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Descriptions of eight new species of *Ligophorus* Euzet & Suriano, 1977 (Monogenea: Ancyrocephalidae) from Red Sea mullets

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Abstract Eight new species of *Ligophorus* Euzet & Suriano, 1977 (Monogenea: Ancyrocephalidae) are described from two species of mullets from the Red Sea. *Ligophorus bykhowskyi* n. sp. and *L. zhangi* n. sp. from *Crenimugil crenilabris* (Forsskål) differ from other species of the genus in the structure of the male copulatory organ, which has a simple accessory piece and a wide copulatory tube that arises from a large, single-chambered, expanded base. *Ligophorus simpliciformis* n. sp., *L. bipartitus* n. sp., *L. campanulatus* n. sp., *L. mamaevi* n. sp., *L. lebedevi* n. sp. and *L. surianoae* n. sp. from *Liza carinata* (Valenciennes) are differentiated on the basis of the morphometrics of the hard parts of the haptor and male copulatory organ. The eight species represent the first records of species directly attributed to *Ligophorus* from the Red Sea. Measurements of the haptoral hard-parts and the male copulatory organ of the new species are analysed with the aid of Principal Component Analysis. Three morphological types of male copulatory organ, five types of anchor, and two types of ventral and three types of dorsal bars were distinguished among these species. *L. bykhowskyi* and *L. zhangi* from *C. crenilabris* have the same type of male copulatory organ and anchors. Those species from *Liza carinata* have only one common morphological character, a thick copulatory tube, but have two types of accessory piece, four types of anchors and three types of bars. All species of *Ligophorus* found on mullets in the Red Sea have an accessory piece without a distal bifurcation and thus differ from most species of this genus from other regions of the world's oceans.

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Introduction

To date 33 nominal species of *Ligophorus* Euzet & Suriano, 1977 are known to science and all of them have been described from the Atlantic and Pacific Oceans and their associated seas (Parona & Perugia, 1890; Hargis, 1955; Euzet & Suriano, 1977; Zhang & Ji, 1981; Euzet & Sanfilippo, 1983; Fernandez-Bargiela, 1987; Gusev, 1985; Hu & Li, 1992; Dmitrieva & Gerasev, 1996; Pan, 1999; Zhang et al., 2001; Miroshnichenko & Maltsev, 2004; Sarabeev & Balbuena, 2004; Sarabeev et al., 2005; Rubtsova et al., 2006; Dmitrieva et al., 2007; Rubtsova et al., 2007; Abdallah et al., 2009; Failla Siquier & Ostrowski de Núñez, 2009; Marcotegui & Martorelli, 2009).

Since the first paper on monogeneans in the Red Sea by Paperna (1965), there have been a small number of other papers on this group (e.g. Ramadan, 1983; Strona et al., 2005; Galli et al., 2007) and mentions of Red Sea material in broader studies (e.g. Paperna & Overstreet, 1981; Oliver & Paperna, 1984; Parukhin, 1989), but very few records from mugilid fishes. The present work represents the first report of species directly attributed to *Ligophorus* from the Red Sea. Eight new species are described below from two mugilid hosts, *Crenimugil crenilabris* (Forsskål) and *Liza carinata* (Valenciennes). Both of these fishes are essentially Indian Ocean forms and do not occur in the Mediterranean basin (Froese & Pauly, 2011), from where many species of *Ligophorus* have been described.

Materials and methods

Heads of three specimens of *Crenimugil crenilabris* and three specimens of *Liza carinata* caught in the Red Sea from the Ras Mohammed National Park (Nabq area) (27°45.150′N; 34°15.590′E) on October 21, 2005, were immediately fixed in 4% formalin and examined during 2006 in the following way. The excised gills were washed in distilled water, after which both the gills and the water were examined under a stereo-microscope at a magnification of ×30. All worms collected from the gills and water were soaked in distilled water over a period of 12–24 hours at 5°C until their body had become flexible. They were then mounted in glycerine jelly (prepared with 0.5 g of carbolic acid per 100 ml) and the mounts sealed with varnish.

Drawings and light micrographs were made using a Carl Zeiss Jena Amplival microscope, at magnifications of ×20 and ×100, fitted with phase-contrast optics, a drawing tube and an Olympus C180 digital camera.

In the descriptions, details of features which are the same in all species, such as the general form of the marginal hooks and composition of the male copulatory organ, are given for the first species but not repeated for the others. The measurement scheme employed follows Gerasev et al. (2010) (Fig. 1). Abbreviations of the linear measurements and angles determined are as follows: V, ventral anchor; D, dorsal anchor; VI, DI, inner length of anchors; VD, DD, length of distal part of anchors; VS, DS, length of anchor shafts; VP, DP, length of anchor points; VIP, DIP, inner length of proximal part of anchors; VOP, DOP, outer length of proximal part of anchors; VSR, DSR, span between roots of anchors; VB, ventral bar; DB, dorsal bar; VBH, DBH, bar heights; VBW, DBW, bar widths; VBP, height of anterior bar processes; VBS, span between anterior bar processes; MCO, male copulatory organ; CTL, length of copulatory tube; APL, length of MCO accessory piece; APW, width of MCO accessory piece; VL, length of vagina; V*I*, D*I*, angles between VOP and VIP and DOP and DIP, respectively; V*II*, D*II*, angles between VI, DI and VIP, DIP; V*III*, D*III*, angles between VP, DP and VS, DS; and V*IV*, D*IV*, angles between VS, DS and VIP, DIP (the latter is the angle of inclination of the distal part in relation to the proximal part of the anchor; Fig. 1). The sizes of the body are given for mounted and flattened but unruptured worms; width was measured at the ovarian level. All linear dimensions are given in micrometres, with the smallest division of the graticule used for measuring being 1 μm. The mean, standard error and range were used to describe the linear measurements. Angle dimensions are given in degrees and were calculated using the program Image J 1.38 only for those anchors for which all parts were clearly visible at one level of focus. Morphological analysis was carried out using Principal Component Analysis based on the correlation matrix (all measurements were ln-transformed) using the Statistica 6 for Windows software package.

Results

A total of 138 monogenean specimens were found. Their general internal morphology and haptoral armaments (Fig. 2) all conform to those described

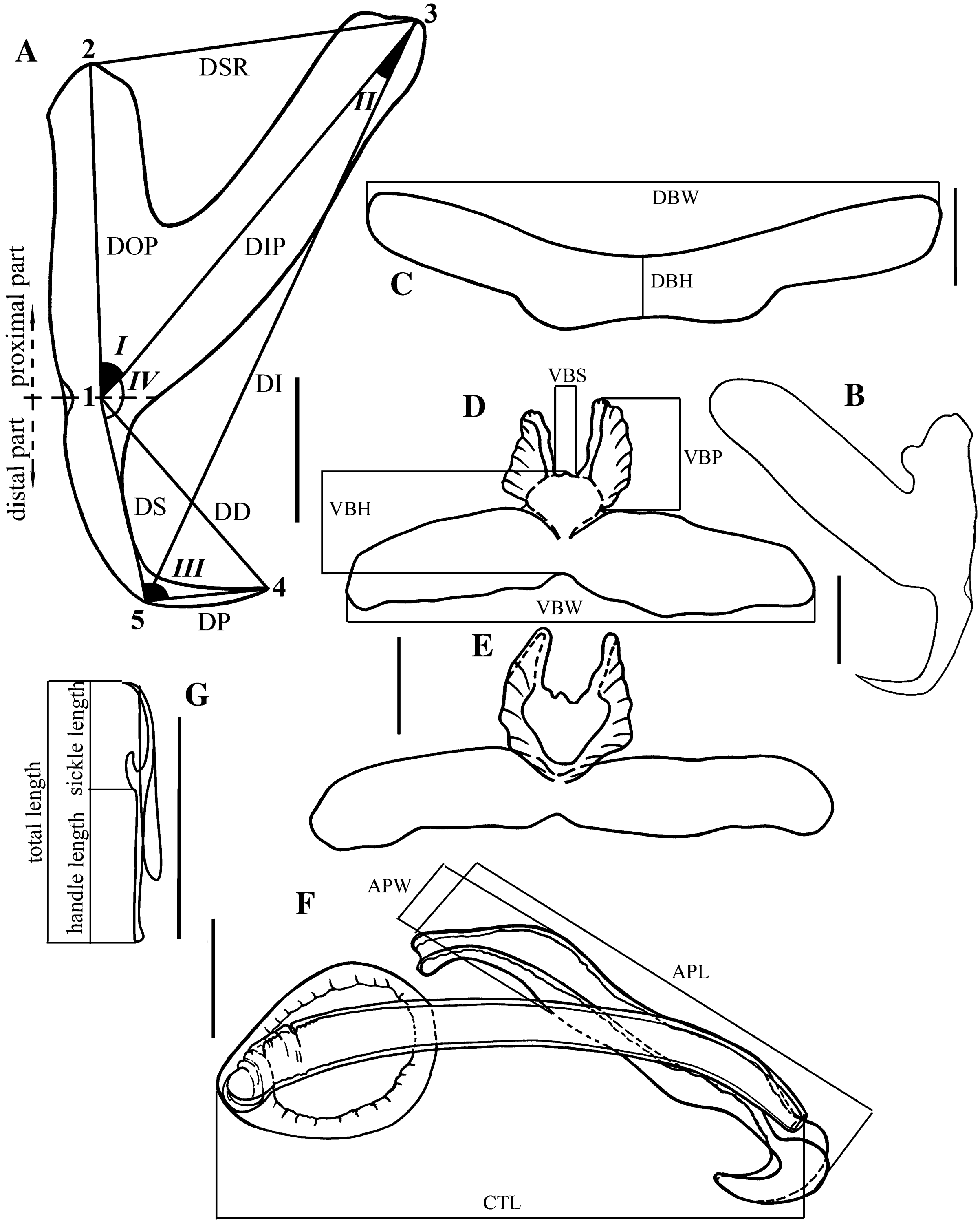


Fig. 1 The haptoral and copulatory hard-parts of *Ligophorus bykhowskyi* n. sp. from *Crenimugil crenilabris* in the Red Sea, showing the linear measurements and angles made for this and other *Ligophorus* spp. A, dorsal anchor; B, ventral anchor; C, dorsal bar; D, ventral bar (ventral view); E, ventral bar (dorsal view); F, male copulatory organ; G, marginal hook; 1–5, measurements; *I–IV* angles. *Abbreviations*: See 'Materials and methods'. *Scale-bars*: 10 µm

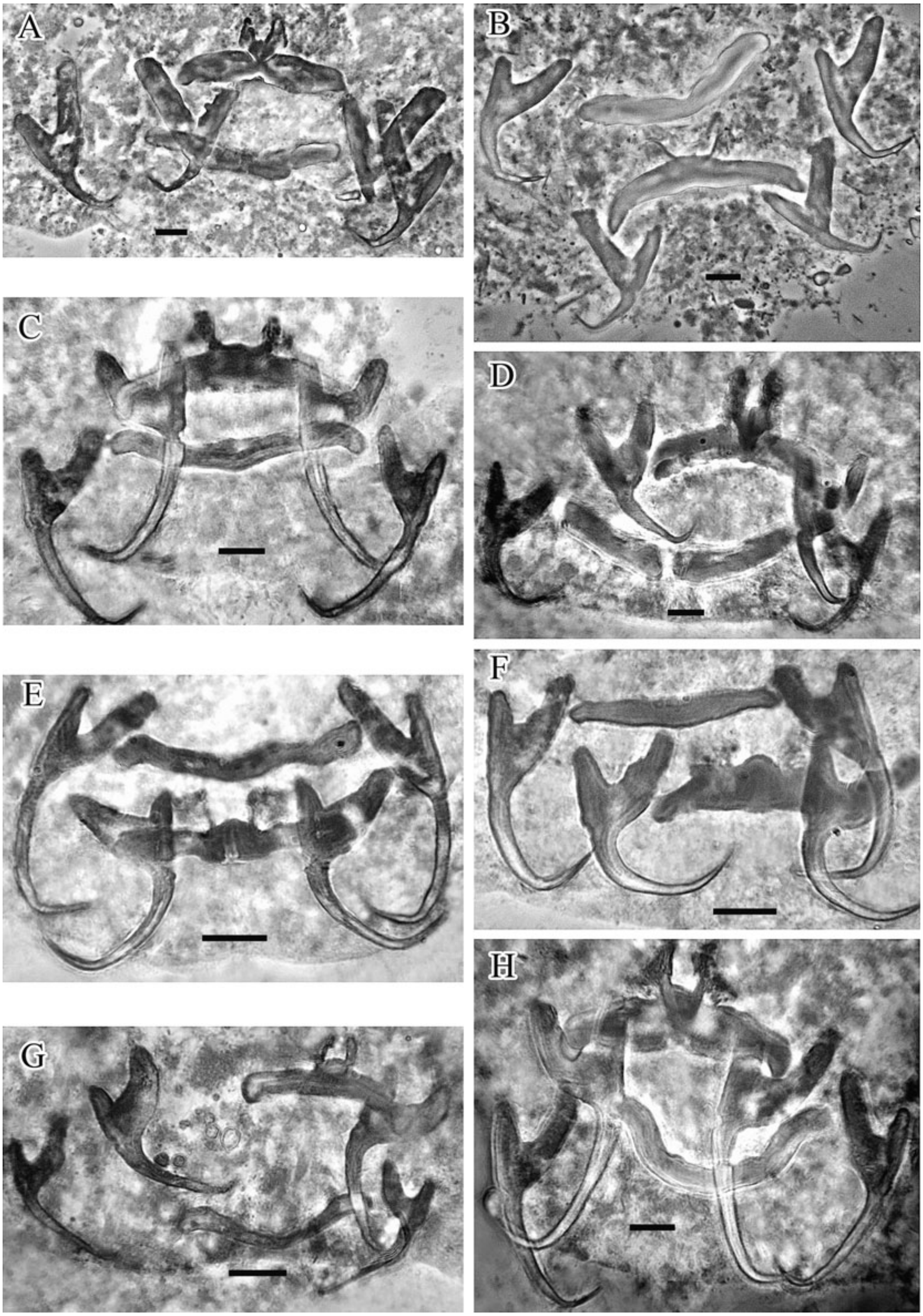


Fig. 2 Haptors of the eight new species of *Ligophorus* from the Red Sea: *L. bykhowskyi* n. sp. (A) and *L. zhangi* n. sp. (B) ex *Crenimugil crenilabris*, *L. simpliciformis* n. sp. (C), *L. bipartitus* n. sp. (D), *L. campanulatus* n. sp. (E), *L. mamaevi* n. sp. (F), *L. lebedevi* n. sp. (G) and *L. surianoae* n. sp. (H) ex *Liza carinata*. *Scale-bar*: 10 µm

by Euzet & Suriano (1977) for *Ligophorus* spp. Eight new species were identified among these worms.

Ligophorus bykhowskyi n. sp.

Type-host: *Crenimugil crenilabris* (Forsskål).
Type-locality: Ras Mohammed National Park, Red Sea (27°45.150′N; 34°15.590′E).
Site on host: Gills.
Type-specimens: 15 specimens. Holotype and 3 paratypes deposited in the Zoological Institute (ZIN) RAS, St Petersburg (holotype: No. 12234, paratypes: Nos 12235-12237). Additional paratypes are in the collections of the Natural History Museum, London (BMNH No. 2011.11.17.1-4), the Institute of Biology of the Southern Seas (IBSS), Sevastopol (No. 516/1-5) and the Museo di Storia Naturale di Milano, Italy (MSNM Pi 4911-12).
Etymology: The species is named for Dr Boris E. Bychowsky, the renowned Russian specialist on the Monogenea.

