L. lentjan*, Arabian Gulf, probably belonging to 2 or 3 species [together with specimens of *Calydiscoides difficilis* (Yamaguti, 1953) Young, 1969 (see Rascalou & Justine, 2007)].

Haliotrema spp., MNHN, 10–15 species, mostly unidentified, from mullids off New Caledonia: *Parupeneus barberinoides* (Bleeker) (JNC2415); *P. ciliatus* (Lacépède) (JNC1916, JNC2525); *P. cyclostomus* (Lacépède) (JNC1599, JNC1922); *P. heptacanthus* (Lacépède) (JNC1075, JNC2984); *P. indicus* (Shaw) (JNC2444); *P. multifasciatus* (Quoy & Gaimard) (JNC1005, 1205, 1224, 1420, 2413, 2445); *P. pleurostigma* (Bennett) (JNC2443); *P. spilurus* (Bleeker) (JNC2444); *Upeneus tragula* (Richardson) (JNC2428, JNC2429).

Haliotrema leporinum Sun, Yang & Kritsky, 2007 (emend.), marked paratype, MNHN JNA41, from *Acanthurus nigrofuscus* (Forsskål), South China Sea (Sun et al., 2007).

Haliotrema pratasense Sun, Yang & Kritsky, 2007 (emend.), marked paratype, MNHN JNA42, from *Acanthurus olivaceus* Bloch & Schneider, South China Sea (Sun et al., 2007).

Lethrinitrema n. g.

Diagnosis. Ancyrocephalidae Bychowsky, 1937 [*sensu* Gusev (1978)]. Body elongate, flattened dorsoventrally; haptor not well demarcated from body. Three pairs of head organs; 2 pairs of dorsal eye-spots. Mouth subterminal, ventral. Pharynx muscular. Intestine bifurcates just posterior to pharynx; 2 intestinal caeca, confluent posterior to testis, forming cyclocoel, but extend further posteriorly as 2 diverticula. Haptor small in relation to body proper, armed with dorsal and ventral pairs of anchors, dorsal and ventral connecting bars and 14 larval-type hooks. Ventral anchors with superficial lateral groove on each lateral side and well-developed inner root with crown-like piece on its tip. Dorsal anchors without lateral grooves. Dorsal and ventral connecting bars well developed. Two pear-shaped haptoral reservoirs, each associated with ventral anchor; elongate tubular extension of each reservoir bifurcates prior to entering lateral groove along each side of ventral anchor (Fig. 2A). Gonads intercaecal, tandem. Testis postovarian. Vas deferens originates from anterior region of testis, passes ovary dorsally, loops around sinistral caecum to ventral side, distends to form seminal vesicle, ascends and enters initial part (base) of copulatory tube. Two elongate, pyriform prostatic reservoirs; prostatic duct connects with base of male copulatory organ. Male copulatory organ a simple, short, tapered copulatory tube with wide initial part, sometimes with distal, slightly sclerotised accessory piece. Ovary elongate, smaller than testis, at mid-body. Oviduct arises from anterior side of ovary, receives duct from vagina (seminal receptacle not observed) and right and left vitelline ducts, forms oötype surrounded by Mehlis' gland-cells. Female

duct continues to ascend medially as uterus; uterine pore opens ventrally near atrium of male copulatory organ. Prominent, muscular vaginal bulb, dextrolateral; duct from vagina connects with oviduct; seminal receptacle not observed. Vitelline system approximately co-extensive with intestinal caeca; anterior confluence of lateral vitelline fields just posterior to intestinal bifurcation, medial confluence just anterior to ovary and posterior confluence just posterior to cyclocoel but anterior to haptor. Parasitic on gills of lethrinid fishes (Perciformes).

Type-species: *Lethrinitrema gibbus* n. sp. from *Lethrinus rubrioperculatus* off New Caledonia.

Other species (see Table 2 for synonyms of fish names):

Lethrinitrema dossenus n. sp. from *Lethrinus rubrioperculatus*, off New Caledonia.

Lethrinitrema chrysostomi (Young, 1968) n. comb. from *Lethrinus miniatus* and allegedly (see below) *Diagramma picta* (Haemulidae), off Australia.

Lethrinitrema fleti (Young, 1968) n. comb. from *Lethrinus laticaudis*, *L. miniatus* and *L. nebulosus* off Australia.

Lethrinitrema lethrini (Yamaguti, 1937) n. comb. from *Lethrinus haematopterus* off Japan and *L. miniatus* off Australia.

Table 2 Distribution patterns of the present five species of *Lethrinitrema* n. g.

Lethrinitrema species[4]	Synonym	Host name in original publication	Updated host name	Locality	Reference
L. chrysostomi (Young, 1968) n. comb.	*Haliotrema chrysostomi* Young, 1968	*Lethrinus chrysostomus* (type-host)	*Lethrinus miniatus*[1]	Off Heron Island, Australia (type-locality)	Young (1968)
		Plectorhinchus pictus	*Diagramma picta*[2]	Off Heron Island, Australia	Young (1968)
		Lethrinus miniatus	*Lethrinus miniatus*	Off Queensland, Australia	Rohde et al. (1994)
L. fleti (Young, 1968) n. comb.	*Haliotrema fleti* Young, 1968	*Lethrinus fletus* (type-host)	*Lethrinus laticaudis*[3]	Moreton Bay, Australia (type-locality)	Young (1968)
		Lethrinus chrysostomus	*Lethrinus miniatus*[1]	Moreton Bay, Australia	Young (1968)
		Lethrinus miniatus		Off Queensland, Australia	Rohde et al. (1994)
		Lethrinus nebulosus		South China Sea	Zhang et al. (2001, 2003)
L. lethrini (Yamaguti, 1937) n. comb.	*Haliotrema lethrini* (Yamaguti, 1937) Young, 1968; *Ancyrocephalus lethrini* Yamaguti, 1937	*Lethrinus haematopterus* (type-host)		Off Japan (type-locality)	Yamaguti, (1937); Young (1968)
		Lethrinus miniatus		Off Queensland, Australia	Rohde et al. (1995)
L. dossenus n. sp.		*Lethrinus rubrioperculatus* (type-host)		Off New Caledonia (type-locality)	Present study
L. gibbus n. sp.		*Lethrinus rubrioperculatus* (type-host)		New Caledonia (type-locality)	Present study

[1] Randall & Wheeler (1991)

[2] Considered a lethrinid by Young (1968), now a haemulid (Froese & Pauly, 2010)

[3] Carpenter (2001)

[4] In addition to the named species, "*Haliotrema* sp." was listed from *Lethrinus nebulosus* in the Heron Island list of Lester & Sewell (1989)

Remarks

Members of *Lethrinitrema* n. g. possess four anchors, one ventral and one dorsal connecting bars, 14 morphologically similar marginal hooks, tandem gonads (ovary pretesticular), a non-sclerotised muscular, dextrolateral vaginal bulb, a male copulatory organ lacking an accessory piece or with a thinly sclerotised accessory piece, and a ventral male genital pore. These characteristics can also be found in many ancyrocephalids, particularly in *Haliotrema* spp. (see Lim & Justine, 2007). In fact, many previously described species exhibiting these features were assigned as *Haliotrema*, resulting in *Haliotrema* spp. being distributed on a wide diversity of marine fish species. *Haliotrema* is the 'catch-all' genus for many of the marine monogeneans with four anchors, two bars and 14 marginal hooks, whereas *Ancyrocephalus* Creplin, 1839 (*sensu stricto*) seems to be its freshwater counterpart.