Description (Figs. 1–4; Table 1)

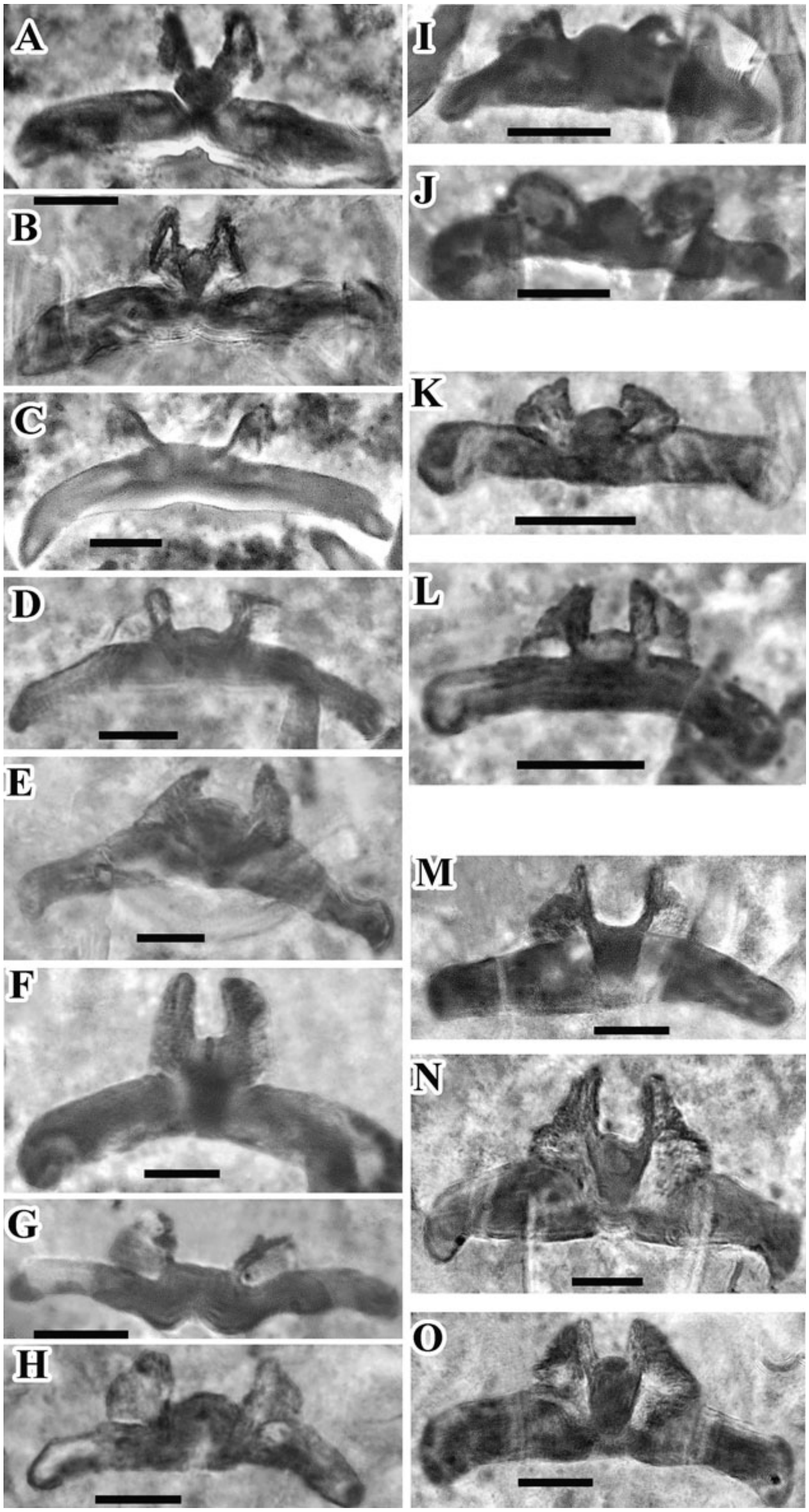
Large worms, with flattened body, 1,110 ± 18 (1,080–1,180) long, 377 ± 7 (350–405) wide. Measurements of haptoral and reproductive hard parts of this and other species are presented in Table 1. Both pairs of anchors equal in length (Table 1: VI *vs* DI) and similar in shape (Figs. 1, 2A); distal part shorter than proximal part (Table 1: VD *vs* VIP and DD *vs* DIP); distal and proximal parts form obtuse angle (Table 1: V*IV*, D*IV*); inner length of proximal part larger than outer (Table 1: VIP *vs* VOP and DIP *vs* DOP); distal part with straightened shaft; point almost at right angle (Table 1: V*III*, D*III*). Marginal hooks (Fig.1G), unhinged, consist of sickle formed by short base with upright small thumb and slightly curved blade, and straight shaft, as in all following species. Dorsal bar larger than ventral bar (Table 1: DBW *vs* VBW), slightly concave, with shallow, wide prominence in middle of posterior margin (Fig. 1C). Ventral bar with 2 long, digitiform anterior processes positioned closely together (Figs. 1D,E; 3A,B; Table 1: VBP, VBS); dorsal side of ventral bar (Figs. 1E, 3B) with 2 narrow, wing-shaped laminae attached to each anterior process and entirely surrounding lateral margins of median knoll, which protrudes beyond anterior margin of bar (Fig. 3A,B).

Male copulatory organ (MCO) of this and all following species consists of copulatory tube, with expanded base, and accessory piece (Fig. 4); latter not articulated with other parts of MCO. Expanded base single-chambered, 18 long, 15 wide, extending 1/3 of tube length (Figs. 1F, 4A). Copulatory tube very wide (Table 1: CTW). Accessory piece forms gutter which is U-shaped in cross-section, with distal end beak-shaped and turned-in so that accessory piece resembles shape of golf-club (Figs. 1F, 4B). Muscular sheath, which usually surrounds copulatory tube, and sclerotised flange of expanded base, to which it attaches, not distinguished in specimens examined. Vagina not observed.

Differential diagnosis

Ligophorus bykhowskyi n. sp. differs from all known representatives of the genus by possessing the widest copulatory tube (4 *vs* 1–2 µm in other species). This new species most closely resembles *L. leporinus* (Zhang & Ji, 1981), described from *Mugil cephalus* L. in the East China Sea (Zhang & Ji, 1981), in the shape of the haptoral hardparts and MCO, but differs from it in: (1) the greater lengths of the ventral anchor roots (inner root length 20–27 *vs* 10–12 and the outer root length 10–14 *vs* 7–10 µm) and the ratio of the inner in relation to the outer root lengths which is 2 in *L. bykhowskyi* and ≤1.5 in *L. leporinus*; (2) the shorter copulatory tube (CTL 60–65 *vs* 120–151 µm); (3) the greater length of the MCO accessory piece (APL 32–42 *vs* 17–27 µm); (4) the ratio of the copulatory tube length to the length of the accessory piece, which is 1.2–1.5 in *L. bykhowskyi vs* 5–7 in *L. leporinus*; (5) the greater expansion of the base of the MCO, which equals 1/3 of the tube length in *L. bykhowskyi* but is <1/10 in *L. leporinus* (Fig. 1F *vs* fig. 2 of Zhang & Ji, 1981); and (7) the shape of the accessory piece, which possesses a distal extremity distinctly turned in, as opposed to lacking this curvature in *L. leporinus* (Fig. 1F *vs* fig. 2.3 of Zhang & Ji, 1981) (comparative data from Zhang & Ji, 1981).

Ligophorus ellochelon Zhang, Yang & Liu, 2001, which infects *Liza* spp. in the South China Sea, *Ligophorus chongmingensis* Hu & Li, 1992, a parasite of *Mugil cephalus* L. in the Yellow Sea, and *L. kaohsianghsieni* (Gusev, 1962), from *Liza haematocheilus*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◀**Fig. 3** Ventral bars of *Ligophorus bykhowskyi* n. sp. (A, ventral view; B, dorsal view) and *L. zhangi* (C, ventral view) ex *Crenimugil crenilabris* and *L. simpliciformis* n. sp. (D, ventral view; E, dorsal view), *L. bipartitus* n. sp. (F, dorsal view), *L. campanulatus* n. sp. (G, ventral view; H, dorsal view), *L. mamaevi* n. sp. (I, ventral view; J, dorsal view), *L. lebedevi* n. sp. (K, ventral view; L, dorsal view) and *L. surianoae* n. sp. (M, ventral view; N, O, dorsal view) ex *Liza carinata* from the Red Sea. *Scale-bar*: 10 μm

(Temminck & Schlegel) in the Sea of Japan, are similar to *Ligophorus bykhowskyi* in the shape of the anchors. However, the new species differs from *L. ellochelon* in: (1) the similar lengths of both pairs of anchors, as opposed to being of different lengths in *L. ellochelon*; (2) the greater length of the ventral anchors (VI 37–42 *vs* 33–35 μm); (3) the shorter length of the dorsal anchors (DI 38–46 *vs* 50–55 μm); (4) the shorter points of all anchors (VP 6–7, DP 9–10 *vs* 8–12, 20–24 μm); (5) the well-pronounced and long anterior processes of the ventral bar *vs* feebly distinguished in *L. ellochelon*; (6) the size of the MCO, which has a considerably shorter tube and accessory piece (CTL 60–65 *vs* 135–148, APL 32–42 *vs* 59–64 μm); and (7) the shape of the MCO accessory piece which lacks processes, as opposed to having three distal processes in *L. ellochelon* (Fig. 1F *vs* fig.10-70.2 of Zhang et al., 2001) (comparative data from Zhang et al., 2001). In relation to *L. chongmingensis* and *L. kaohsianghsieni*, the new species can be distinguished as follows: (1) the copulatory tube is shorter (60–65 *vs* 118–236 in *L. chongmingensis* and 250–265 μm in *L. kaohsianghsieni*); (2) the ratio of the length of the copulatory tube to the length of the accessory piece is considerably smaller (1.2–1.5 *vs* 5–6 in *L. chongmingensis* and 4–6 in *L. kaohsianghsieni*); and (3) the distal end of the accessory piece is beak-shaped and turned-in in *L. bykhowskyi*, whereas it is bifurcate in the other two species (Fig. 1F *vs* fig. 1.3 of Hu & Li, 1992, and Fig. 2e of Dmitrieva, 1996) (comparative data from Hu & Li, 1992, and Dmitrieva, 1996, respectively).

Ligophorus zhangi n. sp.

Type-host: *Crenimugil crenilabris* (Forsskål).
Type-locality: Ras Mohammed National Park, Red Sea (27°45.150′N; 34°15.590′E).
Site on host: Gills.
Type-specimens: 3 specimens. Holotype and 2 paratypes deposited in the ZIN RAS (holotype: No. 12238, paratypes: Nos 12239, 12240).
Etymology: The species is named for Prof. Zhang Jiangying, the well-known Chinese monogenean specialist and author of several species of *Ligophorus*.

Description (Figs. 2B, 3C, 4C, 5; Table 1)

Body flattened, 650 long, 370 wide (measureable in single specimen). Both pairs of anchors equal in length (Table 1: VI *vs* DI) and similar in shape (Figs. 2B, 5); distal part significantly shorter than proximal part (Table 1: VD *vs* VIP and DD *vs* DIP); distal and proximal parts form obtuse angle (Table 1: V*IV*, D*IV*); inner length of proximal part greater than outer length (Table 1: VIP *vs* VOP and DIP *vs* DOP); distal part arcuate, with length greater than shaft length (Table 1: VD *vs* VS and DD *vs* DS); point at slightly obtuse angle (Table 1: V*III*, D*III*). Bars equal in length (Table 1: DBW *vs* VBW). Dorsal bar equal in height along its entire width, bowed, with lateral extremities slightly down-turned (Fig. 5C). Ventral bar with 2 long, digitiform anterior processes set wide apart (Figs. 3C, 5D; Table 1: VBP, VBS). Dorsal side of ventral bar not clearly seen.

Copulatory tube wide (Figs. 4C, 5E; Table 1: CTW); basal expansion 14 long, 8 wide, single-chambered. Accessory piece forms gutter, U-shaped in cross-section, with 2 symmetrical T-shaped projections situated at its proximal end (Fig. 5E). Muscular sheath, which usually surrounds copulatory tube, and vagina not seen.

Differential diagnosis

Ligophorus zhangi n. sp. is very similar to *L. bykhowskyi* n. sp. in the shape of the anchors and MCO but differs by: (1) the generally smaller dimensions of the anchors (Table 1: VI, VIP, VSR, DI, DIP, DOP), but (2) larger point lengths (Table 1: VP, DP); (3) a tighter curvature of the distal part of the both anchors, resulting in smaller angles (Table 1: V*IV*, D*IV*); (4) the shape of the ventral bar, which is equal in height along its entire width, and has shorter anterior processes which are set wider apart, as opposed to the bar having its greatest height in the middle and longer and more closely positioned processes in *L. bykhowskyi* (Fig. 1D,E *vs* Fig. 5D; Table 1: VP, VS); (5) the

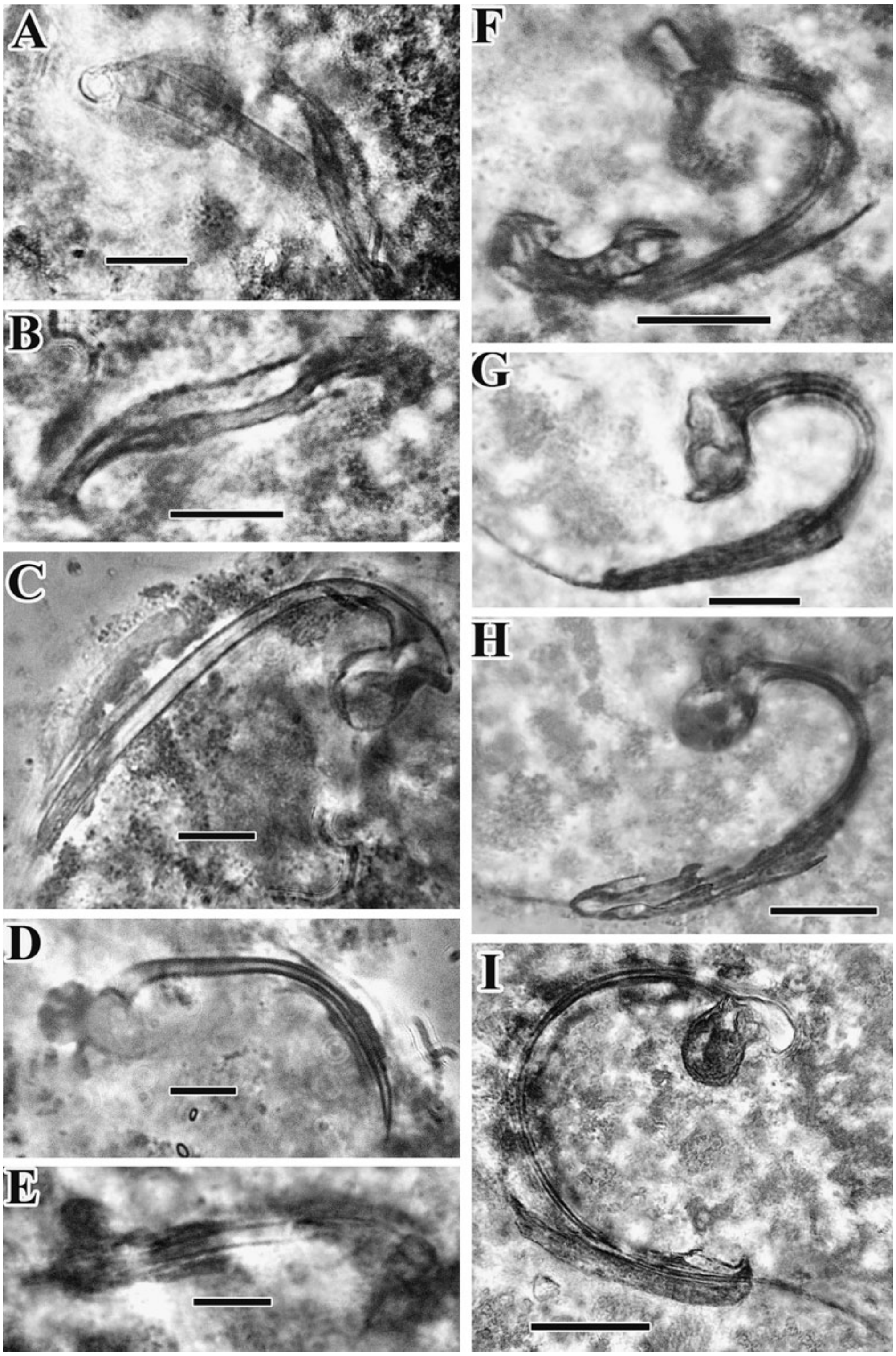

Fig. 4 Copulatory organs of *Ligophorus bykhowskyi* n. sp. (A, MCO tube; B, accessory piece) and *L. zhangi* n. sp. (C) ex *Crenimugil crenilabris* and *L. simpliciformis* n. sp. (D), *L. bipartitus* n. sp. (E), *L. campanulatus* n. sp. (F), *L. mamaevi* n. sp. (G), *L. lebedevi* n. sp. (H) and *L. surianoae* n. sp. (I) ex *Liza carinata* from the Red Sea. *Scale-bar*: 10 μm

Table 1 Linear dimensions, as the range and mean ± standard error, of the haptoral and copulatory hard-parts and angles between different parts of the anchors of eight new *Ligophorus* spp. from the Red Sea

New species No. of specimens	*bykhowskyi* 12	*zhangi* 2	*simpliciformis* 20	*bipartitus* 6	*campanulatus* 24	*mamaevi* 8	*lebedevi* 8	*surianoae* 12
Ventral anchors								
VI*	37–42 40 ± 0.8	32, 35	39–42 40 ± 0.3	31–33 32 ± 0.4	28–33 30 ± 0.3	25–28 26 ± 0.3	26–28 27 ± 0.4	51–56 52.5 ± 0.4
VD	14–15 14 ± 0.2	14, 15	26–27 26.5 ± 0.1	17–18 17.5 ± 0.3	20–23 22 ± 0.2	19–21 19.5 ± 0.2	17–19 18.5 ± 0.3	33–34 33.5 ± 0.1
VS	11–13 12 ± 0.3	12, 13	25–26 25.5 ± 0.1	16–17 16.5 ± 0.3	19–21 20 ± 0.1	16–18 16.5 ± 0.2	17–19 18 ± 0.2	32–34 33 ± 0.2
VP	6–7 7 ± 0.2	8	8	5–6 5.3 ± 0.3	9	9	3	9
VIP	27–36 33 ± 1	25, 26	21–24 22.5 ± 0.3	20–22 21 ± 0.3	18–20 19 ± 0.2	17–19 18.5 ± 0.2	14–16 15.5 ± 0.3	27–34 28.5 ± 0.5
VOP	19–26 22 ± 0.8	19, 21	17–19 18.5 ± 0.2	18–20 19 ± 0.4	12–15 13 ± 0.2	13–14 13.5 ± 0.2	9–11 10 ± 0.2	24–30 25.5 ± 0.4
VSR	20–28 24 ± 1.5	16, 19	13–15 14 ± 0.2	14–17 16 ± 0.6	12–15 14 ± 0.2	13–15 14 ± 0.3	9–10 10 ± 0.1	15–19 17.5 ± 0.3
Angles								
V*I*	48–50	50–54	45–47	40–43	53–58	48–50	35–38	42–44
V*II*	14–16	24–25	35–38	25–27	43–46	37–39	35–39	31–34
V*III*	95–97	95–96	90–92	89–91	86–90	95–97	95–97	87–89
V*IV*	117–120	103–107	107–110	120–123	92–95	92–95	108–111	116–118
Dorsal anchor								
DI	38–46 43 ± 0.7	34, 35	36–40 38 ± 0.3	28–30 29 ± 0.4	38–42 40 ± 0.3	32–35 33 ± 0.6	22–24 23 ± 0.4	46–50 47 ± 0.3
DD	17–19 18 ± 0.3	18, 19	24–25 24.5 ± 0.1	15–17 16 ± 0.5	22–23 22 ± 0.1	19–21 20 ± 0.2	16–17 16.5 ± 0.2	27–29 27.5 ± 0.2
DS	13–15 14 ± 0.2	13, 14	23–25 24 ± 0.2	14–16 15 ± 0.5	21–23 22 ± 0.1	17–20 19 ± 0.4	16–17 16.5 ± 0.2	26–29 27 ± 0.2
DP	9–10 10 ± 0.1	11, 12	7	6–7 6 ± 0.2	8	10	1	7–8 8 ± 0.1
DIP	30–36 33 ± 0.5	25, 27	20–23 21 ± 0.3	20–21 20.5 ± 0.2	21–25 24 ± 0.2	17–19 18 ± 0.2	11–13 12 ± 0.3	25–28 27 ± 0.2
DOP	20–24 22 ± 0.5	17, 18	14–16 15.5 ± 0.2	17–18 17.5 ± 0.2	15–19 17 ± 0.3	13–15 14 ± 0.2	7–10 8.5 ± 0.4	18–20 18.5 ± 0.2
DSR	18–22 20 ± 0.5	17, 18	11–13 12 ± 0.2	13–15 13.5 ± 0.4	11–14 12 ± 0.2	10–11 10 ± 0.15	7–8 7 ± 0.2	14–16 14.5 ± 0.2
Angles								
D*I*	40–43	44–45	37–40	48–50	30–35	29–32	43–46	33–37
D*II*	14–16	20–21	35–37	28–30	24–28	22–26	44–46	28–32
D*III*	90–92	94–96	87–90	95–97	83–84	92–95	85–87	93–94
D*IV*	129–132	120–122	117–120	111–112	126–128	132–135	105–107	121–124
Marginal hooks								
Total length	12	12	13	13	12–13 13 ± 0.1	12	13	13–14 13 ± 0.1

Table 1 continued

New species No. of specimens	*bykhowskyi* 12	*zhangi* 2	*simpliciformis* 20	*bipartitus* 6	*campanulatus* 24	*mamaevi* 8	*lebedevi* 8	*surianoae* 12
Sickle length	6	6	6	6	6	6	6	6
Handle length	6	6	7	7	6–7 7 ± 0.1	6	7	7–8 7 ± 0.1
Ventral bar								
VBH	7–9 8 ± 0.3	8, 9	7–12 10 ± 0.4	10–13 11.5 ± 0.6	6–8 7 ± 0.2	5–11 8 ± 0.8	4–6 5 ± 0.4	10–15 12.5 ± 0.4
VBW	45–52 49.5 ± 0.6	50, 53	45–60 48 ± 1.5	45–52 48.5 ± 1.3	33–42 37 ± 0.5	32–41 36 ± 1.4	27–31 29 ± 0.6	47–53 50 ± 0.4
VBP	9 –13 10.5 ± 0.4	6, 8	6–8 6.5 ± 0.2	10–12 11 ± 0.3	5–8 6 ± 0.2	4–5 4.5 ± 0.2	4–5 4.5 ± 0.2	9–11 10 ± 0.2
VBS	2–3 2 ± 0.2	8, 9	5–8 6.5 ± 0.3	2–5 3 ± 0.4	4–7 6 ± 0.15	6–8 7 ± 0.2	3–5 3.5 ± 0.3	4–7 5 ± 0.3
Dorsal bar								
DBH	6–8 7 ± 0.2	5, 6	5–6 5.5 ± 0.1	6–8 7 ± 0.3	4–6 4 ± 0.1	3–6 5 ± 0.35	2–3 2.5 ± 0.2	5–7 5.5 ± 0.2
DBW	50–60 56 ± 0.9	50, 52	43–57 47.5 ± 1.2	53–62 59 ± 1.3	32–44 38 ± 1	30–34 32 ± 0.5	28–33 31 ± 0.7	48–68 56 ± 1.5
MCO								
CTL	60–65 63 ± 0.7	50, 52	40–45 43 ± 0.5	38–45 42 ± 1.7	40–45 43 ± 0.3	80–90 85 ± 1.7	52–54 53 ± 0.4	95–103 99 ± 0.6
CTW	4	3	2	2	1	1	1	1
APL	32–42 37.5 ± 1	30, 32	20–23 21.5 ± 0.5	23–26 24.5 ± 0.6	28–32 30 ± 0.3	25–30 27 ± 1.7	22–25 23 ± 0.7	32–38 34 ± 0.5
APW	5–6 5.5 ± 0.2	6	3–4 3 ± 0.1	4	4–6 5 ± 0.1	4	3–4 3 ± 0.2	5–8 6.5 ± 0.3
Vagina								
VL	–	–	–	–	34–38 36 ± 1.15	30 + ?	38–40 39 ± 0.7	42–47 44 ± 0.7

* *Abbreviations*: See 'Materials and methods'

smaller copulatory tube (Table 1: CTL, CTW) and smaller expanded base (14 × 8 *vs* 18 × 15 µm); and (6) the shape of the accessory piece, the distal end of which is straight rather than being beak-shaped and turned-in as in *L. bykhowskyi* (Fig. 1F *vs* Fig. 5E).

Compared with *L. leporinus* from Chinese waters, which resembles *L. zhangi* in the shape of the anchors and the MCO accessory piece, the new species differs in that: (1) the dorsal anchor has a considerably longer point (DP 11–12 *vs* 5–8 µm); (2) both bars are smaller in terms of width (VBW 50–53, DBW 50–52 *vs* 56–61, 69–78 µm) and height (VBH + VBP 14–17 *vs* 24–29 and DBH 5–6 *vs* 6–15 µm); (3) the anterior processes of the ventral bar are set further apart (Fig. 5D *vs* Fig. 2 of Zhang & Ji, 1981); (4) the copulatory tube is significantly shorter (CTL 50–52 *vs* 120–151 µm); and (5) the MCO accessory piece is longer (APL 30–32 *vs* 17–27 µm) (comparative data from Zhang & Ji, 1981).

Among the other species of *Ligophorus*, *L. ellochelon*, *L. chongmingensis* and *L. kaohsianghsieni*, parasites of mullets in the NE Pacific region, appear similar to the new species in the shape of the anchors. However, *L. zhangi* can be distinguished from the former by: (1) the two pairs of anchors being of equal length, rather than the dorsal anchors being

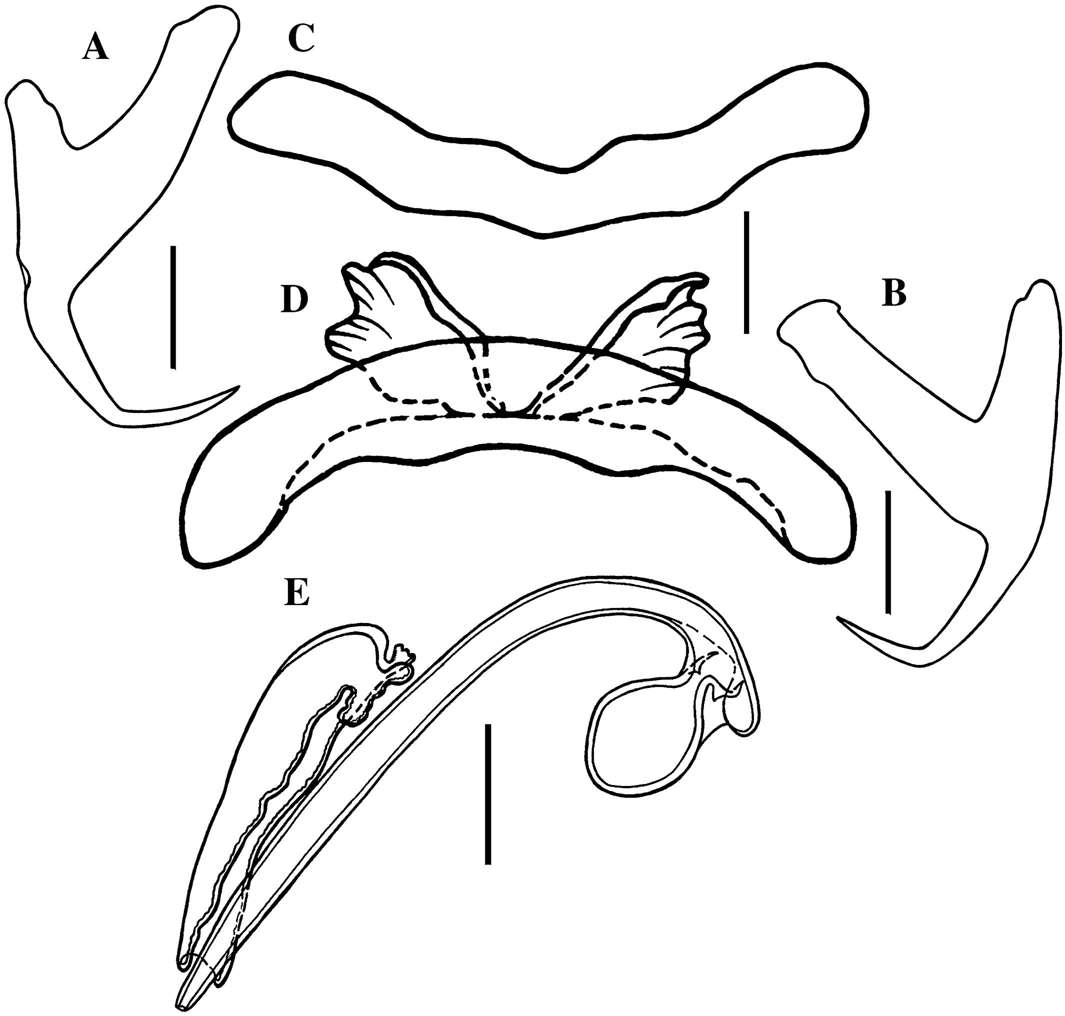

Fig. 5 *Ligophorus zhangi* n. sp. from *Crenimugil crenilabris* in the Red Sea. A, dorsal anchor; B, ventral anchor; C, dorsal bar; D, ventral bar (ventral view); E, male copulatory organ. *Scale-bars*: 10 μm

significantly longer, as in *L. ellochelon*; (2) smaller dorsal anchors (DI 34–35, DP 11–12 *vs* 50–55, 20–24 μm); (3) a dorsal bar with a smaller width (DBW 50–52 *vs* 69–76 μm); (4) a ventral bar with long, distinct rather than indistinct anterior processes, as in *L. ellochelon* (Fig. 5D *vs* fig. 10-70.1 of Zhang et al., 2001); (5) a shorter copulatory tube (CTL 50–52 *vs* 135–148 μm) and accessory piece (APL 30–32 *vs* 59–64 μm); and (6) the absence *vs* presence in *L. ellochelon* of distal processes on the MCO accessory piece (Fig. 5E *vs* fig. 10-70.2 of Zhang et al., 2001) (comparative data from Zhang et al., 2001). From *L. chongmingensis* and *L. kaohsianghsieni*, the new species differs in that: (1) the ventral bar has the same height along its entire width and the anterior processes are set wide apart, as opposed to a bar with the greatest height in the middle and more closely positioned processes in both compared species (Fig. 5D *vs* fig. 1.2 of Hu & Li, 1992, and Fig. 2a of Dmitrieva, 1996); (2) the copulatory tube is significantly shorter (CTL 50–52 *vs* 118–236 μm in *L. chongmingensis* and 250–289 in *L. kaohsianghsieni*); and (3) the MCO accessory piece lacks distal processes rather than possessing a distal bifurcation as in *L. chongmingensis* and *L. kaohsianghsieni* (Fig. 5E *vs* fig. 1.3 of Hu & Li, 1992, and Fig. 2e of Dmitrieva, 1996) (comparative data from of Hu & Li, 1992, and Dmitrieva, 1996).

Ligophorus simpliciformis **n. sp.**

Type-host: *Liza carinata* (Valenciennes).
Type-locality: Ras Mohammed National Park, Red Sea (27°45.150′N; 34°15.590′E).
Site on host: Gills.
Type-specimens: 33 specimens Holotype and 8 paratypes deposited in the ZIN RAS (holotype: No. 12241, paratypes: Nos 12242-12249). Additional paratypes are in the BMNH (No. 2011.11.17.5-11), IBSS (No. 517/1-10) and MSNM (No. Pi 4913-18).
Etymology: The species name refers to the simple shape of the MCO accessory piece; from the Latin *simplex*, simple and *forma*, shape.

Description (Figs. 2C, 3D,E, 4D, 6; Table 1)

Body flattened, 665 ± 14 (610–770) long, 220 ± 7 (190–260) wide. Both pairs of anchors elongate, similar in size and shape (Figs. 2C, 6); distal parts significantly longer than proximal parts (Table 1: VD *vs* VIP and DD *vs* DIP); distal and proximal parts form obtuse angle (Table 1: V*IV*, D*IV*); inner length of proximal part greater than outer (Table 1: VIP *vs* VOP and DIP *vs* DOP); distal part with long, straight shaft and short point, with latter at right angle (Table 1: V*III*, D*III*). Bars equal in length (Table 1: DBW *vs* VBW). Dorsal bar equal in height along its entire width, slightly bowed, with down-turned ends (Fig. 6C). Ventral bar with 2 long, digitiform anterior processes set quite far apart (Figs. 3D,E, 6D,E; Table 1: VBP, VBS); dorsal side with 2 wide wing-shaped laminae attached to each anterior process; median knoll, with flat or occasionally prominent anterior margin, situated between laminae (Fig. 3E).

Copulatory tube relatively wide, short (Table 1: CTL, CTW); expanded base bipartite. Accessory piece very simple, with straight, flattened gutter resembling elongate plate with slightly turned-in or thickened walls (Figs. 4D, 6F). Muscular sheath surrounds copulatory tube and attaches to proximal end of accessory piece.

Entire vagina not observed, but vaginal opening funnel-shaped (Fig. 6G).

Differential diagnosis

Ligophorus simpliciformis n. sp. is unique among the known species of the genus in having the simplest MCO accessory piece, i.e. it is in the form of a straight, flattened gutter without any accessory structures. In other species the accessory piece differs in terms of shape, size and the disposition of various processes, projections or windings.

This new species differs from *Ligophorus bykhowskyi* n. sp. and *L. zhangi* n. sp. in that: (1) the anchor shafts are longer (Table 1: VS, DS); (2) the inner lengths of the proximal parts of the anchors are shorter (Table 1: VIP, DIP); (3) the distal parts of both anchors are longer rather than shorter than their proximal parts (VIP/VD 0.8 *vs* 1.8 and 1.4, and DIP/DD 0.8 *vs* 2.3 and 1.8, in *L. bykhowskyi* and *L. zhangi*, respectively); (4) the distance between the anchor roots is smaller (Table 1: VSR, DSR); (5) the copulatory tube is thinner and shorter (Table 1: CTL, CTW); and (6) the accessory piece is also shorter (Table 1: APL).

Among the species known from other hosts and regions, *L. simpliciformis* has similarities in the shape of the haptoral hard-parts with species infecting *Liza* spp. in the Mediterranean and Black Seas, namely *Ligophorus vanbenedeni* Euzet & Suriano, 1977, *L. acuminatus* Euzet & Suriano, 1977, *L. heteronchus* Euzet & Suriano, 1977, *L. minimus* Euzet & Suriano, 1977, *L. imitans* Euzet & Suriano, 1977, *L. macrocolpos* Euzet & Suriano, 1977, *L. parvicirrus* Euzet & Sanfilippo, 1983 and *L. euzeti* Dmitrieva & Gerasev, 1996. From all of these species, *L. simpliciformis* differs in having a shorter (40–45 *vs* >60 µm for all the other species) but wider (2 *vs* 1 µm for all the other species except *L. parvicirrus*) copulatory tube. Moreover, *L. simpliciformis* can also be distinguished from *L. vanbenedeni*, *L. heteronchus*, *L. minimus*, *L. imitans*, *L. parvicirrus* and *L. euzeti* by having larger bars (VBW 45–60, DBW 45–57 *vs* <42 µm), and additionally from *L. heteronchus*, *L. minimus* and *L. parvicirrus*, plus *L. macrocolpos*, by having shorter anchors (VI 31–33, DI 28–30 *vs* >36 and 33 µm, respectively). It can also be differentiated from *L. parvicirrus* by having a narrower copulatory tube (2 *vs* 3.5 µm) (comparative data from Euzet & Suriano, 1977, Euzet & Sanfilippo, 1983, and Dmitrieva & Gerasev, 1996).

Ligophorus bipartitus **n. sp.**

Type-host: *Liza carinata* (Valenciennes).
Type-locality: Ras Mohammed National Park, Red Sea (27°45.150′N; 34°15.590′E).