Lethrinitrema spp. can be distinguished from the other marine ancyrocephalids by having two pear-shaped haptoral reservoirs, in which the elongate tubular extension bifurcates prior to contact with the superficial lateral grooves along both sides of the ventral anchors (Fig. 2A). In this study we have also examined several undescribed *Lethrinitrema* spp. from other *Lethrinus* spp. off New Caledonia (see 'Introduction') and have re-examined type- and voucher specimens of *Haliotrema* spp. from lethrinids, *H. australe* (holotype and paratype), *Haliotrema* spp. from several mullids and *Haliotrema* and *Haliotrema*-like species from different fishes off New Caledonia (see list above). Except for the *Lethrinitrema* spp. and *Haliotrema* spp. from lethrinids (see re-assignments below), all the other monogeneans examined are devoid of haptoral reservoirs. In the new species of *Lethrinitrema* (described below), the caeca form a cyclocoel just posterior to testis and continue as two posterior gut diverticula. Yamaguti (1963) pointed out differences in the intestinal pattern between the original description of *H. australe* compared with the holotype, and differentiated *Haliotrema* (with 'intestinal crura apparently separate, but actually united separately') from *Ancyrocephalus* (with 'intestinal crura not united posteriorly'). We can thus safely consider that species of *Lethrinitrema* n. g., with two haptoral reservoirs and ventral anchors with lateral grooves, are distinct and different from *Haliotrema* (*sensu stricto*) spp. (see below).

It should be noted that the apparent absence of haptoral reservoirs could be due to the method of collection, specimen preparation or the condition of the specimens during collection. According to the literature, there are other ancyrocephalids with two haptoral reservoirs: *Allomurraytrema spari* (Yamaguti 1958) Byrnes, 1986 [syn. of *A. robustum* (Murray, 1931)], *Calceostomella inermis* (Parona & Perugia, 1889) Palombi, 1943, *Cichlidogyrus halli typicus* El-Naggar & Kearn, 1989, *Chauhanellus australis* Kearn & Whittington, 1994, *C. youngi* Kearn & Whittington, 1994, *Hamatopeduncularia arii* Yamaguti 1953, *H. major* Kearn & Whittington, 1994 and *H. pearsoni* Kearn & Whittington, 1994 (see Wong et al., 2008). There are also ancyrocephalids with four haptoral reservoirs, and they include members of *Sundatrema* Lim & Gibson, 2009, *Parancylodiscoides* Caballero & Bravo-Hollis, 1961, *Bravohollisia* Bychowsky & Nagibina, 1970, *Caballeria* Bychowsky & Nagibina, 1970, *Ancyrocephaloides* Yamaguti, 1938 and *Placodiscus* Paperna, 1972, as well as *Haliotrema kurodai* Ogawa & Egusa, 1978 and *Neocalceostomoides brisbanensis* Whittington & Kearn, 1995 (see Lim, 1995b; Lim & Gibson, 2008a, 2009; Wong et al., 2008). *Placodiscus* was proposed for species with four 'opisthaptoral refractile bodies' or 'plaques' from sparids (Paperna, 1972), which are probably haptoral reservoirs. Ogawa & Egusa (1978) suggested that *H. kurodai*, which is also from a sparid, *Acanthopagrus schlegeli* (Bleeker), might eventually be re-assigned; *Placodiscus* is a likely designation. These ancyrocephalids differ from the present new species and from each other not only in the shape and size of their anchors and haptors (e.g. anchors with expanded outer roots in *Chauhanellus* spp., a digitate haptor in *Hamatopeduncularia* spp. and a large circular haptor in *Neocalceostomatoides* spp.) but also in the presence or absence of superficial grooves in the anchors (e.g. no grooves in species of *Haliotrema, Chauhanellus* and *Hamatopeduncularia vs* lateral grooves in all four anchors of *Bravohollisia, Caballeria* and *Ancyrocephaloides* spp. *vs* lateral grooves only in the ventral anchors of *Lethrinitrema* spp.). The species with haptoral reservoirs also differ in the way the haptoral reservoir tubular extension opens to the exterior. In *Chauhanellus, Caballeria* and *Ancyrocephaloides* spp., each non-bifurcate

tubular extension of the four haptoral reservoirs enters a concealed, crevice-like opening on one side of the anchor into a bifurcate channel within the anchor, which directs the secretions into left and right grooves of the anchors (Lim, 1994, 1995a, b, 1996; Lim & Gibson, 2008a; Wong et al., 2008). In the case of the two new species of *Lethrinitrema*, the two extremities of the bifurcate tubular extension of the haptoral reservoirs are associated with the lateral grooves of the ventral anchor (Figs. 2A, 3A). In species such as *Parancylodiscoides chaetodipteri* Caballero & Bravo-Hollis, 1961, *Neocalceostomoides brisbanensis*, *Cichlidogyrus halli typicus*, *Tetraonchus monenteron* Diesing, 1858 and *Sundatrema langkawiense* Lim & Gibson, 2009, the haptoral reservoirs open directly to the exterior close to the site where the anchor point exits the body and the anchors do not have grooves (Lim & Gibson, 2009). All these monogeneans differ from *Lethrinitrema* spp. in their hosts; *Lethrinitrema* spp. are found on members of *Lethrinus* (Lethrinidae), whereas *Sundatrema* and *Parancylodicoides* spp. are found on ephippids, *Ancyrocephaloides* spp. on triacanthids, *Bravohollisia* spp. and *Caballeria* spp. on pomadasyids, *Cichlidogyrus* spp. on cichlids, *Neocalceostomatoides*, *Chauhanellus* and *Hamatopeduncularia* spp. on ariids, and *Placodiscus* spp., *Allomurraytrema* spp. and *Haliotrema kurodai* on sparids. Lim (1995b), Wong et al. (2008) and Lim & Gibson (2008a) proposed that the secretions stored in the haptoral reservoirs of the different species of *Bravohollisia, Caballeria* and *Ancyrocephaloides* assist in attachment and locomotion, with the net-like secretions acting as a belay device. Although no net-like secretions have been observed in the *Lethrinitrema* specimens examined, the same may be true for members of this genus.

The status of dactylogyridean monogeneans with four anchors has been controversial (cf. Kritsky & Boeger, 1989; Lim et al., 2001). In agreement with authors, such as Bychowsky & Nagibina (1978), Gusev (1978) and many more recent workers (e.g. Dmitrieva et al., 2009; Lim et al., 2001; Le Roux & Avenant-Oldewage, 2009; Lim & Gibson, 2008a, b, 2009; Lim & Justine, 2007; Marcotegui & Martorelli, 2009; Pariselle & Euzet, 2009), we recognise the Ancyrocephalidae, and we include *Lethrinitrema* n. g. within this family.

***Lethrinitrema gibbus* n. sp.**

Type-host: *Lethrinus rubrioperculatus* Sato (Lethrinidae).
Type-locality: Lagoon off Nouméa, New Caledonia.
Type-specimens: Holotype JNC988B4 and 13 paratypes, [JNC1424 A1.01, JNC 1016 A7, JNC 1016 A2, JNC 988 B1, JNC 988 B2, JNC 989 A6, JNC 1422 A1, JNC 1422 A1, JNC 1113 A1, JNC 1728.01-03, JNC 1270.08-09], MNHN; 2 paratypes, 2011.1.5.1-2, BMNH; 2 paratypes, 104124, 104125, USNPC; 14 paratypes, [2010.01(P)-06(P), 2010.11(P), 2010.12(P)-2010.18(P)], MZUM(P).
Material studied: 34 specimens studied; 14 specimens measured.
Etymology: The species name *gibbus*, a noun (Latin for 'hump'), refers to the local name of lethrinids, 'bossus', meaning 'humpback'.