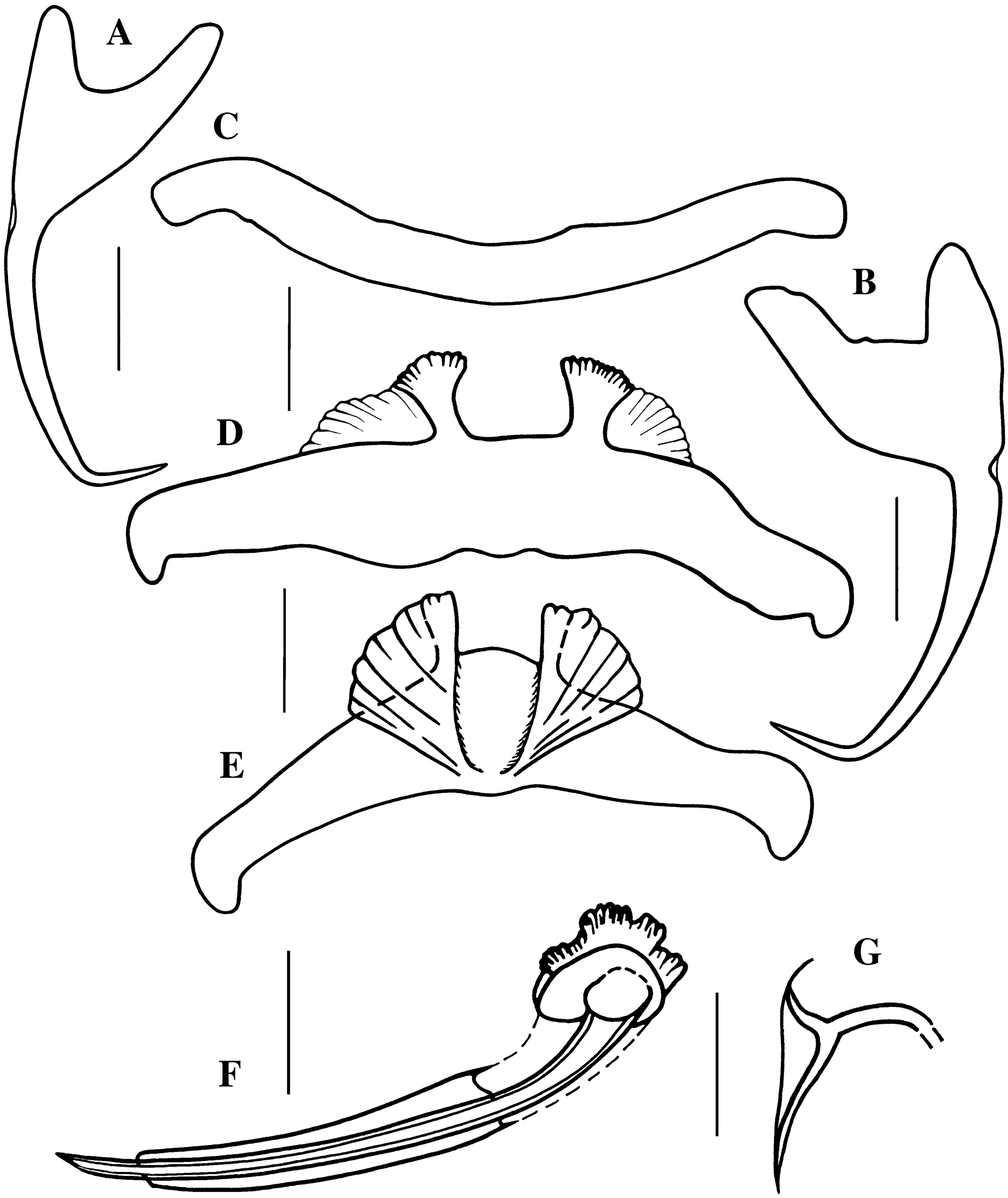

Fig. 6 *Ligophorus simpliciformis* n. sp. ex *Liza carinata* from the Red Sea. A, dorsal anchor; B, ventral anchor; C, dorsal bar; D, ventral bar (ventral view); E, ventral bar (dorsal view); F, copulatory organ; G, vaginal opening. *Scale-bars*: 10 µm

Site on host: Gills.
Type-specimens: 6 specimens. Holotype and 2 paratypes deposited in the ZIN RAS (holotype: No. 12250, paratypes: Nos 12251, 12252). Additional paratypes are in the BMNH (No. 2011.11.17.12-13) and the IBSS (No 518/1).
Etymology: The species name is adjectival and reflects the shape of the dorsal bar, which appears constricted medially into two parts; from the Latin *bi-* + partitus, meaning divided into two parts.

Description (Figs. 2D, 3F, 4E, 7, 8A; Table 1)

Large worms; body flattened, 1,120 ± 21 (1,000–1,150) long, 326 ± 8 (300–350) wide. Dorsal and ventral anchors of similar shape (Figs. 2D, 7);

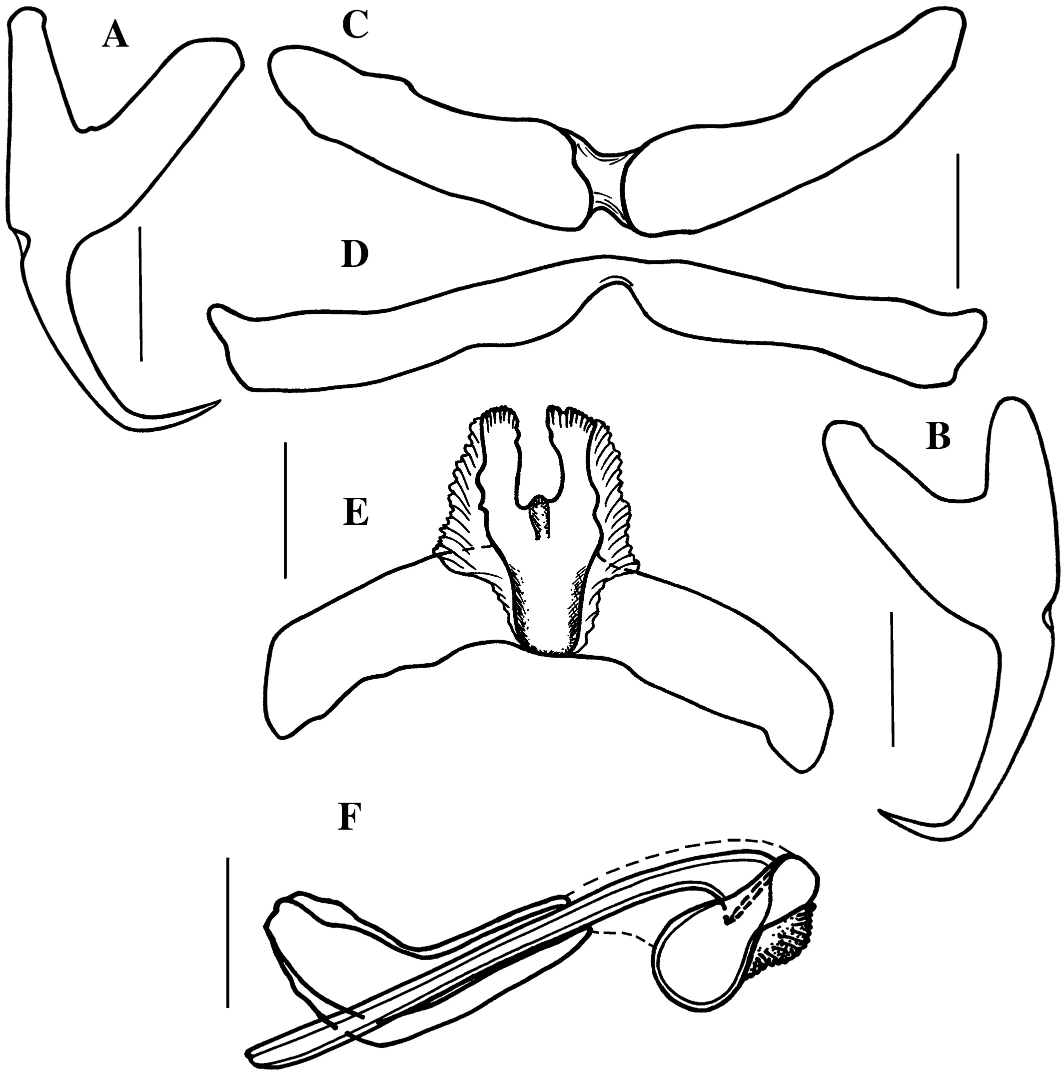

Fig. 7 *Ligophorus bipartitus* n. sp. ex *Liza carinata* from the Red Sea. A, dorsal anchor; B, ventral anchor; C,D, dorsal bar; E, ventral bar (ventral view); F, male copulatory organ. *Scale-bars*: 10 μm

proximal part longer than distal part (Table 1: VIP *vs* VD and DIP *vs* DD); distal and proximal parts form obtuse angle (Table 1: V*IV*, D*IV*); inner length of proximal part slightly greater than outer length (Table 1: VIP *vs* VOP and DIP *vs* DOP); short point almost at right angle (Table 1: V*III*, D*III*). Dorsal anchors have slightly smaller dimensions than ventral anchors (Table 1). Dorsal bar longer than ventral bar (Table 1: DBW *vs* VBW), wide V-shaped, with deep constriction in middle, almost dividing it into 2 parts (Figs. 7C,D, 8A). Ventral bar with 2 long, digitiform anterior processes positioned closely together (Figs. 3F, 7E; Table 1: VBP, VBS); dorsal side of ventral bar with 2 narrow wing-shaped laminae, each attached laterally to anterior process; narrow median knoll, with small, digitiform process arising from its middle close to anterior margin between laminae.

Copulatory tube short and rather wide (Table 1: CTL, CTW); expanded base bipartite. Accessory piece forms shallow, boomerang-shaped gutter, U-shaped in cross-section, without processes (Figs. 4E, 7E). Neither muscular sheath surrounding copulatory tube nor vaginal armature observed.

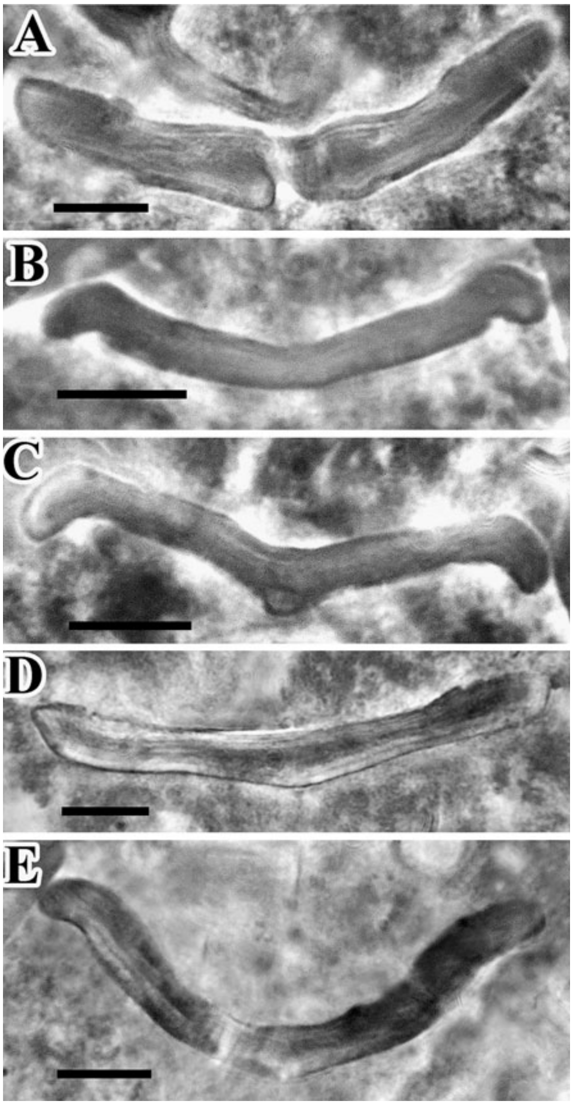

Fig. 8 Dorsal bars of *Ligophorus bipartitus* n. sp. (A), *L. campanulatus* n. sp. (B,C) and *L. surianoae* n. sp. (D,E) ex *Liza carinata* from the Red Sea. *Scale-bars*: 10 µm

Differential diagnosis

With the exception of *L. fluviatilis* (Bychowsky, 1949) n. comb. (see below), *L. bipartitus* n. sp. differs from all known representatives of *Ligophorus* in the shape of the dorsal bar, which has a well-marked constriction in the middle.

This new species can readily be distinguished from the two species described above from *Crenimugil crenilabris* by having an MCO with: (1) a shorter and narrower copulatory tube (Table 1: CTL, CTW); and (2) a shorter accessory piece (Table 1: APL).

Moreover, *L. bipartitus* differs from *L. simpliciformis* n. sp. described from the same host in: (1) the shape of the anchors, the distal part of which is shorter than the proximal part rather than being longer as in *L. simpliciformis* (Table 1: VD *vs* VIP and DD *vs* DIP); and (2) the size of the anchors, which have a shorter inner length and distal part (Table 1: VI, VD, VS, VP and DI, DD, DS, DP); (3) the anterior processes of the ventral bar, which are longer (Table 1: VBP); and (4) the shape of the MCO accessory piece, the distal end of which is boomerang-shaped as opposed to being straight in *L. simpliciformis* (Fig. 6F *vs* Fig. 7F).

Compared to *L. fluviatilis*, a parasite of *Liza abu* in Iran and the most closely related species based on the morphology of the haptoral hard-parts, *Ligophorus bipartitus* can be distinguished by: (1) having larger bars (VBW 48–52, DBW 53–62 *vs* 39–42, 46–49 µm, respectively); (2) having a shorter copulatory tube (38–40 *vs* 50 µm); and (3) the shape of the MCO accessory piece which lacks processes rather than being terminally bifurcate as in *L. fluviatilis* (comparative data from Bychowsky, 1949).

Ligophorus campanulatus n. sp.

Type-host: *Liza carinata* (Valenciennes).
Type-locality: Ras Mohammed National Park, Red Sea (27°45.150′N; 34°15.590′E).
Site on host: Gills.
Type-specimens: 52 specimens. Holotype and 15 paratypes deposited in the ZIN RAS (holotype: No. 12253, paratypes: Nos 12254-12268). Additional paratypes are in the BMNH (No. 2011.11.17.14-23), the IBSS (No. 519/1-16) and the MSNM (No. Pi 4919-28).
Etymology: The species name is adjectival and refers to the shape of the vagina, the distal part of which looks like a bellflower corolla, from the Latin *campanula*, a little bell.

Description (Figs. 2E, 3G,H, 4F, 8B,C, 9, 10A; Table 1)

Body flattened, 475 ± 16 (380–575) long, 170 ± 8 (125–225) wide. Dorsal and ventral anchors differ in shape and size (Figs. 2E, 9A,B). Dorsal anchors larger than ventral (Table 1: DI *vs* VI), elongate; proximal and distal parts equal in length (Table 1: DD *vs* DIP)

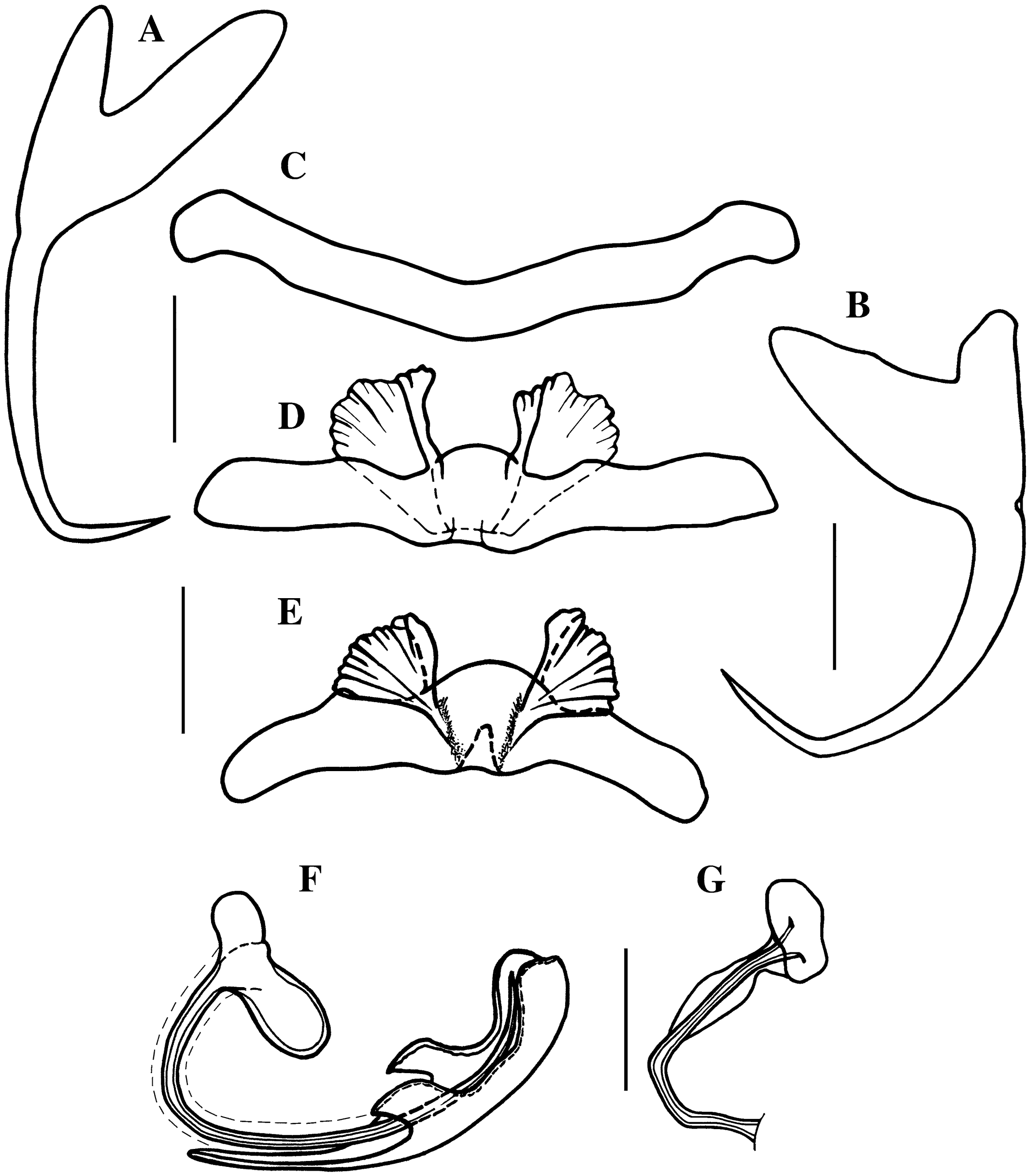

Fig. 9 *Ligophorus campanulatus* n. sp. from *Liza carinata* from the Red Sea. A, dorsal anchor; B, ventral anchor; C, dorsal bar; D, ventral bar (ventral view); E, ventral bar (dorsal view); F, male copulatory organ; G, vagina. *Scale-bars*: 10 µm

and form obtuse angle (Table 1: D*IV*); inner length of proximal part significant larger than outer (Table 1: DIP *vs* DOP); shaft straight, with point at acute angle (Table 1: D*III*). Ventral anchor more arcuate; distal part longer than proximal (Table 1: VD *vs* VIP), at slightly obtuse angle to each other (Table 1: V*IV*); inner length of proximal part significantly greater than outer length (Table 1: VIP *vs* VOP), as for dorsal anchor; shaft bent, with point almost at right angle (Table 1: V*III*). Bars equal in length (Table 1: DBW *vs* VBW). Dorsal bar equal in height along its entire width, bowed in middle, with lateral extremities down-turned; sometimes with rectangular prominence in middle of posterior margin (Fig. C). Ventral bar with 2 long, digitiform anterior processes set quite far apart (Figs. 3G, 9D; Table 1: VBP, VBS); dorsal side of ventral bar with wing-shaped lamina attached to each anterior process; median knoll, with cupola-