Description (Figs. 1–2)

Body leaf-like, 1,288 (1,191–1,458) × 204 (158–236). Three pairs of head organs; four pairs of pigmented eyespots. Mouth subterminal, ventral. Pharynx ovoid. Intestine bifurcates just posterior to pharynx; caeca unite just posterior to testis, continue posteriorly as 2 diverticula. Haptor small, not well demarcated, wider than long, 64 (53–79) × 127 (96–181). Fourteen larval-type hooks, length 12 (11–13). Dorsal anchors, inner length 31 (29–31), outer length 22 (21–23), well-developed inner roots 12 (11–14), outer root 3 (2–4), point 15 (12–16); ventral anchors, inner length 21 (19–22), inner root 12 (9–13) with crown-like piece, outer length 23 (22–24), outer root 4 (3–6), point 8 (7–9); superficial lateral groove along both sides of ventral anchors from shaft to point. Dorsal bar V-shaped, 45 (41–48) × 4 (3–5); ventral bar with posterior prominence, 41 (37–46) × 9 (7–11). Two pear-shaped haptoral reservoirs, each with elongate, tubular extension which bifurcates distally prior to entering lateral groove on each side of ventral anchor (Fig. 2A).

Testis ovoid to bilobed, postovarian. Vas deferens leaves anterior region of testis, passes ovary dorsally, loops around sinistral caecum to ventral side, distends to form seminal vesicle, narrows, ascends and then enters initial part (base) of copulatory tube. Two elongate, pyriform prostatic reservoirs; prostatic duct

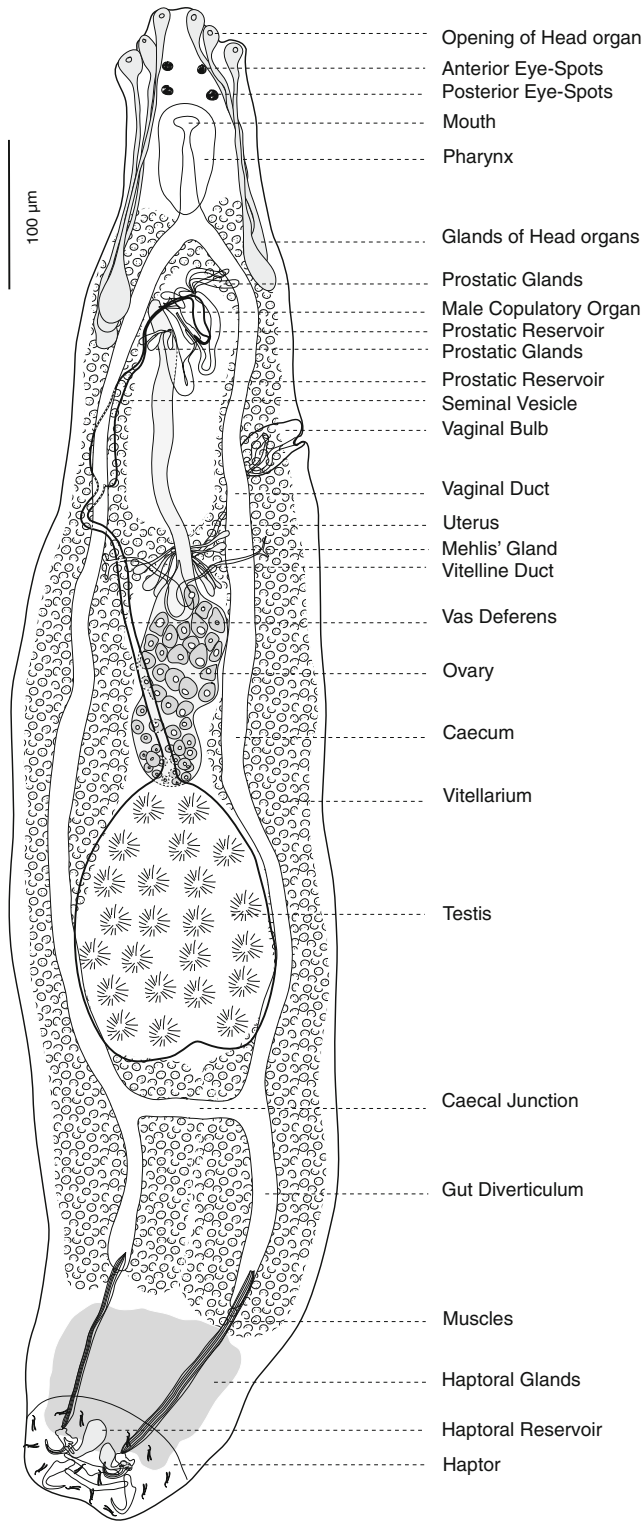

Fig. 1 Composite illustration of *Lethrinitrema gibbus* n. g., n. sp. from *Lethrinus rubrioperculatus*, dorsal view

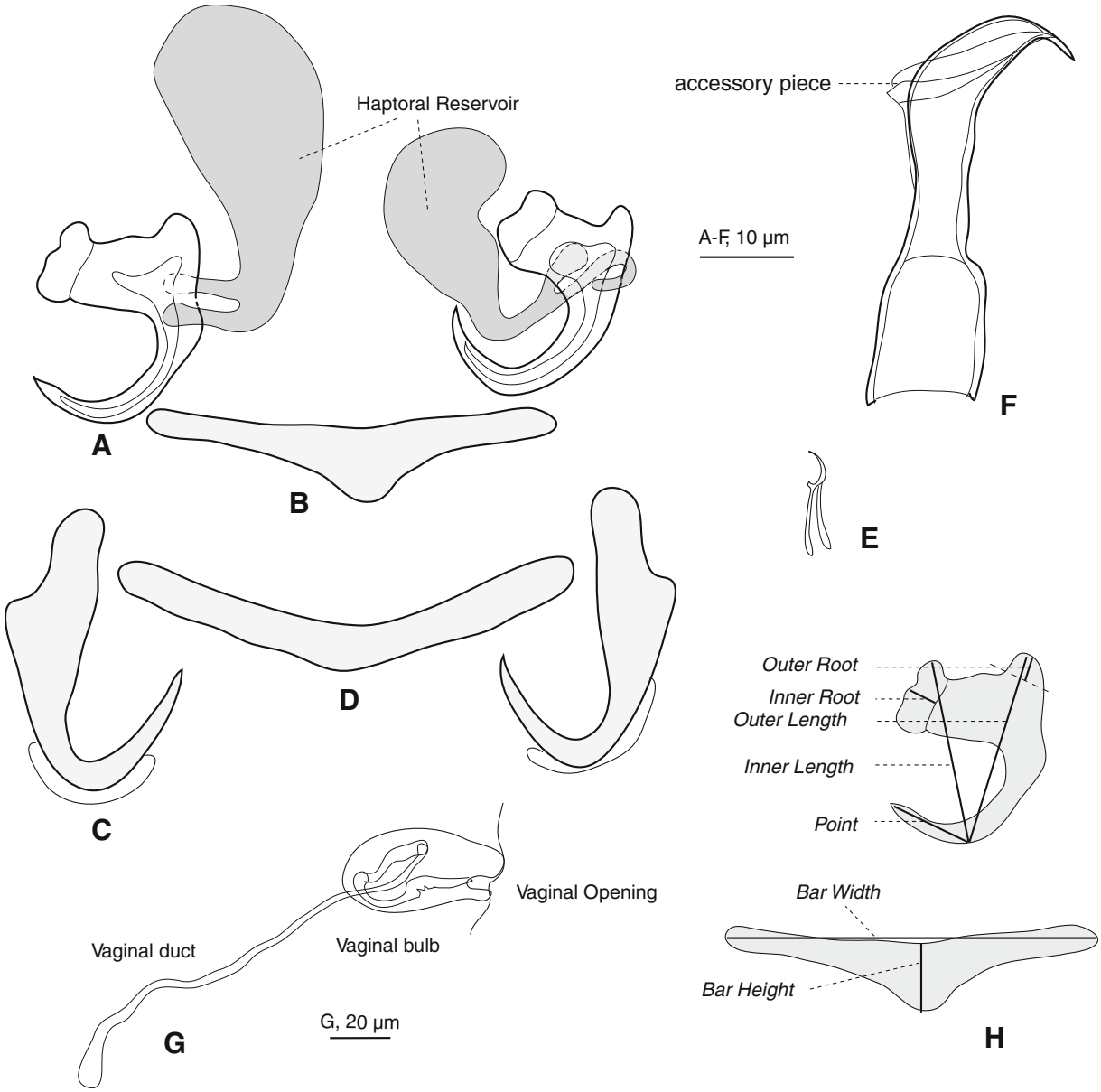

Fig. 2 Sclerotised parts of *Lethrinitrema gibbus* n. g., n. sp. A, ventral anchors; B, ventral bar; C, dorsal anchor; D, dorsal bar; E, hook; F, male copulatory organ; G, vaginal system; H, parameters measured

connects with base of male copulatory organ. Male copulatory organ consists of simple tapered copulatory tube, length 40 (40–45), with long base (or initial part), recurved distally; thin accessory piece arises from distal end of tube. Prostatic gland ducts drain into anterior part of prostatic reservoir. Ovary in mid-body, smaller than testis. Vaginal bulb dextrolateral, muscular; vaginal duct leaves vaginal bulb and unites with oviduct; seminal receptacle not observed. Oviduct arises from anterior side of ovary, receives vaginal duct and both right and left vitelline ducts, ascends as oötype surrounded by Mehlis' gland-cells, continues to ascend medially as uterus; uterine pore opens ventrally near atrium of male copulatory organ. Vitelline system approximately co-extensive with intestinal caeca; anterior confluence of lateral vitelline fields just posterior to intestinal bifurcation, medial confluence just anterior to ovary and posterior

confluence just posterior to cyclocoel but anterior to haptor.

Differential diagnosis

L. gibbus n. sp. is the type-species for *Lethrinitrema* n. g. This species differs from previously described monogeneans with four anchors in having a combination of a pair of haptoral reservoirs with a bifurcate, tubular extension, ventral anchors with a lateral superficial groove on both sides, a prominent muscular vaginal bulb and a simple tapered copulatory tube (see 'Remarks' for *Lethrinitrema* n. g.).

Lethrinitrema dossenus n. sp.

Type-host: *Lethrinus rubrioperculatus* Sato (Lethrinidae).
Type-locality: Lagoon off Nouméa, New Caledonia.
Type-specimens: Holotype JNC988B3 and 16 paratypes, [JNC 984 A1, JNC 1064 A5.01-03, JNC 1424 A1.02-05, JNC 1016 A5.01-03, JNC1728.04, JNC1728.05, JNC1728.06, JNC1720.07 & JNC1720.08] MNHN; 2 paratypes, 2011.1.5.3-4, BMNH; 2 paratypes, 104122, 104123, USNPC; 12 paratypes, [2010.07(P)-10(P), 2010.19(P)–2010.26(P)], MZUM(P).
Material studied: 33 specimens studied; 13 specimens measured.
Etymology: The species name *dossenus*, a noun (Latin for 'humpback'), refers to the local name of lethrinids, 'bossus', meaning 'humpback'.

Description (Fig. 3)

Body leaf-like, 1,148 (970–1,546) × 152 (121–201). Haptor wider than long, 62 (42–91) × 92 (75–123). Fourteen larval type hooks, length 12 (11–13). Dorsal anchors, inner length 32 (30–33), outer length 24 (23–25), well-developed inner roots 2 (11–14), outer root 3 (2–3), point 13 (11–15); ventral anchors, inner length 20 (20–21), outer length 21 (20–24), inner root 12 (11–13) with crown-like piece at tip, outer root 3 (2–3), point 10 (8–13), with lateral groove on each side of shaft to point. Dorsal bar 32 (32–33) × 5 (3–5); ventral bar 37 (35–39) × 7 (6–8). Two pear-shaped hyaline haptoral reservoirs with distal tubular extension bifurcate, as in *L. gibbus*.

Arrangement of male and female organs similar to *L. gibbus*. Male copulatory organ consists of funnel-shaped copulatory tube, length 25 (24–30), short initial part and inconspicuous accessory piece at its distal end. Prominent dextrolateral muscular vaginal bulb, as in *L. gibbus.*

Differential diagnosis

This species differs from *L. gibbus* n. sp. in the shape and size of the copulatory tube: in *L. dossenus* it is a short, funnel-like tube (24–30 μm in length) with short initial part and a lightly sclerotised (inconspicuous) accessory piece, whereas in *L. gibbus* the copulatory tube (40–45 μm in length) has a recurved distal tip, long initial part and a thin accessory piece (cf. Fig. 4E, F). The present species is also different from *L. gibbus* in the shape and size of the dorsal connecting bar (Table 3). Although there is some overlap, it also has dorsal anchors with shorter recurved points of 13 (11–15) μm, compared to 15 (12–16) μm in *L. gibbus*, and ventral anchors with a longer point of 10 (8–13) μm, compared to 8 (7–9) μm in *L. gibbus.*

Lethrinitrema chrysostomi (Young, 1968) n. comb.

Syn. *Haliotrema chrysostomi* Young, 1968

Type-host: *Lethrinus chrysostomus* Richardson [now *L. miniatus* (Forster)] (Lethrinidae).
Other host: *Plectorhinchus pictus* (Thunberg) [now *Diagramma picta* (Thunberg)] (Haemulidae) (Young, 1968; Table 2).
Material studied: Paratype from *L. miniatus*; paratype from *P. pictus*.

Brief redescription (Fig. 4)

Measurements given in Table 3. Two haptoral reservoirs, 15 × 11 ('paratype 1'), 12×7 ('paratype 4') (length 27–38 in original description). Testis 70 × 35 ('paratype 1'). Measurements of anchors not possible because of poor orientation.

Comments

There are discrepancies between the measurements in the description given by Young (1968) and our measurements of the paratypes. However, measurements