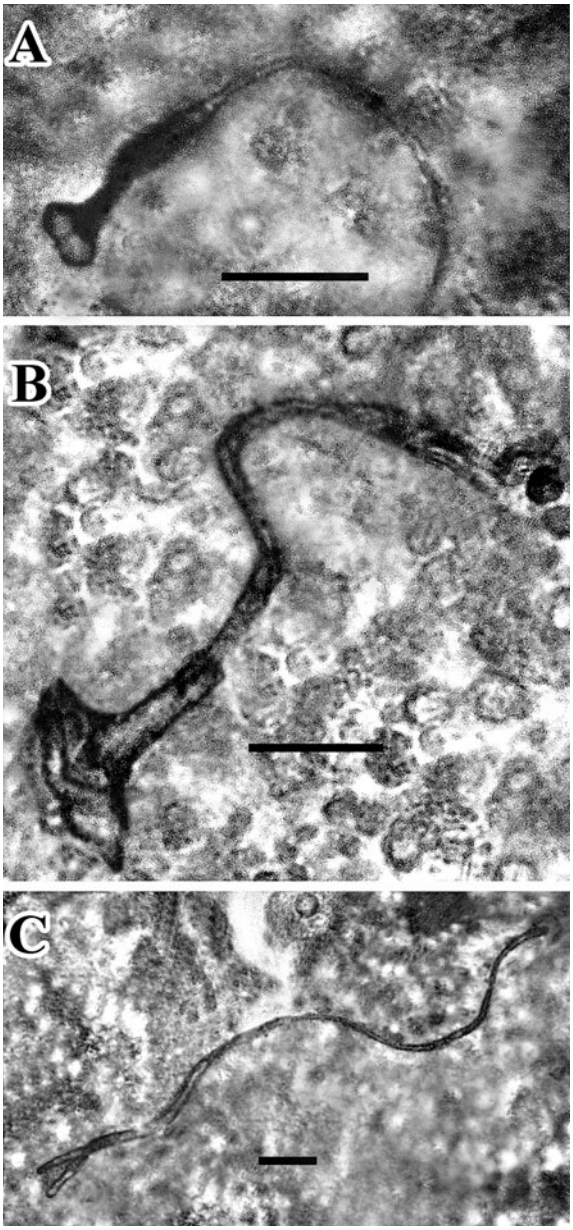

Fig. 10 Vagina of *Ligophorus campanulatus* n. sp. (A), *L. lebedevi* n. sp. (B) and *L. surianoae* n. sp. (C) ex *Liza carinata* from the Red Sea. *Scale-bars*: 10 μm

shaped anterior margin, situated between laminae (Figs. 3H, 9E).

Copulatory tube very narrow and rather short (Table 1: CTL, CTW); expanded base bipartite. Accessory piece gutter-shaped, deep U-shaped in cross-section, tapers towards proximal end; pair of short, symmetrical, knife-shaped processes arise from about mid-length, directed towards proximal end (Figs. 4F, 9F). Muscular sheath surrounding copulatory tube attaches close to distal end of accessory piece.

Vagina typical for genus, in form of narrow tube, with armature represented by solid wall; distal region of tube 12–14 from vaginal pore strongly reinforced; distal extremity of vagina in form of deep, wide funnel *c.*7 in diameter (Figs. 9G, 10A).

Differential diagnosis

Ligophorus campanulatus n. sp. differs from the two new species described above from *Crenimugil crenilabris* in: (1) the shorter and narrower copulatory tube (Table 1: CTL, CTW); (2) the different rather than similar shape of the dorsal and ventral anchors; and (3) the shape of both anchors, the proximal and distal parts of which have equal lengths, as opposed to the proximal part being significantly longer than the distal in both compared species (VIP/VD 0.9 and DIP/DD 1.1 *vs* 1.8 and 1.4 in *L. bykhowskyi* n. sp., 2.3 and 1.8 in *L. zhangi* n. sp., respectively); and (4) the smaller bars (Table 1: VBW, DBW).

From the two species described above from the same host, *Liza carinata*, *Ligophorus campanulatus* can be distinguished by: (1) the different rather than similar shape of the dorsal and ventral anchors; (2) the greater dimensions of the MCO accessory piece (Table 1: APL, APW); and (3) its shape, with two symmetrical, knife-shape processes directed towards the proximal end, as opposed to a simple shape without processes in *L. simpliciformis* and *L. bipartitus* (Fig. 9F *vs* Figs. 6F, 7F). Moreover, it can be differentiated from *L. simpliciformis* n. sp. by: the smaller dimensions of the ventral anchors (Table 1: VI, VD, VS, VIP, VOP) and the ventral bar (Table 1: VBW); and from *L. bipartitus* n. sp. by: the shape of the anchors, the proximal and distal parts of which are practically equal in length rather than the proximal part being significantly longer than the distal part, as in *L. bipartitus* (Table 1: VD *vs* VIP and DD *vs* DIP); the smaller sizes of the both bars (VBW, VBH, DBW, DBH); the shape of the dorsal bar, which is equal in height along its entire width, as opposed to having a well-marked constriction in the middle in *L. bipartitus* (Fig. 9C *vs* Fig. 7C,D); and finally the shape of the ventral bar with the shorter and more widely positioned anterior processes (Table 1: VBP, VBS).

Ligophorus campanulatus resembles species from *Liza* spp. in the Mediterranean, namely *Ligophorus confusus* Euzet & Suriano, 1977, *L. szidati* Euzet & Suriano, 1977 and *L. angustus* Euzet & Suriano, 1977, in the different shapes of the dorsal and ventral anchors. However, it differs from these species in: (1) the proportions of the distal part of the ventral anchors, which have a longer shaft and a significantly shorter point (VP 9 *vs* 17–18 in *L. confusus* and *L. szidati*, 13–15 µm in *L. angustus*); (2) the anterior processes of the ventral bar, which are set quite widely apart rather than being positioned closely together, as in the compared species (Fig. 9D,E *vs* figs. 6, 29, 35 of Euzet & Suriano, 1977); (3) the shorter copulatory tube (40–45 *vs* 90–100 µm in *L. confusus*, *L. szidati* and *L. angustus*); (4) the shape of the accessory piece, which has a pair of small symmetrical processes directed towards the proximal end, as opposed to one large process directed towards the distal end (the so-called as distal bifurcation) in the Mediterranean species (Fig. 9F *vs* figs. 7, 30, 36 of Euzet & Suriano, 1977) (comparative data from Euzet & Suriano, 1977).

Ligophorus mamaevi n. sp.

Type-host: *Liza carinata* (Valenciennes).
Type-locality: Ras Mohammed National Park, Red Sea (27°45.150′N; 34°15.590′E).
Site on host: Gills.
Type-specimens: 11 specimens. Holotype and 2 paratypes deposited in the ZIN RAS (holotype: No. 12269, paratypes: Nos 12270, 12271). Additional paratypes are in the BMNH (No. 2011.11.17.24-26), the IBSS (No. 520/1-3) and the MSNM (No. Pi 4929-31).
Etymology: The species is named for the late Dr Yuri L. Mamaev, the well-known Russian specialist on monogeneans of fishes from the Pacific Ocean.

Description (Figs. 2F, 3I,J, 4G, 11; Table 1)

Small worms, 449 ± 8 (440–480) long, 178 ± 7 (160–190) wide, with flattened body. Dorsal and ventral anchors differ in shape and size (Figs. 2F, 11A,B). Dorsal anchors larger than ventral (Table 1: DI *vs* VI), elongate; distal and proximal parts form obtuse angle (Table 1: D*IV*); roots of proximal part short, set rather close; shaft only slightly curved, with point almost at right angle (Table 1: D*III*). Ventral anchors different in shape to dorsal anchors, arcuate, with distal and proximal parts almost at right angle (Table 1: V*IV*); roots of proximal part set rather wide apart; distal part longer than proximal part (Table 1: VD *vs* VIP); shaft curved, but point rather straight. Both pair of anchors similar in that inner length of proximal part is greater than that of outer part (Table 1: VIP *vs* VOP and DIP *vs* DOP). Dorsal bar slightly smaller than ventral bar (Table 1: DBW *vs* VBW). Dorsal bar somewhat elongate-fusiform, with slightly down-turned lateral extremities (Fig. 11C). Ventral bar with 2 short, digitiform anterior processes set quite widely apart (Figs. 3I,J, 11D,E; Table 1: VBP, VBS); dorsal side of ventral bar with 2 relatively wide, wing-shaped laminae attached laterally to anterior processes; median knoll with indistinct cupola-shaped anterior margin, situated between laminae (Figs. 3J, 11E).

Copulatory tube very narrow and rather long (Table 1: CTL, CTW); expanded base bipartite. Accessory piece forms shallow gutter, U-shaped in cross-section, tapers towards distal end, extremity of which is turned-up (Fig. 4G). Muscular sheath surrounding copulatory tube attaches close to distal end of accessory piece.

Vagina typical for genus, in form of narrow tube with armature represented by solid walls; distal opening in form of shallow funnel, giving hard-parts shape of bent nail in lateral view (Fig. 11G). Full extent of vagina not visible for measuring.

Differential diagnosis

From *Ligophorus bykhowskyi* n. sp. and *L. zhangi* n. sp., described above from *Crenimugil crenilabris*, *L. mamaevi* n. sp. differs in: (1) its longer and narrower copulatory tube (Table 1: CTL, CTW); (2) the different rather than similar shape of the dorsal and ventral anchors (Fig. 2F *vs* Fig. 2A,B); and (3) the smaller ratio of the proximal in relation to the distal parts of both anchors (VIP/VD and DIP/DD 0.9 *vs* 1.8 and 1.4 in *L. bykhowskyi*, 2.3 and 1.8 in *L. zhangi*).

From *L. campanulatus* n. sp., *L. simpliciformis* n. sp. and *L. bipartitus* n. sp., described above from *Liza carinata*, *Ligophorus mamaevi* can be distinguished mainly by the fact that its copulatory tube is twice as long (Table 1: CTL). Of these three species, *L. campanulatus* is similar to *L. mamaevi* in the shape of the anchors, but the latter differs in: (1) the shape of both bars, which have their greatest height in the

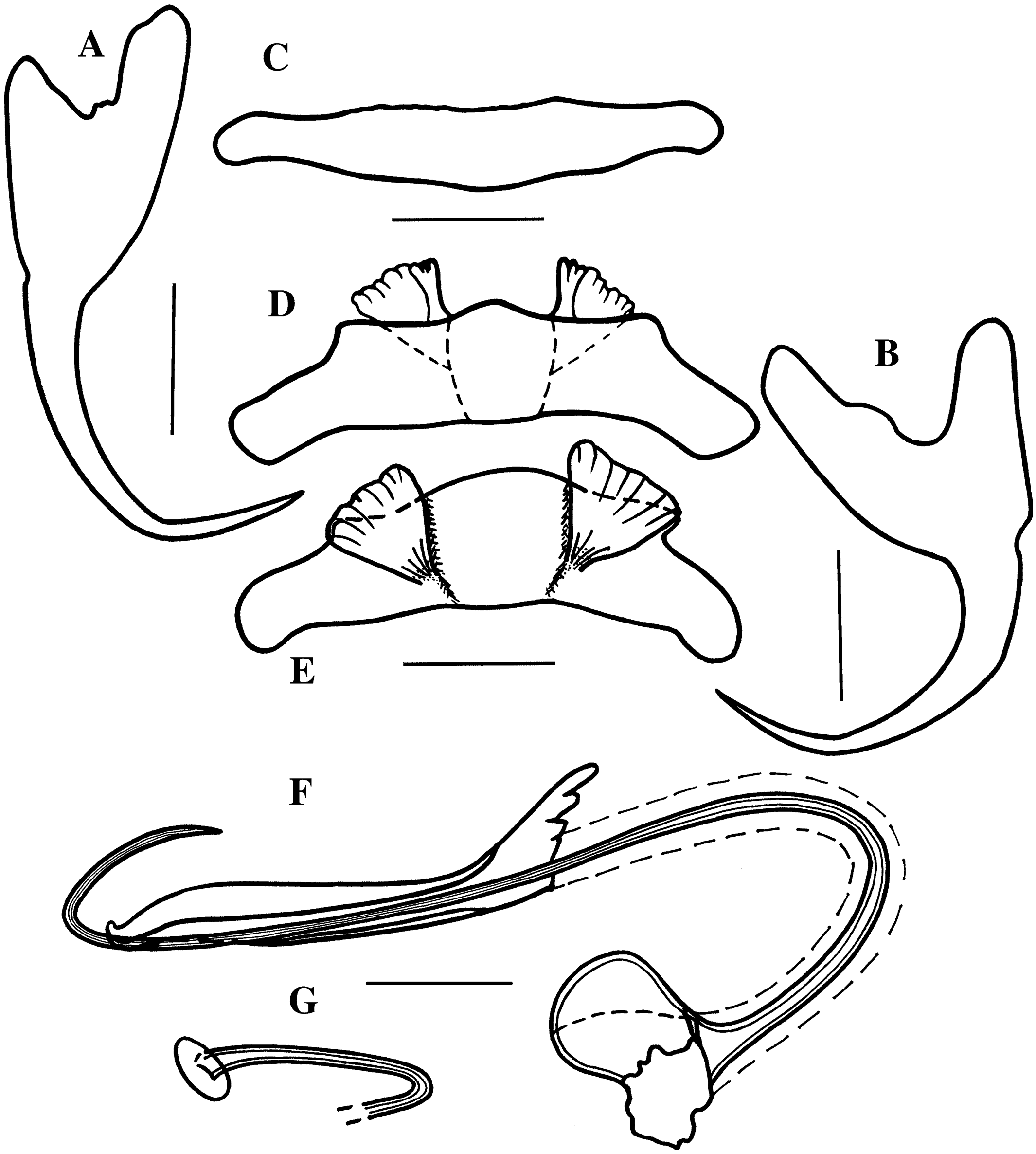

Fig. 11 *Ligophorus mamaevi* n. sp. ex *Liza carinata* from the Red Sea. A, dorsal anchor; B, ventral anchor; C, dorsal bar; D, ventral bar (ventral view); E, ventral bar (dorsal view); F, male copulatory organ; G, vagina. *Scale-bars*: 10 µm

middle and taper laterally, rather than being more elongate and similar in height throughout their entire width, as in *L. campanulatus* (Fig. 11C–E *vs* Fig. 9C–E); (2) the shape of the MCO accessory piece is simple without processes, as opposed to bearing two symmetrical knife-shape processes in *L. campanulatus* (Fig. 11F *vs* Fig. 9F); and (3) the vaginal tube wall is of equal thickness along its entire length and the distal extremity is in the form of a small funnel, rather than the distal part of the vaginal tube being strongly reinforced and the funnel-shaped opening wider and deeper, as in *L. campanulatus* (Fig. 11G *vs* Fig. 9G).

With regard to the two other species, *L. simpliciformis* and *L. bipartitus*, *L. mamaevi* is similar in the shape of the MCO accessory piece, which has no processes, but differs significantly by having: (1) differently shaped rather than similar dorsal and ventral anchors (Fig. 2F *vs* Fig. 2C,D); (2) smaller bars (Table 1: VBW, DBW); and (3) a wider copulatory tube (Table 1: CTW).

Of the other representatives of the genus, *L. mamaevi* appears similar to *L. confusus*, *L. szidati* and *L. angustus*, all parasites of *Liza* spp. in the Mediterranean Sea, which also have anchors which differ in shape and ventral anchors that are more curved than the dorsal pair. However, *Ligophorus mamaevi* can be distinguished from the Mediterranean species by: (1) the shape of the ventral anchors, the distal part of which has a long, arcuate shaft and a relatively short point, as opposed to a short, rather straight shaft and a long, curved point (VP 9 *vs* 17–18 µm in *L. confusus* and *L. szidati*, 13–15 µm in *L. angustus*); (2) the anterior processes of the ventral bar are set further apart (Fig. 11D,E *vs* figs. 6, 29, 35 of Euzet & Suriano, 1977); and (3) the MCO accessory piece is undivided rather than bifurcate at the distal end, as in the Mediterranean species (Fig. 11F *vs* figs. 7, 30, 36 of Euzet & Suriano, 1977) (comparative data from Euzet & Suriano, 1977).

Ligophorus lebedevi n. sp.

Type-host: *Liza carinata* (Valenciennes).
Type-locality: Ras Mohammed National Park, Red Sea (27°45.150′N; 34°15.590′E).
Site on host: Gills.
Type-specimens: 9 specimens. Holotype and 2 paratypes deposited in the ZIN RAS (holotype: No. 12272, paratypes: Nos 12273, 12274). Additional paratypes are in the BMNH (No. 2011.11.17.27-28), the IBSS (No. 521/1-2) and the MSNM (No. Pi 4932-33).
Etymology: The species is named for the late Dr Boris E. Lebedev, the well-known Russian monogenean specialist.

Description (Figs. 2G, 3K,L, 10B, 12)

Body flattened, 605 ± 18 (540–650) long, 220 ± 9 (195–255) wide. Both pairs of anchors elongate, similar in shape (Figs. 2G, 12A,B); distal part longer than proximal part (Table 1: VD *vs* VIP and DD *vs* DIP); distal and proximal parts form obtuse angle (Table 1: V*IV*, D*IV*); inner length of proximal part greater than outer length (Table 1:VIP *vs* VOP and DIP *vs* DOP); distal part with relatively straight shaft and very short point. Dorsal anchors smaller than ventral anchors (Table 1: DI *vs* VI) and with shorter point, which is almost at right angle to shaft (Table 1: D*III*), whereas in ventral anchors point is at slightly obtuse angle (Table 1: V*III*). Bars equal in length (Table 1: DBW *vs* VBW). Dorsal bar bowed in middle, with broad, slightly down-turned lateral extremities (Fig. 12C). Ventral bar with 2 short, digitiform anterior processes set quite closely together (Figs. 3K,L, 12D,E; Table 1: VBP, VBS); dorsal side of ventral bar with short, wide, wing-shaped lamina attached to each anterior process; median knoll with cupola-shaped anterior margin, situated between laminae (Figs. 3L, 12E).