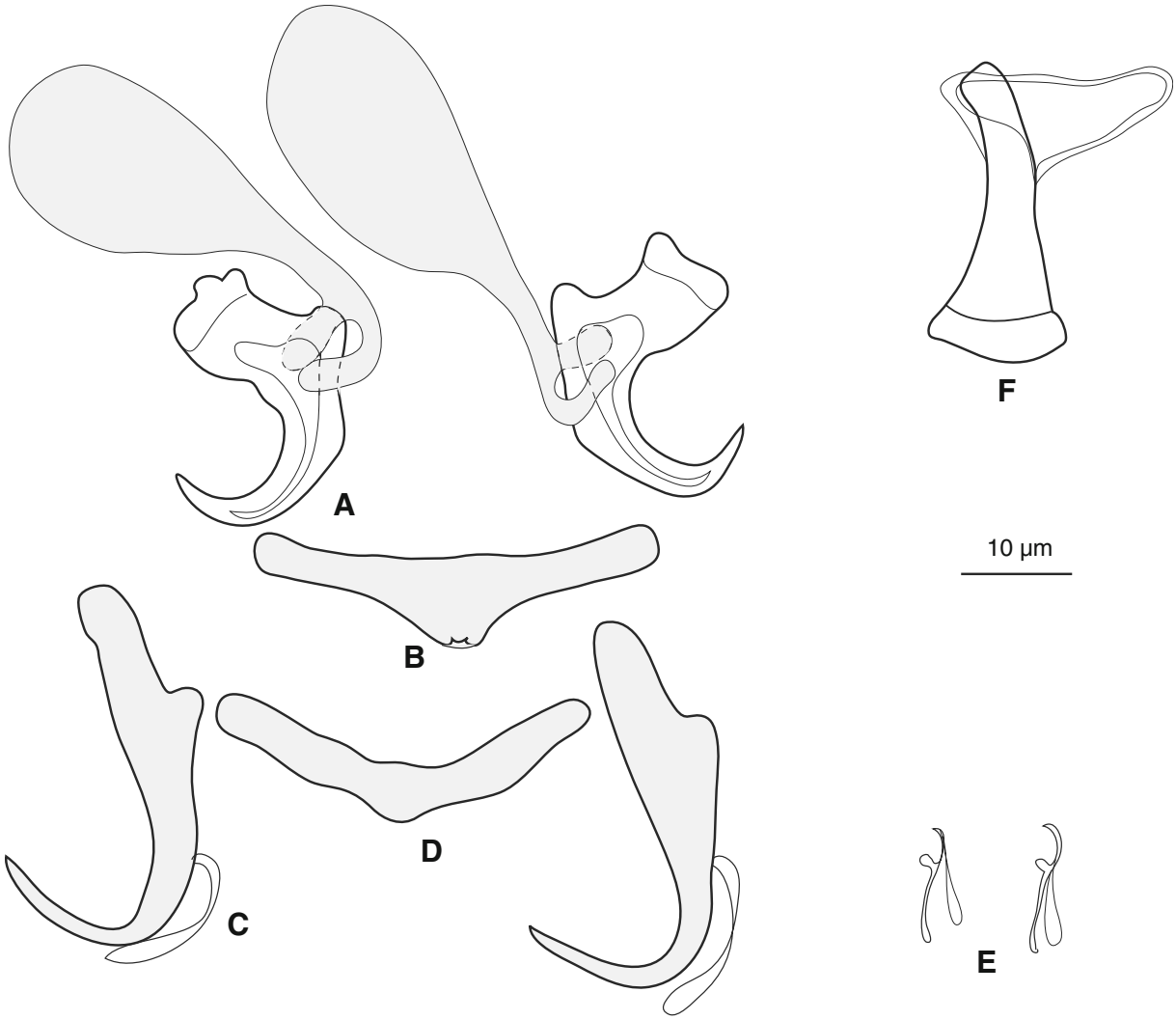

Fig. 3 Sclerotised parts of *Lethrinitrema dossenus* n. g., n. sp. A, ventral anchor; B, ventral bar; C, dorsal anchor; D, dorsal bar; E, hooks; F, male copulatory organ

of the original figures of Young (1968) using the given scale-bar correspond to our measurements of the paratypes (Table 3). Rohde et al. (1994) also provided a drawing of the male copulatory organ of *Haliotrema chrysostomi* from *Lethrinus miniatus*, and the length of the male copulatory organ in their figure 11 is 32 µm, which is comparable to our measurements of the paratypes and our measurement of the original figure of Young.

From our examination of the two paratypes of *H. chrysostomi*, we have to accept Young's interpretation that the specimens from *L. miniatus* (Lethrinidae) and *Plectorhinchus pictus* (Haemulidae) are the same species, since the paratypes from the two host species are similar, particularly in the structure of the male copulatory organ. *P. pictus* (Thunberg) is now designated as *Diagramma picta*, although *Plectorhinchus pictus* (Tortonese) nec (Thunberg) is valid. We have examined several specimens of *D. picta*, and several species of *Plectorhinchus*, from off New Caledonia, but we have not found any ancyrocephalids, although other monogeneans were present on the gills. The work of Young is not without fish misidentifications (Justine

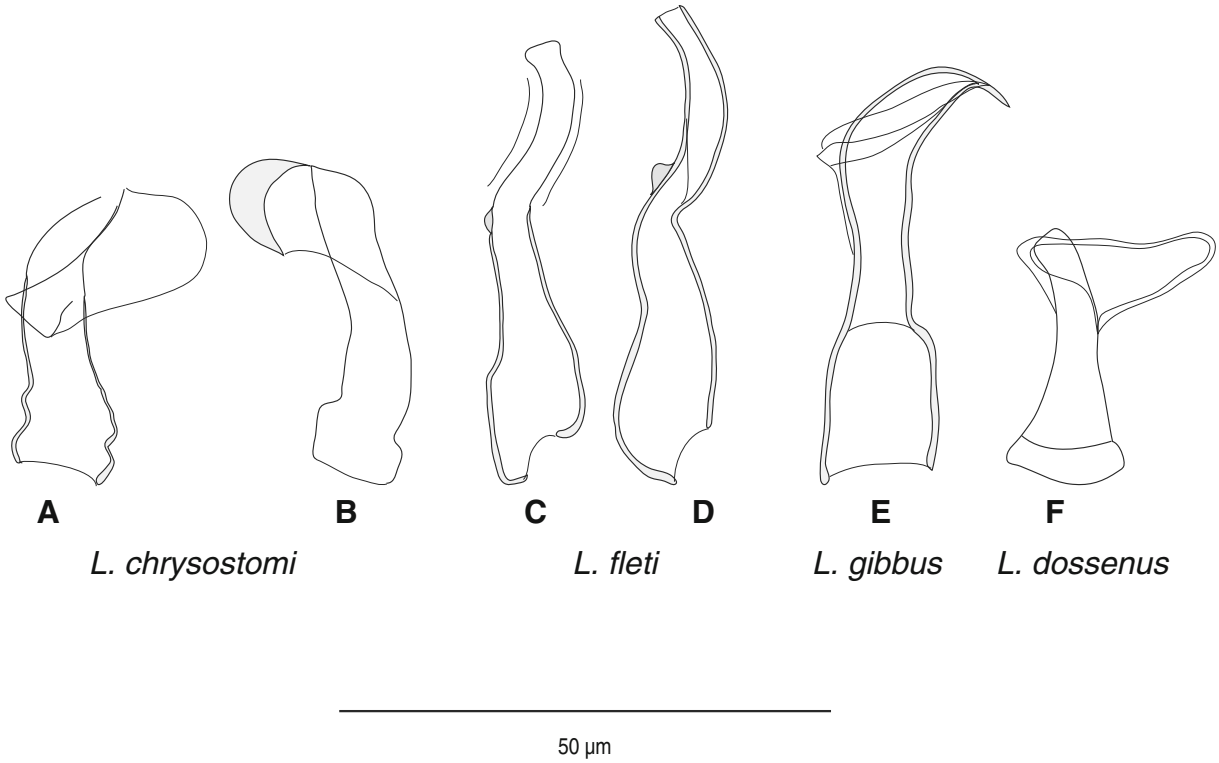

Fig. 4 Sclerotised male copulatory organs of four species of *Lethrinitrema* n. g. A, B, *L. chrysostomi* (Young, 1968) n. comb., USNPC 61283 (A, 'paratype 4'; B, 'paratype 1'); C, D, *L. fleti* (Young, 1968) n. comb., USNPC 61285 (C, 'paratype 1', D, 'paratype 2'); E, *L. gibbus* n. sp.; F, *L. dossenus* n. sp.

et al., 2009*)* and lethrinids can be easily confused for small haemulids; hence, the presence of *Lethrinitrema chrysostomi* on a haemulid needs to be confirmed.