Copulatory tube rather short and narrow (Table 1: CTL, CTW); expanded base bipartite. Accessory piece forms shallow gutter, U-shaped in cross-section, tapers towards proximal end; 2 short, proximally oriented, barb-shaped processes arise close to middle of each side-wall; 2 symmetrical bulb dilatations with long, pointed, horn-shaped processes arising from each of them, situated at distal end (Figs. 4H, 12F). Muscular sheath, surrounding copulatory tube, attaches to these rod-shaped processes.

Vagina typical for genus, forming narrow tube, with its armature represented by solid walls; latter thickened along one side of distal quarter of vaginal tube; distal aperture funnel-shaped, resembling screw-head in side view; proximal end also slightly trumpet-shaped (Figs. 10B, 12G).

Differential diagnosis

From all known species of *Ligophorus*, except for *L. hamulosus* Pan & Zhang in Pan, 1999 and those described in the present study, *L. lebedevi* n. sp. differs mainly in the shape of the anchors, which bear the smallest points (1–3 *vs* >5 µm for all known species, excluding *L. hamulosus*).

Moreover, this new species differs from *L. bykhowskyi* n. sp. and *L. zhangi* n. sp., described above from *Crenimugil crenilabris*, in: (1) the sizes and proportions of the anchors, which are smaller in terms of length (Table 1: VI, DI) [however, although the measurements of their proximal parts are 2–3 times smaller (Table 1: VOP, VIP, VSR, DOP, DIP, DSR), the distal parts are larger (Table 1: VD, VS, DD, DS), so the ratio of the proximal to the distal part in both anchors are smaller (VIP/VD 0.8 and DIP/DD 0.7 *vs* 1.8 and 1.4 for *L. bykhowskyi* and 2.3 and 1.8 for *L. zhangi*, respectively)]; and the MCO, which has (2)

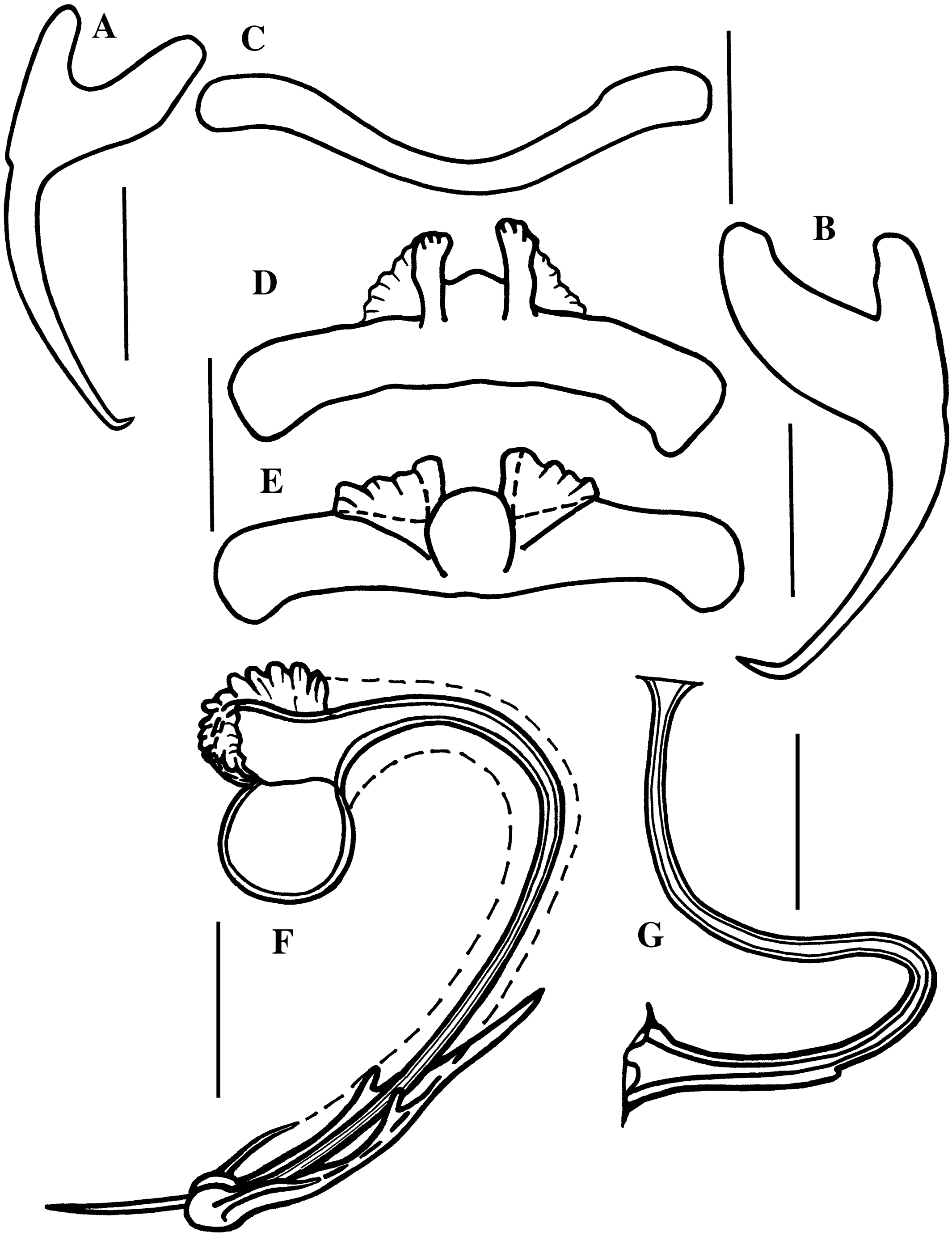

Fig. 12 *Ligophorus lebedevi* n. sp. ex *Liza carinata* from the Red Sea. A, dorsal anchor; B, ventral anchor; C, dorsal bar; D, ventral bar (ventral view); E, ventral bar (dorsal view); F, copulatory organ; G, vagina. *Scale-bars*: 10 µm

a smaller tube and (3) a shorter accessory piece (Table 1: CTW, APL).

L. campanulatus n. sp., described from *Liza carinata*, has some similarities with *Ligophorus lebedevi* in the shape of the MCO, but the latter species differs in: (1) the ventral and dorsal anchors being similar in shape rather than of a different shape and size, as in *L. campanulatus* (Fig. 2G *vs* Fig. 2E); (2) smaller dimensions of the dorsal anchor (Table 1); (3) a shorter proximal part of the ventral anchor (Table 1: VIP, VOP, VSR); and (4) a longer copulatory tube (Table 1: CTL).

From *L. simpliciformis* n. sp., *L. bipartitus* n. sp. and *L. mamaevi* n. sp., described from the same host as *L. campanulatus*, the present new species can be distinguished by the fact that the MCO accessory piece has two different pairs of symmetrical processes directed towards its proximal end, whereas no processes are present in the former three species (Fig.12F *vs* Figs. 6F, 7F, 11F, respectively). Compared with *L. simpliciformis* and *L. bipartitus*, *L. lebedevi* has smaller bars (Table 1: VBW, DBW) and a longer copulatory tube (Table 1: CTL). Moreover, compared with *L. bipartitus*, the dorsal bar narrows only slightly in the middle, rather than having a deep constriction (Fig. 12C *vs* Fig. 7C,D). In comparison with *L. mamaevi*, the ventral and dorsal anchors are similar in shape rather being different (Fig. 2G *vs* Fig. 2F), the proximal parts of the anchors have smaller dimensions (Table 1: VIP, VOP, VSR, DIP, DOP, DSR), the dorsal bar narrows in the middle rather than being wider, as in *L. mamaevi* (Fig. 12C *vs* Fig. 11C), and the copulatory tube is shorter (Table 1: CTL).

Among the species known from other hosts and regions, *L. hamulosus* Pan & Zhang in Pan, 1999, described from *Liza macrolepis* in the South China Sea, appears to be the most similar to *Ligophorus lebedevi* based on the morphology of the haptoral hard-parts. The new species differs from *L. hamulosus* in: (1) the smaller sizes of both bars (VBW 27–31 *vs* 33–38 and DBW 28–33 *vs* 38–40 µm); (2) the shorter dorsal anchor point (DP 1 *vs* 3 µm); (3) the shorter copulatory tube (CTL 52–54 *vs* 55–63 µm); (4) the shape of the MCO accessory piece, which has two different pairs of symmetrical processes directed towards the proximal end rather than being simple, without processes, as in *L. hamulosus* (Fig. 12F *vs* fig. 2 of Pan, 1999); and (5) a longer vaginal tube (VL 38–40 *vs* 20–23 µm) (comparative data from Pan, 1999).

***Ligophorus surianoae* n. sp.**

Type-host: *Liza carinata* (Valenciennes).
Type-locality: Ras Mohammed National Park, Red Sea (27°45.150′N; 34°15.590′E).
Site on host: Gills.
Type-specimens: 18 specimens. Holotype and 4 paratypes deposited in the ZIN RAS (holotype: No. 12275, paratypes: Nos 12276-12279). Additional paratypes are in the BMNH (No. 2011.11.17.29-32), the IBSS (No. 522/1-5) and the MSNM (No. Pi 4934-36).
Etymology: This species is named for Dr Delia M. Suriano, the Argentinean parasitologist who co-authored the genus *Ligophorus*.

Description (Figs. 2H, 3M–O, 4I, 8D,E, 10C, 13; Table 1)

Middle-sized worms, 760 ± 15 (700–800) long, 225 ± 12 (190–250) wide, with flattened body. Both pairs of anchors elongate (Figs. 2H, 12A,B), with distal and proximal parts of similar length (Table 1: VD *vs* VIP and DD *vs* DIP) and forming obtuse angle (Table 1: V*IV*, D*IV*); point short, almost at right angle (Table 1: V*III*, D*III*). Ventral anchors larger than dorsal (Table 1: VI *vs* DI), with inner and outer lengths of proximal part virtually equal (Table 1: VIP *vs* VOP). Dorsal anchors with inner length of proximal part significantly longer than outer (Table 1: DIP *vs* DOP). Dorsal bar slightly larger than ventral (Table 1: DBW *vs* VBW). Dorsal bar, in most cases, slightly curved (Fig. 8D), equal in height along its entire width, with slight prominence in middle of posterior margin and lateral extremities slightly up-turned (Fig. 13C) or, rarely, bowed (Fig. 8E). Ventral bar with 2 long, digitiform anterior processes positioned relatively closely together (Figs. 3M–O, 13D,E; Table 1: VBP, VBS); dorsal side of ventral bar with rather narrow, wing-shaped laminae attached to each anterior process; median knoll, in most cases, with flat (Fig. 3N) or sometimes slightly prominent anterior margin (Fig. 3O), situated between laminae.

Copulatory tube narrow and rather long (Table 1: CTL, CTW); expanded base bipartite. Accessory piece forms gutter with deep, U-shaped cross-section, partly encloses copulatory tube (Fig. 4I), tapers proximally, with 2 small processes directed towards distal end situated not far from distal extremity; side-walls of accessory piece drawn close together at distal end, practically surrounding tube near distal opening. Muscular sheath surrounding copulatory tube attaches close to distal end of accessory piece.

Vagina typical for genus, forming narrow, sinuous tube with armature represented by solid walls; distal

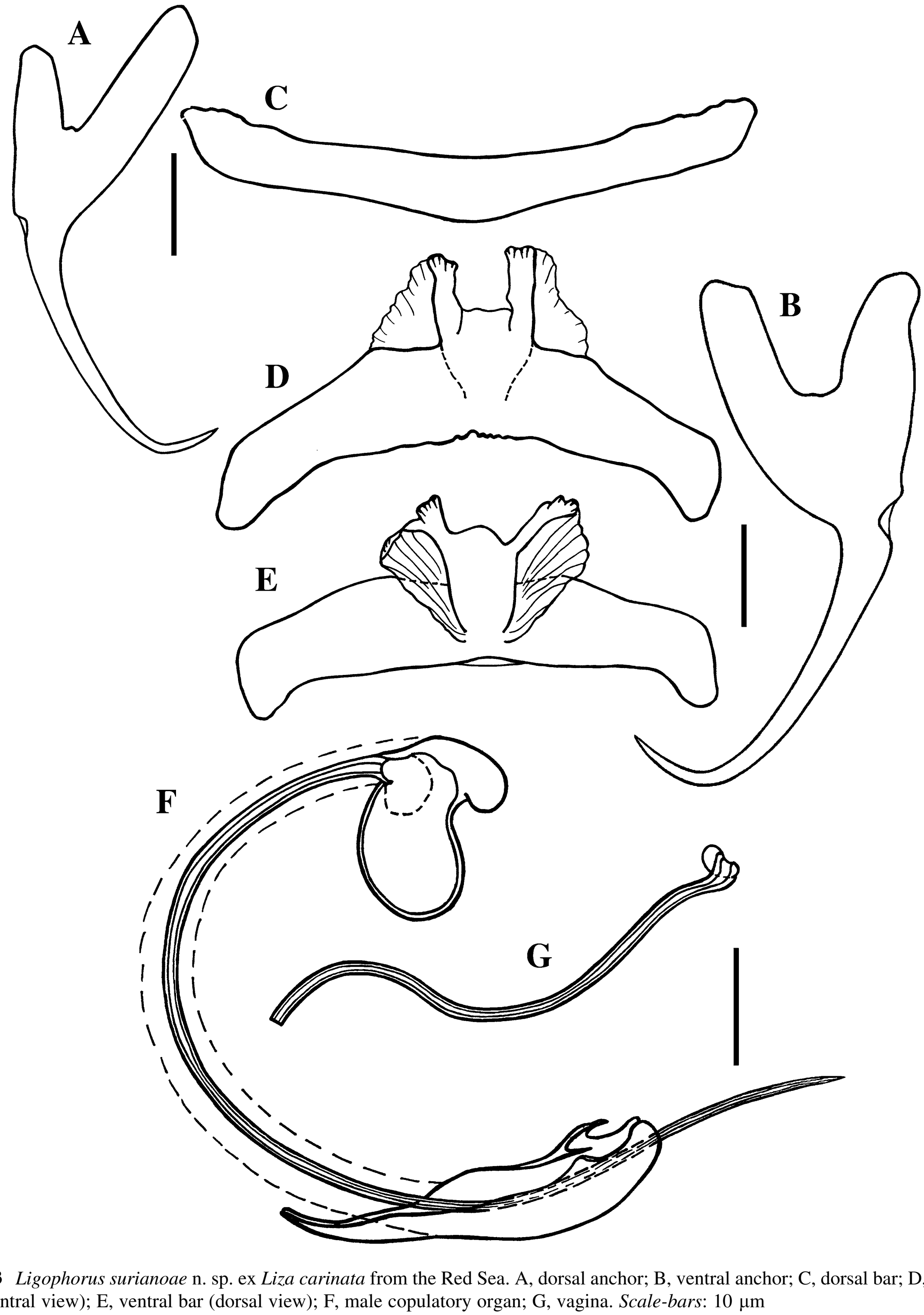

Fig. 13 *Ligophorus surianoae* n. sp. ex *Liza carinata* from the Red Sea. A, dorsal anchor; B, ventral anchor; C, dorsal bar; D, ventral bar (ventral view); E, ventral bar (dorsal view); F, male copulatory organ; G, vagina. *Scale-bars*: 10 µm

aperture in form of shallow funnel resembling nail-head in side view (Figs. 10C, 13G).

Differential diagnosis

Ligophorus surianoae n. sp. differs from *L. bykhowskyi* n. sp. and *L. zhangi* n. sp., described above from *Crenimugil crenilabris*, by having: (1) the MCO with a longer and thinner copulatory tube (Table 1: CTL, CTW); and (2) anchors with a greater total length (Table 1: VI, DI) and (3) greater length of the proximal parts (Table 1: VD, VS, DD, DS), such that (4) the ratio of the distal part to the proximal is equal or slightly less than unity, rather than being significantly greater than unity (VIP/VD 0.8 and DIP/DD 1.0 *vs* 1.8 and 1.4 in *L. bykhowskyi*, and 2.3 and 1.8 in *L. zhangi*, respectively).

In relation to all of the species described above from *Liza carinata*, *Ligophorus surianoae* can be distinguished mainly by: (1) most dimensions of the anchors; and (2) the greater length of the copulatory tube (Table 1). Among these species, *L. simpliciformis* n. sp. appears to be the most similar to *L. surianoae* based on the morphology of the haptoral hard-parts, but the latter differs by having: (1) a thinner copulatory tube (Table 1: CTW); and (2) an MCO accessory piece which tapers significantly towards its proximal end, has side-walls which are drawn together at the distal end and bears two small processes situated near the distal aperture, rather than being practically equal in width along its entire length and devoid of processes, as is the case for *L. surianoae* (Fig. 13F *vs* Fig. 6F).

L. surianoae resembles *L. vanbenedeni*, *L. acuminatus*, *L. heteronchus*, *L. minimus*, *L. imitans*, *L. macrocolpos*, *L. parvicirrus* and *L. euzeti*, which parasitise mullets of the genus *Liza* in the Mediterranean and Black Seas, in the shape of the haptoral hard-parts, but differs from these species by having: (1) a longer ventral anchor (VI 51–56 *vs* 32–46 µm for all of the above-listed species); and (2) the MCO accessory piece has small processes, rather than the clearly visible and significantly longer distal processes of all the compared species. Moreover, the new species can also be distinguished as follows: in *Ligophorus vanbenedeni*, *L. heteronchus*, *L. minimus*, *L. imitans*, *L. parvicirrus* and *L. euzeti* the bars have a greater width (VBW 47–53, DBW 48–68 *vs* < 42 µm); in *L. acuminatus* and *L. minimus*, the vagina is longer (42–47 *vs* 25–27, 20–25 µm, respectively); and in *L. macrocolpos*, the vagina is shorter (42–47 *vs* 115–120 µm) (comparative data from Euzet & Suriano, 1977, Euzet & Sanfilippo, 1983, and Dmitrieva & Gerasev, 1996).

Morphological analysis of the eight new species of *Ligophorus*

Principal Component Analysis (PCA) was carried out on four separate datasets of morphological dimensions [available as Suppl. Data]: four characters of the MCO, seven characters of each anchor pair (data from 93 specimens for these analyses) and 4 characters of the ventral bar (data from 88 specimens).

The four dimensions describing the main proportions of the MCO were reduced to two principal components (PCs) (i.e. factors) which explained 80% of the overall variance (Fig. 14). The width of the copulatory tube (CTW) contributed most to this separation (Fig. 14B). As a result of this PCA, 93 specimens grouped in eight clusters corresponding to the eight species; these in turn formed two distinctly distant groups (Fig. 14A).

One group was formed by specimens of *Ligophorus bykhowskyi* n. sp. and *L. zhangi* n. sp. from *Crenimugil crenilabris* (Fig. 14A: 1, 2). The MCO of these species has a wide, thick-walled and relatively short copulatory tube arising from a large unipartite, expanded base (Figs. 1F, 5E; Table 1) and the accessory piece is a broad, simple gutter lacking any sort of bifurcation or processes. This is ‘first’ type of MCO among the analysed species.

The other group includes specimens of six species described from *Liza carinata* (Fig. 14A: 3-8). All these species have an expanded base of the copulatory tube consisting of two parts (Figs. 6, 7, 9, 11, 12, 13F) and an accessory piece of the MCO forming an undivided gutter. *Ligophorus simpliciformis* n. sp. and *L. bipartitus* n. sp. were positioned closest together (Fig. 14A: 3, 4). They have the shortest and widest copulatory tube (Fig. 14B: CTL, CTW) and the simplest shape of the MCO accessory piece which lacks processes (Figs. 6, 7F). This MCO shape is referred to as the ‘second’ type. *L. campanulatus* n. sp., *L. lebedevi* n. sp. and *L. surianoae* n. sp. have an MCO accessory piece with a different shape and bearing processes (Figs. 9, 12, 13F). However,

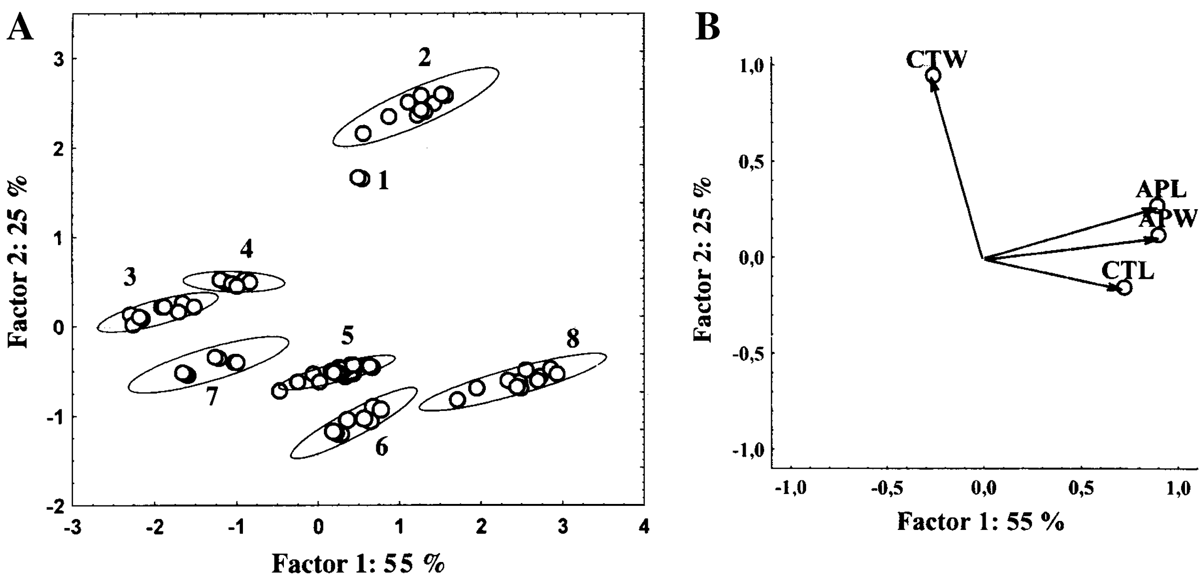

Fig. 14 A, PCA plot of 93 *Ligophorus* specimens based on their scores in the first plane of the PCA run on metrical data for four characters of the male copulatory organ: 1, *L. zhangi* n. sp. (n = 2); 2, *L. bykhowskyi* n. sp. (n = 10); 3, *L. simpliciformis* n. sp. (n = 20); 4, *L. bipartitus* n. sp. (n = 6); 5, *L. campanulatus* n. sp. (n = 24); 6, *L. mamaevi* n. sp. (n = 9); 7, *L. lebedevi* n. sp. (n = 8); 8, *L. surianoae* n. sp. (n = 14); B, PCA plot of the contributions made by these characters for the first two factors. Ellipse coefficient, 95%; →, direction of increasing of measurements. *Abbreviations*: see 'Materials and methods'

L. surianoae was clearly separated from the other two species by having the longest copulatory tube (Fig. 14B: CTL) and, because of this, grouped with *L. mamaevi* n. sp. *L. mamaevi* has an MCO accessory piece lacking processes, as in *L. simpliciformis* and *L. bipartitus*, but differs from the latter species in the deeper gutter of the accessory piece, the side-walls of which draw together at the distal end and surround the copulatory tube close to the distal aperture (Fig. 11F). These details of the accessory piece and the rather long, thick copulatory tube group *L. mamaevi* with *L. campanulatus*, *L. lebedevi* and *L. surianoae*, which together represent the 'third' type of MCO.

Seven dimensions describing the main parameters of the anchors were reduced to two principal components (factors) describing 86% of the overall variance for the ventral anchor (Fig. 15A) and 88% for the dorsal anchor (Fig. 15C).

Specimens of *L. bykhowskyi* and *L. zhangi* grouped closely together in both PCA plots (Fig. 15A,C: 1–2) and were separated from other species by the proportions of their anchors, which have distal parts with the smallest length (Fig. 15B,D: VD, VS, DD, DS) and proximal parts with the greatest dimensions (Fig. 15B,D: VOP, VIP, VSR, DOP, DIP, DSR). Both pairs of anchors of these two species are of the same morphological type (referred to as the 'first' type), i.e. with well-developed proximal parts, long inner roots, distal parts with a rather short, somewhat straight, shaft which forms an angle of >100° with the proximal parts, and relatively long points of more than half the shaft length (Figs. 1, 5A,B; Table 1).

All other new species were displaced on the plots (Fig. 15A,C) to positions indicating a decreased length of the proximal parts (VOP, VIP, VSR, DOP, DIP, DSR) and an increased length of the distal parts (VD, VS, DD, DS) in both pairs of anchors (Fig. 15B,D) relative to the species from *Crenimugil crenilabris*. Specimens of *L. lebedevi* (Fig. 15A,C: 7) were clearly separated in the plots from the others by having small inner lengths for both pairs of anchors (VI, DI), the smallest lengths of their proximal parts (VOP, VIP, DIP, DOP) and the shortest point (VP, DP), which were <3 µm, representing only a fifth of the shaft length in both pairs of anchor (Fig. 15B,D). These anchors of *L. lebedevi* (Fig. 12A,B) belong to the 'second' morphological type among the described species. Conversely, specimens of *L. surianoae* were separated by having the largest dimensions of the anchors (Fig. 15A,C: 8). The anchors in this species represent a 'third' type of anchor, with the distal part

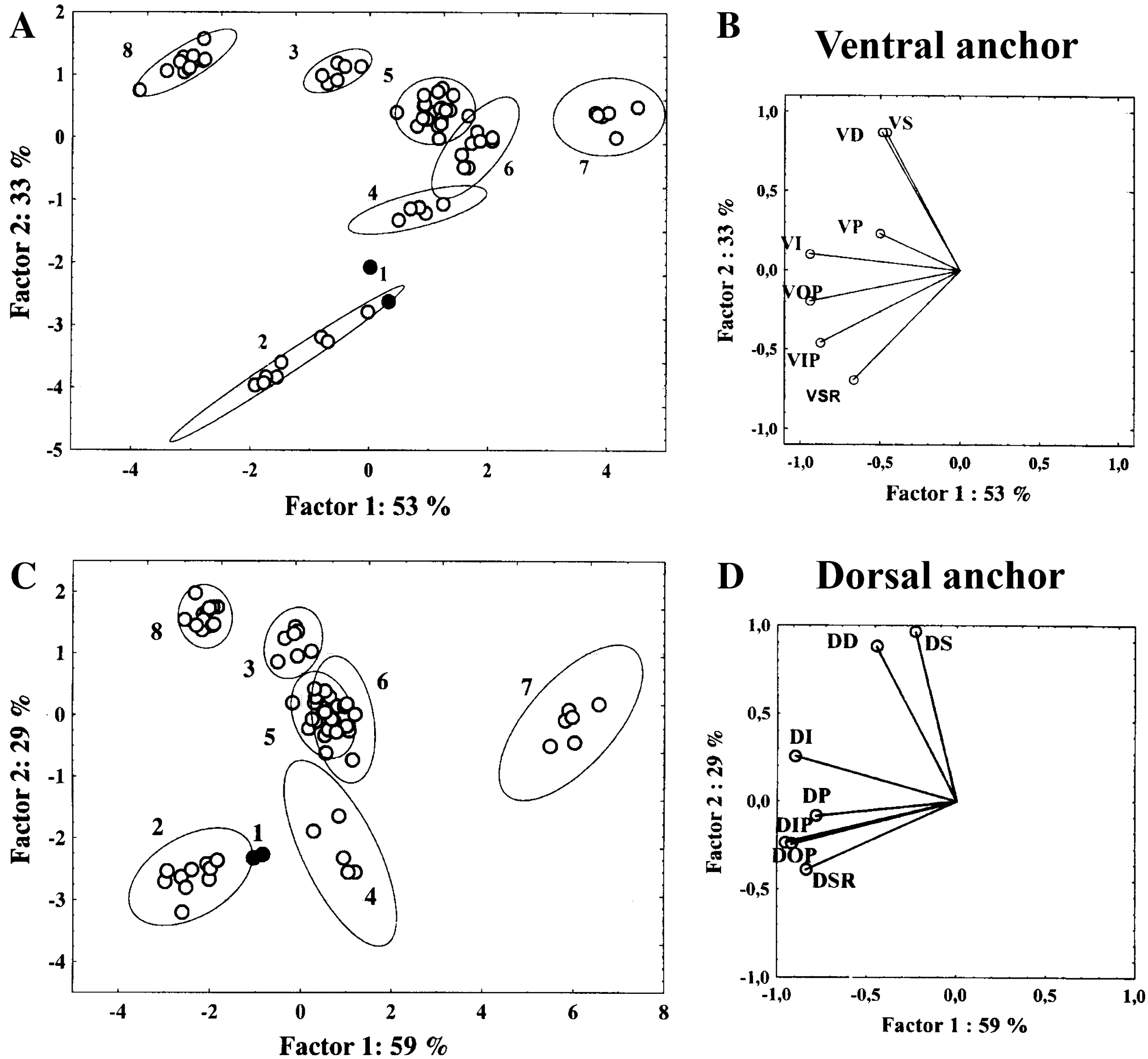

Fig. 15 A, C, PCA plots of 93 *Ligophorus* specimens based on their scores in the first plane of the PCA run on metrical data for seven characters of the each pair of anchors: 1, *L. zhangi* n. sp. (n = 2); 2, *L. bykhowskyi* n. sp. (n = 10); 3, *L. simpliciformis* n. sp. (n = 20); 4, *L. bipartitus* n. sp. (n = 6); 5, *L. campanulatus* n. sp. (n = 24); 6, *L. mamaevi* n. sp. (n = 9); 7, *L. lebedevi* n. sp. (n = 8); 8, *L. surianoae* n. sp. (n = 14); B,D, PCA plot of the contributions made by these characters for the first two factors. Ellipse coefficient, 95%; →, direction of increasing of measurements. *Abbreviations*: see 'Materials and methods'

having a greater length than the proximal part, a relatively long, rather straight shaft, which forms an angle of >100° with the proximal part (Table 1: V*IV*), and a relatively short point with a length of less than half of the shaft length. Also included in this anchor type are both dorsal and ventral anchors of *L. simpliciformis* (Fig. 6A,B) and the dorsal anchors of *L. campanulatus* and *L. mamaevi* (Figs. 9A, 11A). The ventral anchors of the latter two species (Figs. 9B, 11B) belong to a 'fourth' type of anchor, which has an arcuate distal part, forms an angle of <100° with the proximal part (Table 1: V*IV*) and has a relatively short point which is about half of the shaft length. The anchors of *L. bipartitus* (Fig. 7A,B) represent the 'fifth' type among the studied species; this type has the distal and proximal parts of equal length, roots of equal in length and a relatively short point of less than half of the shaft length.

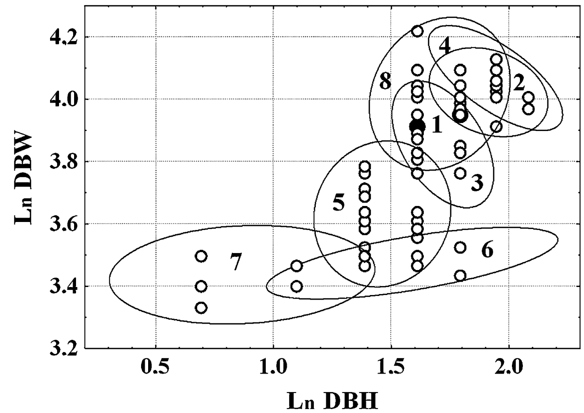

Fig. 17 Scatterplot of the coordinates of ln-transformed dorsal bar dimensions of 88 *Ligophorus* specimens: 1, *L. zhangi* n. sp. (n = 2); 2, *L. bykhowskyi* n. sp. (n = 10); 3, *L. simpliciformis* n. sp. (n = 20); 4, *L. bipartitus* n. sp. (n = 6); 5, *L. campanulatus* n. sp. (n = 23); 6, *L. mamaevi* n. sp. (n = 7); 7, *L. lebedevi* n. sp. (n = 7); 8, *L. surianoae* n. sp. (n = 13). Ellipse coefficient, 90%. *Abbreviations*: see 'Materials and methods'

Four dimensions describing the main parameters of the ventral bars were reduced to two PCs (factors) describing 89% of the overall variance (Fig. 16A). As a result of this PCA, 88 specimens grouped in two clusters (Fig. 16A).

One cluster was formed by specimens of *L. bykhowskyi*, *L. bipartitus* and *L. surianoae*, which have rather large bars (Fig. 16A: 2, 4, 8). The ventral bars of these species possess a well-pronounced median knoll, which protrudes well above the anterior margin of the remaining part of the bar and long, digitiform anterior processes positioned relatively closely together (Figs. 1D,E, 7E, 13D,E; Table 1). These species were not clearly separated from others by the height and width of the dorsal bar (Fig. 17), but the shape of this structure is different. The dorsal bars of *L. bykhowskyi*, *L. bipartitus* and *L. surianoae* are straight or have slightly turned-up lateral extremities, whereas that of *L. bipartitus* has a peculiar shape (Fig. 7C,D), somewhat similar to that described for *L. fluiviatilis* n. comb. (see below) by Bychowsky (1949).

The second cluster on a PCA plot based on metrical data from the ventral bars (Fig. 16A) includes the specimens of *L. zhangi*, *L. simpliciformis*, *L. campanulatus*, *L. mamaevi* and *L. lebedevi*. These specimens correspond primarily in their rather short and widely separated anterior processes on the ventral bar (Fig. 16B: VBP, VBS). Moreover, they have quite wide, wing-shaped laminae attached to each anterior process, and a median knoll, in most cases with a flat or sometimes prominent anterior margin, situated between the laminae (Figs. 5D, 6, 9, 11, 12D,E; Table 1). The dorsal bars of these species also differ with regard to their lateral extremities, which are slightly down-turned (Figs. 5, 6, 9, 11, 12C)

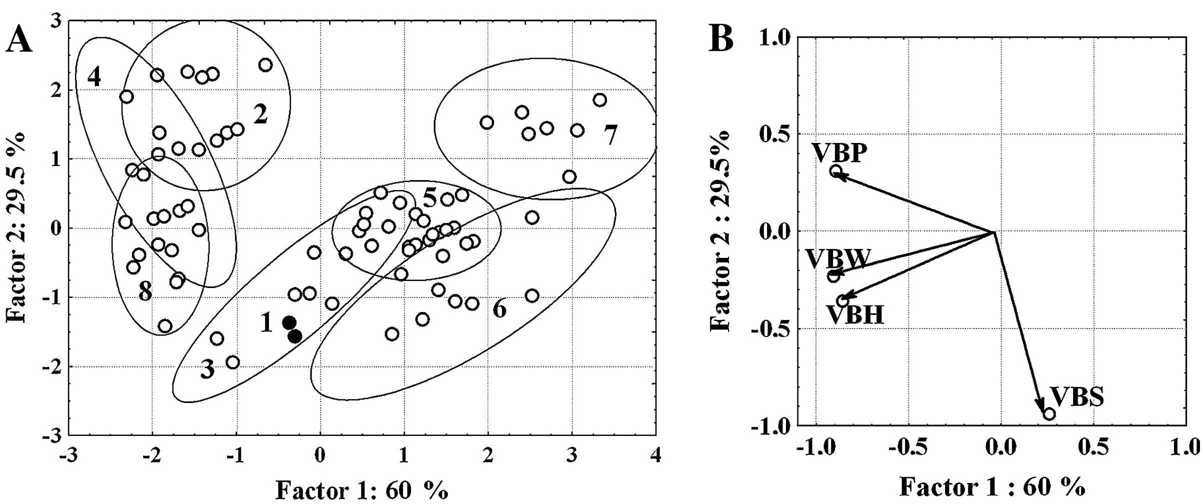

Fig. 16 A, PCA plots of 88 *Ligophorus* specimens based on their scores in the first plane of the PCA run on metrical data for four characters of the ventral bars: 1, *L. zhangi* n. sp. (n = 2), 2, *L. bykhowskyi* n. sp. (n = 10); 3, *L. simpliciformis* n. sp. (n = 20); 4, *L. bipartitus* n. sp. (n = 6); 5, *L. campanulatus* n. sp. (n = 23); 6, *L. mamaevi* n. sp. (n = 7); 7, *L. lebedevi* n. sp. (n = 7); 8, *L. surianoae* n. sp. (n = 13); B, PCA plot of the contributions made by these characters for the first two factors. Ellipse coefficient, 90%; →, direction of increasing of measurements. *Abbreviations*: see 'Materials and methods'

Thus three morphological types of MCO, five types of anchor, two types of ventral bar and three types of dorsal bar were distinguished for the described species based on PCAs of metrical data from their haptoral and MCO hard parts and, in some cases, on their shape.