***Lethrinitrema fleti* (Young**, 1968**) n. comb.**
Syn. *Haliotrema fleti* Young, 1968

Type-host: *Lethrinus fletus* Whitney [now *L. laticaudis* Alleyne & Macleay] (Lethrinidae)
Other hosts: *Lethrinus chrysostomus* Richardson [now *L. miniatus* (Forster)] (see Rohde et al., 1994; Young, 1968); *L. nebulosus* (Forsskål) (see Zhang et al., 2001, 2003) (Table 2).
Material studied: Two paratypes from *L. fletus*.

Brief redescription (Fig. 4)

Measurements given in Table 3. Two haptoral reservoirs, 80 × 25 ('paratype 1'), 70 × 25 ('paratype 2') (original description: 57–79). Testis 200 × 70 ('paratype 2'). Measurements of anchors not possible because of poor orientation. Male copulatory organ in both specimens similar.

Comments

The measurements of *Haliotrema fleti* in the original text of Young (1968) do not correspond with either those obtained from the type-specimens or those obtained by measuring the original illustrations, particularly that of the haptoral reservoirs (Table 3). This species has the largest haptoral reservoirs, compared with the other species examined in this study. Rohde et al. (1994) also provided a drawing of the male copulatory organ of *H. fleti* from *Lethrinus miniatus*, but gave no other information; the curved length of the male copulatory organ, measured on their figure 11, is 55 µm.

Lethrinitrema chrysostomi n. comb., *L. fleti* n. comb., *L. gibbus* n. sp. and *L. dossenus* n. sp. can be distinguished on the basis of their male copulatory tube (Table 3; Fig. 4). In *L. chrysostomi* the copulatory tube is 29–30 µm long, with a terminal

Table 3 Selected measurements of species of *Lethrinitrema* n. g. from different sources

Lethrinitrema species Data source	*L. chrysostomi* Young (1968)	*L. chrysostomi* Our measurement of 'Paratype 1' (USNPC 61283):	*L. chrysostomi* Our measurement of 'Paratype 4' (USNPC 61283):	*L. fleti* Young (1968)	*L. fleti* Our measurement of 'Paratype 1' (USNPC 61285)	*L. fleti* Our measurement of 'Paratype 2' (USNPC 612850	*L. lethrini* Yamaguti (1937)	*L. gibbus* Present data	*L. dossenus* Present data
Host names (as in the original description; updated names given in Table 2)	*Lethrinus chrysostomus; Plectorhinchus pictus*	*Lethrinis chrysostomus*	*Plectorhinchus pictus*	*Lethrinis fletus L. chrysostomus*	*Lethrinus fletus*	*Lethrinus fletus*	*Lethrinus haemopterus*	*Lethrinus rubrioperculatus*	*Lethrinus rubrioperculatus*
Body length	506–693[a]	600	530	748–1,210[a]	1,050+	1,200	1,400–1,700	1,191–1,458	970–1,546
Length of male copulatory organ	65–76[a] 32[b]; 27[c]	29	30	34–36[a] 23[b]; 27[c]	44	48	150	40–45	24–30
Ventral bar	81–100[a] 43[b]; 37[c]	36	36	44–50[a] 31[b]; 37[c]	60	60	45–57	37–46	35–39
Dorsal bar	91–92[a] 41[b]; 34[c]	31	42	54–60[a] 27[b]; 32[c]	50	47	54–80	41–48	32–33
Reservoirs	27–38[a]	15 × 11	12 × 7	57–79[a]	80 × 25	70 × 22			

[a] From original text

[b] From figures, based on scale in legend

[c] From figures, based on scale bar in figures of Young (1968)

Table 4 Some characteristics of *Lethrinitrema* spp.

Lethrinitrema species	Characteristics			
	Two haptoral reservoirs	Vaginal bulb	Vitelline duct	Gut diverticula
L. chrysostomi	+	+	?	+
L. fleti	+	+	?	+
L. lethrini	+	+	?	?
L. dossenus	+	+	+	+
L. gibbus	+	+	+	+

'hook' ('swollen complex tip' in the original description); in *L. fleti* the copulatory tube is 44–48 μm long, with a crest at mid-length, probably similar to the spiral piece around the tube in the original drawing given by Young (1968); in *L. gibbus* it is 40–45 μm long, with a recurved distal extremity and a thin, distal accessory piece; and in *L. dossenus* it is a short (24–30 μm), funnel-shaped tube, with a lightly sclerotised distal accessory piece. According to Young (1968), the accessory piece is absent in *L. chrysostomi*, although the 'hook' at the extremity of the male copulatory organ could be interpreted as an accessory piece similar to the reduced accessory piece in *L. gibbus* and *L. dossenus.*

***Lethrinitrema lethrini* (Yamaguti**, 1937) **n. comb.**
Syns *Ancyrocephalus lethrini* Yamaguti, 1937; *Haliotrema lethrini* (Yamaguti, 1937) Young, 1968

We were unable to examine the type-specimens of *Haliotrema lethrini* from *Lethrinus haematopterus*. However, this species possesses features [two haptoral reservoirs and a copulatory tube described as a 'slender, curved, chitinous tube enclosed proximally in a muscular pouch' (Yamaguti, 1937)], which are similar to those of the new species described above. *H. lethrini* is herein re-assigned as *Lethrinitrema lethrini* n. comb. (Table 2). This species is easily distinguished from the other four species of *Lethrinitrema* by the length of its copulatory tube (150 μm) and the shape of its anchors (see Yamaguti, 1937).

Discussion

There are five species of *Lethrinitrema*, *L. dossenus* n. sp., *L. gibbus* n. sp., *L. fleti* n. comb., *L. chrysostomi* n. comb. and *L. lethrini* n. comb. with the characteristics summarised in Table 4. In *L. chrysostomi*, *L. fleti*, *L. gibbus* and *L. dossenus* the caeca form two posterior gut diverticula which extend back from the cyclocoel; this feature was not mentioned in the description of *L. lethrini*. These two posterior gut diverticula are not visible in the specimens deposited by Young (1968) but are mentioned in the descriptions. The haptoral reservoirs of *L. fleti* are larger than in other species. *L. lethrini* is the largest species and *L. chrysostomi* the smallest (Table 3). The five species also differ in the detailed morphology of their male copulatory organs (Fig. 4) and bars, in particular, the size of the ventral bar (Table 3), which is wider in *L. fleti* than in the other species.

We could ascertain that the five known species of *Lethrinitrema* have two haptoral reservoirs (Table 4) and a similar male copulatory organ in the form of a simple, tapering tube either without an accessory piece or with an inconspicuous accessory piece (Fig. 4). There is, however, a need to collect and re-examine specimens of the reassigned species, and in particular the two species described by Young (1968), in order to determine whether their internal anatomy is similar to that of the two new species, whether their haptoral reservoirs have a distal bifurcation and whether lateral grooves are present on their ventral anchors. In the paratype specimens examined, the anchors were not well oriented and we could not check for the presence of the 'crown' on the inner roots of the ventral anchors or for lateral grooves.