L. bykhowskyi and *L. zhangi*, from *Crenimugil crenilabris*, have the same type of MCO (both in terms of tube width and the shape of the accessory piece) and anchors, differing significantly from those of the species described from *Liza carinata*. Those species from *L. carinata* have only one common morphological trait, i.e. a narrow copulatory tube, yet have two types of accessory piece and four types of anchors and bars. *Ligophorus simpliciformis* and *L. bipartitus* have a similar type of MCO but utterly different anchors and bars. All of the remaining species have a similar type of MCO, but, when one examines in detail the length of the copulatory tube and the armature of the vagina, two pair of related species can be separated; these are *L. campanulatus* + *L. lebedevi* and *L. surianoae* + *L. mamaevi*. Furthermore, three different forms of the attachment structures can be distinguished among these species, and although *L. campanulatus* and *L. mamaevi* are similar in relation to these structures, they differ significant in the shape of the MCO and vagina.

It is also worth mentioning that all of the species of *Ligophorus* described from Red Sea mullets have an accessory piece lacking a distal bifurcation, which is different from the situation occurring in most species of this genus from other regions of the world, with the exception of *L. leporinus* and *L. hamulosus* from the South and East China Seas (Zhang & Ji, 1981; Pan, 1999; Zhang et al., 2001).

Discussion

As indicated above, there have been no previous published records of species directly attributed to *Ligophorus* from the Red Sea, or indeed from the Indian Ocean region. It is, however, worth mentioning that we have determined that there is one previous record from freshwaters in Iran, but the species has not previously been attributed to *Ligophorus*. This is material of *Ancyrocephalus fluviatilis* Bychowsky, 1949 described on the basis of specimens collected from *Liza abu* (Heckel) caught in the River Karkheh, Iran, which flows into the Persian Gulf (Bychowsky, 1949). We have examined the type-material in the ZIN collection and consider it to be a species of *Ligophorus*, to which we transfer it as *L. fluviatilis* (Bychowsky, 1949) n. comb. Paperna (1972), in his paper on Red Sea dactylogyrids of littoral and reef fishes, listed *A. fluviatilis* as a synonym of *Haliotrema vanbenedenii* (Parona & Perugia, 1890), which he reported, but did not describe, from *Mugil* spp. in the Gulf of Suez. It seems likely that this material may also have belonged to *Ligophorus*, since *H. vanbenedenii* was transferred to this genus by Euzet & Suriano (1977). Whereas Paperna & Overstreet (1981) considered that this was a variable species which extended from the Atlantic though the Indian Ocean to the Pacific, their concept more likely includes a complex of similar species. It is unlikely that Paperna's (1972) record represents *L. vanbenedenii* (*sensu stricto*), which is a parasite of *Liza* spp. in the Atlantic region (Table 2[1]), but rather a mix of related, perhaps undescribed, species. Moreover, Paperna & Overstreet (1981) listed *Haliotrema mugilis* (Tripathi, 1959) from *Liza subviridis* in India and from one and the same host, as well as *Valamugil seheli* and *Crenimugil crenilabis*, in the northern Red Sea. *H. mugilis* was placed by Young (1968), in his analysis of *Haliotrema* spp., in a group with *H. vanbenedenii*, so it seems likely that these records also represent a species or multiple species of *Ligophorus*.

Eight new species of *Ligophorus* are described above from two of the 10 species of mullets inhabiting the Red Sea (Froese & Pauly, 2011). Two of these species (*L. bykhowskyi* and *L. zhangi*) were found on *Crenimugil crenilabris* and six species (*L. simpliciformis*, *L. bipartitus*, *L. campanulatus*, *L. mamaevi*, *L. lebedevi* and *L. surianoae*) were recorded from *Liza carinata*. Moreover, one of the latter host specimens was infected by all six of the new species recorded from this host and the other two fishes by four and five species, respectively.

Analysis of the occurrence of *Ligophorus* spp. on mullets in different parts of the world's oceans shows that most host species are parasitised by two or more species of these monogeneans in one and the same region (Table 2). In fact six mugilid species, *Liza saliens*, *L. haematocheilus*, *Mugil liza*, *M. cephalus*, *Valimugil engeli* and *V.seheli* can harbour between

[1] Records listed from other regions are, in our view, questionable.

Table 2 Occurrence of *Ligophorus* spp. on mullet species in different regions of the world's oceans

Region	Host species	Species of *Ligophorus*	Source of data
NE Atlantic and Mediterranean Basin:			
Off British Isles	*Chelon labrosus*	*L. angustus* Euzet & Suriano, 1977	Anderson, 1981: Llewellyn & Anderson, 1984
Caspian Sea	*Liza saliens*	*L. heteronchus* Euzet & Suriano,1977	Ibragimov, 1988; Mamedova, 2009
	Liza aurata	*L. szidati* Euzet & Suriano, 1977	Ibragimov, 1988; Mamedova, 2009
		L. vanbenedenii (Parona & Perugia, 1890)	
Sea of Azov	*Mugil cephalus*	*L. cephali* Rubtsova, Balbuena, Sarabeev, Blasco-Costa & Euzet, 2006	Rubtsova, 2008
		L. mediterraneus Sarabeev, Balbuena & Euzet, 2005	
	Liza haematocheilus	*L. pilengas* Sarabeev & Balbuena, 2004*	Rubtsova, 2008
		L. kaohsianghsieni (Gusev, 1962)	
		L. llewellyni Dmitrieva, Gerasev & Pronkina, 2007	
	Liza aurata	*L. szidati*	Miroshnichenko & Maltsev, 1998; Rubtsova, 2008
		L. vanbenedeni	
		L. kaohsianghsieni	
	Lisa saliens	*L. szidati*	Rubtsova, 2008
		L. vanbenedenii	
Black Sea	*Liza aurata*	*L. vanbenedenii*	Dmitrieva & Gerasev, 1996; Dmitrieva, 1996; Pankov, 2011
		L. szidati	
		L. kaohsianghsieni	
		L. macrocolpos Euzet & Suriano, 1977	
	Liza saliens	*L. acuminatus* Euzet & Suriano, 1977	Dmitrieva & Gerasev, 1996; Rubtsova, 2008; Pankov, 2011
		L. euzeti Dmitrieva & Gerasev, 1996	
		L. szidati	
		L. heteronchus	
		L. macrocolpos Euzet & Suriano, 1977	
		L. minimus Euzet & Suriano, 1977	
		L. imitans Euzet & Suriano, 1977	
		L. vanbenedenii	
	Liza haematocheilus	*L. kaohsianghsieni*	Dmitrieva, 1996; Sarabeev & Balbuena, 2004; Dmitrieva et al., 2007; Pankov, 2011
		L. pilengas	
		L. lewellyni	
		L. vanbenedenii	
	Mugil cephalus	*L. mediterraneus*	Sarabeev et al, 2005; Rubtsova et al., 2006;
		L. cephali	
		L. vanbenedenii	Pankov, 2011
		L. szidati	
Sea of Marmara	*Liza ramada*	*L. confusus* Euzet & Suriano, 1977	Oguz & Bray, 2009

Table 2 continued

Region	Host species	Species of *Ligophorus*	Source of data
Mediterranean Sea	*Liza aurata*	*L. vanbenedenii* *L. szidati*	Euzet & Suriano, 1977; Mariniello et al., 2004
	Liza saliens	*L. macrocolpos* *L. acuminatus* *L. minimus* *L. heteronchus*	Euzet & Suriano, 1977; Merella & Garippa, 2001; Mariniello et al., 2004
	Liza ramada	*L. imitans* Euzet & Suriano, 1977 *L. confusus* *L. parvicirrus* Euzet & Sanfilippo, 1983	Euzet & Suriano, 1977; Euzet & Sanfilippo, 1983; Hassan et al., 1990; Caltran et al., 1995; Abu Samak & Hassan, 1999; Merella & Garippa, 2001; Mariniello et al., 2004
	Mugil cephalus	*L. cephali* *L. chabaudi* Euzet & Suriano, 1977 *L. mediterraneus*	Euzet & Suriano, 1977; Merella & Garippa, 2001; Mariniello et al., 2004; Sarabeev et al., 2005; Rubtsova et al., 2006
	Chelon labrosus	*L. angustus*	Euzet & Suriano, 1977; Merella & Garippa, 2001; Mariniello et al., 2004
NW Atlantic:			
Caribbean Sea	*Mugil curema*	*L. mugilinus* (Hargis, 1955)	Garcia & Williams, 1985; Fuentes & Nasir, 1990
Off coast of USA	*Mugil cephalus*	*L. vanbenedenii*	Zwerner & Lawler, 1972
Gulf of Mexico	*Mugil cephalus*	*L. mugilinus*	Hargis, 1955
SW Atlantic:			
Off Argentina	*Mugil platanus*	*L. saladensis* Macrotegui & Martorelli, 2009 *L. uruguayensis* Failla Siquier & Ostrowski de Núñez, 2009 (emend.)	Marcotegui & Martorelli, 2009; Failla Siquier & Ostrowski de Núñez, 2009
Off Brazil	*Mugil liza*	*L. tainhae* Abdallah, Azevedo & Luque, 2009 *L. brasiliensis* Abdallah, Azevedo & Luque, 2009 *L. guanduensis* Abdallah, Azevedo & Luque, 2009 *L. lizae* Abdallah, Azevedo & Luque, 2009	Abdallah et al., 2009
NE Pacific:			
Off Mexico	*Mugil curema*	*L. vanbenedenii*	Pérez-Ponce de Leon et al. (1999)

Table 2 continued

Region	Host species	Species of *Ligophorus*	Source of data
NW Pacific:			
South China Sea	*Liza vaigiensis*	*L. ellochelon* Zhang, Yang & Liu, 2001	Zhang et al., 2001
		L. leporinus (Zhang & Ji, 1981)	
	Liza macrolepis	*L. leporinus*	Zhang et al., 2001
		L. hamulosus Pan & Zhang in Pan, 1999	
	Liza affinis	*L. leporinus*	Zhang et al., 2001; New unpublished data
		L. pacificus Rubtsova Balbuena & Sarabeev, 2007 [syn. *L. vanbenedenii* sensu Zhang et al., 2001]	
	Liza haematocheilus	*L. kaohsianghsieni*	Zhang et al., 2003
	Liza carinata	*L. hamulosus*	Li et al., 2009
	Valimugil engeli	*Ligophorus* spp. 1–7 of Gerasev et al. (2011a)	Gerasev et al., 2011a
	Valimugil seheli	*Ligophorus* spp. 8–11 of Gerasev et al. (2011b)	Gerasev et al., 2011b
East China Sea	*Liza haematocheilus*	*L. kaohsianghsieni*	Zhang et al., 2003
		L. mugilinus	
		L. vanbenedenii	
		L. chabaudi	
	Mugil cephalus	*L. leporinus*	Zhang & Ji, 1981; Zhang et al., 2003; New unpublished data
		L. chabaudi	
		L. mugilinus	
		L. kaohsianghsieni	
		L. pacificus	
Yellow Sea	*Mugil cephalus*	*L. chongmingensis* Hu & Li, 1992	Hu & Li,1992
		L. chenzhenensis Hu & Li, 1992	
Sea of Japan	*Liza haematocheilus*	*L. kaohsianghsieni*, *L. pilengas*, *L. llewellyni*	Gusev, 1985; Rubtsova, 2009
	Mugil cephalus	*L. chabaudi*, *L. pacificus*	Rubtsova et al., 2007; Dmitrieva et al., 2009
		L. domnichi Rubtsova, Balbuena & Sarabeev, 2007	
		L. cheleus Rubtsova, Balbuena & Sarabeev, 2007	
Tumen River (opens into Sea of Japan)	*Mugil cephalus*	*L.domnichi* and *L.pacificus* [as *Ancyrocephalus vanbenedenii* in Gusev (1955)]	Gusev, 1955; New unpublished data
SE Pacific:			
Off Chile	*Mugil cephalus*	*L. huitrempe* Fernandez-Bargiela, 1987	Fernandez-Bargiela, 1987
Indian Ocean:			
Iran (close to Persian Gulf)	*Liza abu*	*L. fluviatilis* (Bychowsky, 1949) n. comb.	Bychowsky, 1949
Chilka Lagoon, India	*Liza subviridis*	?*Ligophorus* sp. (as *Ancylodiscoides mugilis* Tripathi, 1959)	Tripathi, 1959
Red Sea	*Mugil* spp.	?*Ligophorus* spp. (as *Haliotrema vanbenedenii* (Parona & Perugia, 1890))	Paperna, 1972
	Liza subviridis	?*Ligophorus* sp. (as *Haliotrema mugilis*)	Paperna & Overstreet, 1981

Table 2 continued

Region	Host species	Species of *Ligophorus*	Source of data
	Liza carinata	*L. simpliciformis* n. sp.	Present data
		L. bipartitus n. sp.	
		L. campanulatus n. sp.	
		L. mamaevi n. sp.	
		L. lebedevi n. sp.	
		L. surianoae n. sp.	
	Crenimugil crenilabris	*?Ligophorus* sp. (as *Haliotrema mugilis*)	Paperna & Overstreet, 1981
		L. bykhowskyi n. sp.	Present data
		L. zhangi n. sp	
	Valamugil seheli	*?Ligophorus* sp. (as *Haliotrema mugilis*)	Paperna & Overstreet, 1981

* Also recorded as *L. gussevi* Miroshnichenko & Maltsev, 2004 by Miroshnichenko & Maltsev (2004)

four and seven species of *Ligophorus* in one locality (Table 2). However, this does not necessarily mean that these species occur concurrently on one host specimen, as in some cases data on the occurrence of *Ligophorus* spp. is the sum of results of different studies, carried out at different times, using different sampling methods and by different researchers. The greatest number of named *Ligophorus* spp. collected on one occasion and by the same authors is four, which has been recorded on *Liza saliens* in the Mediterranean Sea (Euzet & Suriano, 1977), on *Mugil liza* off Brazil (Abdallah et al., 2009) and on *M. cephalus* from the Sea of Japan (Dmitrieva et al., 2009) (Table 2). However, Gerasev et al. (2011a, b) have recently reported seven and four un-named species from *Valimugil engeli* and *V. seheli*, respectively, off the coast of Vietnam. The presence of the six named species of *Ligophorus* spp., described in detail in the present study, simultaneously parasitizing a single host specimen indicates that the *Ligophorus*/*Liza carinata* relationship in the Red Sea may represent a useful tool for examining the speciation process in monogeneans, especially in terms of the sympatric and synxenic assemblage of congeners, in addition to site selection and interspecific competition.

The present species of *Ligophorus* are also interesting in that they exhibit a great diversity in the morphology of both their attachment and copulatory hard-parts. Some morphological characters of these species have not previously been recorded, or are very rare, in species of *Ligophorus*. These include the simple shape of the MCO accessory piece in *L. zhangi* and *L. simpliciformis*, the wide MCO tube with a large, single-chambered and expanded base in *L. bykhowskyi* and *L. zhangi*, the strongly reinforced vagina in *L. campanulatus*, the shape of the dorsal bar in *L. bipartitus* and the shape of the anchors in *L. lebedevi*. Only the two species from *Crenimugil crenilabris* (*L. bykhowskyi* and *L. zhangi*) exhibit a similarity in the morphology of the both organ systems. The six species from *Liza carinata* have a greater diversity in the form of the attachment structures than they do in the form of the MCO. However, it has been suggested that most specialist infracommunities of *Dactylogyrus* spp. (species of *Ligophorus* are also undoubtedly specialists) have a similar attachment apparatus but marked differences in the form of the copulatory organs (Jarkovsky et al., 2004). These authors explained the similarity in the form of the haptoral hard-parts as a result of adaptation to a given host. The considerable divergence in the form of the attachment structures and general similarity in the form of the reproductive hard-parts observed in this study can be related to the segregation of closely related species co-existing on the same host at different attachment sites on the gills. It has been shown that sister species of *Dactylogyrus* Diesing, 1850 on one and the same host differ in their position on the gills (Simkova et al., 2004). Although detailed data on the site of the species described in this study were not collected, species of *Ligophorus* parasitising the same host are known to have significant differences in their distribution over the gills (Abu Samak & Hassan, 1998; Pronkina et al., 2010). Furthermore, Simkova et al. (2001) were convinced that specialist monogeneans possess attachment organs closely adapted to their microenvironment on their host.

It should be noted that, at the present time, it is not possible to comment on the number of morphological groups among the species of *Ligophorus* in the Red Sea, their morphological divergence and their distribution among suitable host species, because only two of the 10 mullet species in the region have been investigated for these parasites.

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