To date, many of the species assigned to *Haliotrema* spp., which are restricted to particular host groups, have been reassigned. For example, species of *Ligophorus* Euzet & Suriano, 1977 are restricted to mugilids; *Euryhaliotrematoides* spp. and *Aliatrema*

spp. to chaetodontids; *Volsellituba* spp. and *Pennulituba* spp. to *Mulloidichthys* spp. (Mullidae); *Haliotrematoides* spp. to lutjanids, caesionids, haemulids and sparids; and *Euryhaliotrema* spp. to sciaenids, sparids, haemulids and lutjanids (Euzet & Suriano, 1977; Mendoza-Franco et al., 2009; Kritsky & Boeger, 2002; Kritsky et al., 2009; Plaisance & Kritsky, 2004; Rehulková et al., 2010). All known *Lethrinitrema* spp. are found on members of *Lethrinus* (Lethrinidae), although, as indicated above, *L. chrysostomi* has also been reported on a haemulid. The occurrence of *Lethrinitrema* spp. only on species of *Lethrinus* suggests a history of host-parasite co-evolution. We have several other species of *Lethrinitrema* collected off New Caledonia (which are undescribed due to insufficient numbers of specimens), all from other *Lethrinus* spp. (see 'Introduction'), and there are also possibly two or three *Lethrinitrema* spp. on *Lethrinus lentjan* (Lacépède) in the Arabian Gulf (judging from BMNHN slide 1994.8.10.98-100, which we examined). The geographical distribution of *Lethrinitrema* spp. probably extends from off Japan to South-Eastern Australian waters, and from the Red Sea to New Caledonian waters, following the distribution range of *Lethrinus* spp. It would be of biogeographical interest to check the parasites of *L. atlanticus* in the Atlantic.

Acknowledgements Kent Carpenter (Norfolk, Virginia, USA) helped in identifying *Lethrinus* spp. on photographs. Julie Mounier, a volunteer technician, and Charles Beaufrère, Audrey Guérin, Anaïs Guillou, Amandine Marie, Chloé Journo, Violette Justine, Eric Bureau, Maya Robert, Damien Hinsinger, Aude Sigura and Guilhem Rascalou, all students, participated in the fishing operations and parasitological survey. Angelo di Matteo (IRD) provided technical help and Liew K.S. assisted with the fishing and with the collection and preparation of specimens for this study. Gérard Mou Tham (IRD) spear-fished certain specimens. We would like to thank the French Embassy in Malaysia for funding the visit of the first author and Liew K.S. to New Caledonia.

References

Bychowsky, B. E., & Nagibina, L. F. (1978). [A revision of Ancyrocephalinae Bychowsky, 1937 (Monogenoidea)]. *Parazitologicheskii Sbornik, 28*, 5–15. (In Russian).

Carpenter, K. E. (2001). Lethrinidae. Emperors (emperor snappers). In: Carpenter, K. E. & Niem, V. H. (Eds) *FAO species identification guide for fishery purposes. The living marine resources of the Western Central Pacific. Volume 5. Bony fishes, Part 3 (Menidae to Pomacentridae)*. Rome: FAO, pp. 3004–3030.

Carpenter, K. E., & Allen, G. R. (1989). *FAO Species Catalogue*. Vol. 9. *Emperor fishes and large-eye breams of the world (Family Lethrinidae). An annotated and illustrated catalogue of lethrinid species known to date. FAO Fisheries Synopsis No 125, Volume 9*. Rome: Food and Agriculture Organization of the United Nations, 118 pp.

Dmitrieva, E. V., Gerasev, P. I., Merella, P., & Pugachev, O. N. (2009). Redescription of *Ligophorus mediterraneus* Sarabeev, Balbuena & Euzet, 2005 (Monogenea: Ancyrocephalidae) with some methodological notes. *Systematic Parasitology, 73*, 95–105.

Euzet, L., & Suriano, M. D. (1977). *Ligophorus* n. g. (Monogenea, Ancyrocephalidae) parasite des Mugilidae (Téléostéens) en Méditerranée. *Bulletin du Muséum National d'Histoire Naturelle, Paris, 3ème série, 472*, 797–822.

Froese, R., & Pauly, D. (Eds) (2010). *FishBase. World Wide Web electronic publication.* www.fishbase.org, version (01/2010).

Gusev, A. V. (1978). [Freshwater Indian Monogenoidea. Principles of systematics, analysis of world fauna and its evolution]. *Parazitologicheskii Sbornik, 28*, 96–198. (In Russian).

Johnston, T. A., & Tiegs, O. W. (1922). New gyrodactyloid trematodes from Australian fishes together with a reclassification of the super-family Gyrodactyloidea. *Proceedings of the Linnean Society of New South Wales, 47*, 83–129.

Justine, J.-L. (2005). Species of *Pseudorhabdosynochus* Yamaguti, 1958 (Monogenea: Diplectanidae) from *Epinephelus fasciatus* and *E. merra* (Perciformes: Serranidae) off New Caledonia and other parts of the Indo-Pacific Ocean, with a comparison of measurements of specimens prepared using different methods, and a description of *P. caledonicus* n. sp. *Systematic Parasitology, 62*, 1–37.

Justine, J.-L. (2007). Species of *Calydiscoides* Young, 1969 (Monogenea: Diplectanidae) from lethrinid fishes, with the redescription of all of the type-specimens and the description of *C. euzeti* n. sp. from *Lethrinus rubrioperculatus* and *L. xanthochilus* off New Caledonia. *Systematic Parasitology, 67*, 187–209.

Justine, J.-L. (2010). Parasites of coral reef fish: how much do we know? With a bibliography of fish parasites in New Caledonia. *Belgian Journal of Zoology, 140 (Suppl.)*, 155–190.

Justine, J.-L., & Briand, M. J. (2010). Three new species, *Lamellodiscus tubulicornis* n. sp., *L. magnicornis* n. sp. and *L. parvicornis* n. sp. (Monogenea: Diplectanidae) from *Gymnocranius* spp. (Lethrinidae: Monotaxinae) off New Caledonia, with proposal of the new morphological group 'tubulicornis' within *Lamellodiscus* Johnston & Tiegs, 1922. *Systematic Parasitology, 75*, 159–179.

Justine, J.-L., Dupoux, C., & Cribb, T. H. (2009). Resolution of the discrepant host-specificity of *Pseudorhabdosynochus* species (Monogenea, Diplectanidae) from serranid fishes in the tropical Indo-Pacific. *Acta Parasitologica, 54*, 119–130.

Kritsky, D. C., & Boeger, W. A. (1989). The phylogenetic status of the Ancyrocephalidae Bychowsky, 1937 (Monogenea: Dactylogyroidea). *Journal of Parasitology, 75*, 207–211.

Kritsky, D. C., & Boeger, W. A. (2002). Neotropical Monogenoidea. 41: New and previously described species of Dactylogyridae (Platyhelminthes) from the gills of marine and freshwater perciform fishes (Teleostei) with proposal of a new genus and a hypothesis on phylogeny. *Zoosystema, 24*, 7–40.

Kritsky, D. C., Yang, T., & Sun, Y. (2009). Dactylogyrids (Monogenoidea, Polyonchoinea) parasitizing the gills of snappers (Perciformes, Lutjanidae): Proposal of *Haliotrematoides* n. gen. and descriptions of new and previously described species from marine fishes of the Red Sea, the eastern and Indo-west Pacific Ocean, Gulf of Mexico and Caribbean Sea. *Zootaxa, 1970*, 1–51.

Le Roux, L. E., & Avenant-Oldewage, A. (2009). Checklist of the fish parasitic genus *Cichlidogyrus* (Monogenea), including its cosmopolitan distribution and host species. *African Journal of Aquatic Science, 35*, 21–36.

Lester, R. J. G., & Sewell, K. B. (1989). Checklist of parasites from Heron Island, Great Barrier Reef. *Australian Journal of Zoology, 37*, 101–128.

Lim, L. H. S. (1991). Preparation of Museum specimens – Monogenea. *Fish Health Section Newsletter, 2*, 10–11.

Lim, L. H. S. (1994). *Chauhanellus* Bychowsky & Nagibina, 1969 (Monogenea) from ariid fishes (Siluriformes) of Peninsular Malaysia. *Systematic Parasitology, 28*, 99–124.

Lim, L. H. S. (1995a). *Neocalceostoma* Tripathi, 1957 and *Neocalceostomoides* Kritsky, Mizelle & Bilqees, 1978 (Monogenea: Neocalceostomatidae n. fam.) from ariid fishes of Peninsular Malaysia. *Systematic Parasitology, 30*, 141–151.

Lim, L. H. S. (1995b). *Bravohollisia* Bychowsky & Nagibina, 1970 and *Caballeria* Bychowsky & Nagibina, 1970 (Monogenea: Ancyrocephalidae) from *Pomadasys hasta* (Bloch) (Pomadasyidae), with the description of a new attachment mechanism. *Systematic Parasitology, 32*, 211–224.

Lim, L. H. S. (1996). Eight new species of *Hamatopeduncularia* Yamaguti, 1953 (Monogenea: Ancyrocephalidae) from Ariidae of Peninsular Malaysia. *Systematic Parasitology, 33*, 53–71.

Lim, L. H. S., & Gibson, D. I. (2008a). Redescriptions of species of *Ancyrocephaloides* Yamaguti, 1938 (Monogenea: Ancyrocephalidae) from triacanthid fishes caught off Peninsular Malaysia and a report of their haptoral secretions. *Systematic Parasitology, 69*, 59–73.

Lim, L. H. S., & Gibson, D. I. (2008b). Species of *Triacanthinella* Bychowsky & Nagibina, 1968 (Monogenea: Ancyrocephalidae) from triacanthid teleosts off Peninsular Malaysia, with a generic revision, amended diagnosis and key. *Systematic Parasitology, 70*, 191–213.

Lim, L. H. S., & Gibson, D. I. (2009). A new monogenean genus from an ephippid fish off Peninsular Malaysia. *Systematic Parasitology, 73*, 13–25.

Lim, L. H. S., & Justine, J.-L. (2007). *Haliotrema banana* sp. n. (Monogenea: Ancyrocephalidae) from *Bodianus perditio* (Perciformes: Labridae) off New Caledonia. *Folia Parasitologica, 54*, 203–207.

Lim, L. H. S., Timofeeva, T. A., & Gibson, D. I. (2001). Dactylogyridean monogeneans of the siluriform fishes of the Old World. *Systematic Parasitology, 50*, 159–197.

Malmberg, G. (1957). Om förekomsten av *Gyrodactylus* på svenska fiskar (In Swedish.). *Skrifter Utgivna av Södra Sveriges Fiskeriförening, Årsskrift, 1956*, 19–76.

Marcotegui, P. S., & Martorelli, S. R. (2009). *Ligophorus saladensis* n. sp (Monogenea: Ancyrocephalidae) from *Mugil platanus* Günther in Samborombón Bay, Argentina. *Systematic Parasitology, 74*, 41–47.

Mendoza-Franco, E. F., Reyes-Lizama, C., & González-Solıs, D. (2009). *Haliotrematoides* spp. (Monogenoidea, Dactylogyridae) infecting the gills of grunts (Perciformes: Haemulidae) from the southern coast of Quintana Roo, Mexico. *Journal of Parasitology, 95*, 1360–1363.

Ogawa, K., & Egusa, S. (1978). *Haliotrema kurodai* n. sp. (Monogenea: Dactylogyridae, Ancyrocephalinae), a monogenean parasite obtained from the Japanese black sea bream, *Acanthopagrus schlegeli* (Bleeker). *Bulletin of the Japanese Society of Scientific Fisheries, 44*, 1329–1332.

Paperna, I. (1972). Monogenea of Red Sea Fishes. III. Dactylogyridae from littoral and reef fishes. *Journal of Helminthology, 46*, 47–62.

Pariselle, A., & Euzet, L. (2009). Systematic revision of dactylogyridean parasites (Monogenea) from cichlid fishes in Africa, the Levant and Madagascar. *Zoosystema, 31*, 849–898.

Plaisance, L., & Kritsky, D. C. (2004). Dactylogyrids (Platyhelminthes: Monogenoidea) parasitizing butterfly fishes (Teleostei: Chaetodontidae) from the coral reefs of Palau, Moorea, Wallis, New Caledonia, and Australia: species of *Euryhaliotrematoides* n. gen. and *Aliatrema* n. gen. *Journal of Parasitology, 90*, 328–341.

Randall, J. E. (2005). *Reef and shore fishes of the South Pacific. New Caledonia to Tahiti and the Pitcairn Islands.* Honolulu: University of Hawai'i Press, Honolulu, 707 pp.

Randall, J. E., & Wheeler, A. (1991). Reidentification of seven tropical Pacific fishes collected and observed by the Forsters during the voyage of HMS Resolution, 1772–75. *Copeia, 1991*, 760–767.

Rascalou, G., & Justine, J.-L. (2007). Three species of *Calydiscoides* (Monogenea: Diplectanidae) from five *Lethrinus* spp. (Lethrinidae: Perciformes) off New Caledonia, with a description of *Calydiscoides terpsichore* sp. n. *Folia Parasitologica, 54*, 191–202.

Řehulková, E., Justine, J.-L., & Gelnar, M. (2010). Five new monogenean species from the gills of *Mulloidichthys vanicolensis* (Perciformes: Mullidae) off New Caledonia, with the proposal of *Volsellituba* n. gen. and *Pennulituba* n. gen. (Monogenea: Dactylogyridae). *Systematic Parasitology, 75*, 125–145.

Rohde, K., Hayward, C., & Heap, M. (1995). Aspects of the ecology of metazoan ectoparasites of marine fishes. *International Journal for Parasitology, 25*, 945–970.

Rohde, K., Hayward, C., Heap, M., & Gosper, D. (1994). A tropical assemblage of ectoparasites: gill and head parasites of *Lethrinus miniatus* (Teleostei, Lethrinidae). *International Journal for Parasitology, 24*, 1031–1053.

Sato, T. (1978). A synopsis of the sparoid fish genus *Lethrinus*, with the description of a new species. *The University Museum of Tokyo, Bulletin, 15*, 1–70.

Sun, Y., Kritsky, D. C., & Yang, T. (2007). Two new species of *Haliotrema* (Monogenoidea: Dactylogyridae) from *Acanthurus nigrofuscus* and *Acanthurus olivaceus* (Teleostei: Acanthuridae) in the South China Sea. *Journal of Parasitology, 93*, 781–786.

Wong, W. L., Brennan, G. P., Halton, D. W., Maule, A. G., & Lim, L. H. S. (2008). Secretory products of the haptoral reservoirs and peduncular glands in two species of *Bravohollisia* (Monogenea: Ancyrocephalidae). *Invertebrate Biology, 127*, 139–152.

Yamaguti, S. (1937). *Studies on the helminth fauna of Japan. Part 19. Fourteen new ectoparasitic trematodes of fishes*. Kyoto: S. Yamaguti, 28 pp.

Yamaguti, S. (1963). *Monogenea and Aspidocotylea. Systema helminthum. Volume IV*. New York: Interscience Publishers, 699 pp.

Young, P. C. (1968). Ten new species of *Haliotrema* Johnston and Tiegs, 1922 (Monogenoidea: Dactylogyridae) from Australian fishes and a revision of the genus. *Journal of Zoology, London, 154*, 41–75.

Zhang, J., Yang, T., Liu, L., & Ding, X. (2003). A list of monogeneans from Chinese marine fishes. *Systematic Parasitology, 54*, 111–130.

Zhang, J.-Y., Yang, T.-B., Liu, L., et al. (2001). *Monogeneans of Chinese marine fishes*. Beijing: Agriculture Press, pp. 79–175. (In Chinese, with English descriptions of new taxa).