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EIGHT NEW SPECIES OF *LIGOPHORUS* EUZET & SURIANO, 1977 (MONOGENEA: ANCYROCEPHALIDAE) FROM MUGILIDS OFF PENINSULAR MALAYSIA

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ABSTRACT. — Eight new species of *Ligophorus* Euzet & Suriano, 1977 are described from *Liza subviridis* Valenciennes and *Valamugil buchanani* Bleeker off Carey Island and off Langkawi Island, Peninsular Malaysia. They are *Ligophorus navjotsodhii*, new species, *L. chelatus*, new species, *L. funnelus*, new species, *L. parvicopulatrix,* new species, *L. bantingensis*, new species, and *L. careyensis*, new species, from *Liza subviridis* and *L. kedahensis*, new species, and *L. fenestrum*, new species, from *V. buchanani*. To facilitate differential diagnosis, Principle Component Analysis (PCA) is used to analyse morphometric data of the present *Ligophorus* species and numerical taxonomy (NT) analysis is used to compare the 42 known and eight new *Ligophorus* species based on morphological and metric characters. PCA is able to group the 318 *Ligophorus* specimens into eight groups which correspond to the eight new *Ligophorus* species. The NT analyses based on Jaccard's Index of Similarity and neighbour-joining clustering indicate that eight new and 42 known species of *Ligophorus* are 51% similar to each other and the eight new species are morphologically different from each other and the 42 known species in the size and shape of anchors, bars (particularly the antero-median protuberance (AMP) of the ventral bar) and accessory piece of the copulatory organs. *Ligophorus* is emended to include the lack of a sclerotised vaginal system in some species and the ovary being J- to U-shaped.

KEY WORDS. — *Ligophorus*, Ancyrocephalidae, Monogenea, Mugilidae, *Liza subviridis*, *Valamugil buchanani*

INTRODUCTION

There are 82 species and 18 genera in the Mugilidae (Teleostei), commonly known as mullets (Froese & Pauly, 2012). In the Malaysian waters there are ten species of mullets; *Liza subviridis* Valenciennes, *Chelon planiceps* Valenciennes, *L. vaigiensis* Quoy & Gaimard, *L. melinoptera* Valenciennes, *Mugil cephalus* Linnaeus, *Paramugil parmatus* Cantor, *Valamugil cunnesius* Valenciennes, *Moolgarda seheli* Forsskål, *Valamugil buchanani* Bleeker, and *V. speigleri* Bleeker (Froese & Pauly, 2012). In this study, only *L. subviridis* (49 specimens) and *V. buchanani* (6 specimens) obtained off Carey Island and off Langkawi Island, respectively, were examined for monogeneans.

To date monogeneans recorded from mullets include species of *Ergenstrema* Paperna, 1964 (see Paperna, 1964; Anderson, 1981a), *Polyclithrum* Rogers, 1967 (see Rogers, 1967; Ernst et al., 2000), *Solastamenides* Unnithan, 1971 (see Hargis, 1956; Zhang & Yang, 2001), *Metamicrocotyla* Yamaguti, 1952 (see Yamaguti, 1953, 1968) and *Ligophorus* Euzet & Suriano, 1977 (see Table 1). The generic designation of the type-species, *Ligophorus vanbenedenii* (Parona & Perugia, 1890) Euzet & Suriano, 1977 had been changed several times from its original designation as *Tetraonchus vanbenedenii* Parona & Perugia, 1890 (from *Liza aurata*). It had been reassigned as *Ancyrocephalus vanbenedenii* by Johnston & Tiegs (1922), as *Haplocleidus vanbenedenii* by Palombi (1949), as *Haliotrema vanbenedenii* by Young (1968) and finally as *Ligophorus vanbenedenii* by Euzet & Suriano (1977). Euzet & Suriano (1977) noted inconsistencies in the characteristics of *A. vanbenedenii* (obtained from *Liza aurata* off Sète, France) and *Ancyrocephalus paradoxus* Creplin, 1839 (type species for *Ancyrocephalus* Creplin, 1839). *A. paradoxus* has a digestive system with two unconnected branches, vas deferens looping round the right intestinal branch, two prostatic reservoirs, a median ovary and dextro-lateral vaginal opening (Bychowsky & Nagibina,

1970), whereas in *A. vanbenedenii*, the vas deferens does not overlap the right intestinal branch, there is only one prostatic reservoir and the vagina opens at the medio-ventral part of the body. Based on these differences, Euzet & Suriano (1977) assigned *A. vanbenedenii* as the type species of *Ligophorus* Euzet & Suriano, 1977 (Table 1).

Ligophorus was assigned to Ancyrocephalidae Bychowsky, 1937 by Euzet & Suriano (1977). As already noted the type-species of *Ligophorus* have numerous assignments and re-assignments to different ancyrocephalid genera (see above). Of notable interest is its re-assignment to *Haliotrema*, the catch-all genus for marine monogeneans with four anchors, by Young (1968). Lim & Justine (2011) have noted that many of the marine monogeneans with four anchors, two bars and 14 marginal hooks, assigned to the *Haliotrema* but which are restricted to particular host groups, have been subsequently reassigned as exemplified by the re-assignments of the *Haliotrema* species from the mugilids to *Ligophorus* Euzet & Suriano, 1977; from the chaetodontids to *Euryhaliotrematoides* Plaisance & Kritsky, 2004 and *Aliatrema* Plaisance & Kritsky, 2004; from *Mulloidichthys vanicolensis* (Mullidae) to *Volsellituba* Rehulkova et al., 2010 and *Pennulituba* Rehulkova et al., 2010; from lutjanids, caesionids, haemulids and sparids to *Haliotrematoides* Kritsky et al., 2009; from the sciaenids, sparids, haemulids and lutjanids to *Euryhaliotrema* Kritsky & Boeger, 2002 and recently three species of *Haliotrema* from lethrinids have been transferred to *Lethrinitrema* Lim & Justine, 2011 (see Euzet & Suriano, 1977; Kritsky & Boeger, 2002; Plaisance & Kritsky, 2004; Kritsky et al., 2009; Rehulkova et al., 2010; Lim & Justine, 2011).

Differential diagnoses particularly of new species are becoming increasingly difficult with increasing number of described species, especially if the species are morphologically similar. *Ligophorus* species have high overlapping metric parameters, prompting the use of multivariate analysis such as Principal Component Analysis (PCA) for morphometric discrimination (Sarabeev & Balbuena, 2004; Rubtsova et al., 2006; Dmitrieva et al., 2007; Rubtsova et al., 2007; Dmitrieva et al., 2009, Dmitrieva et al., 2012). Besides species discrimination, PCA has also been used to detect morphovariants within species (Mariniello et al., 2004; Tan et al., 2010). Numerical taxonomy (NT) analytical methods (Sneath & Sokal, 1973) have been used for clustering morphologically similar species (Lim & Furtado, 1987) and also for phylogenetic investigations (Agnarsson, 2004). There are 42 valid *Ligophorus* species from 14 mugilid species and they are all used in the numerical taxonomy analysis (Table 1).

In this investigation, eight *Ligophorus* species were obtained from two species of mullets, off Carey Island and off Langkawi Island, respectively. PCA and NT analyses are used to facilitate differential diagnoses and provide a more objective comparison of the new *Ligophorus* species with each other and with known *Ligophorus* species. In this study, PCA is used to confirm the status of the eight new *Ligophorus* species based on morphometric data from 318 specimens belonging to the present collection. NT analysis is done to see how the eight new *Ligophorus* species are related to each other and to the 42 known *Ligophorus* species, based on categorised metric and morphological characters.

The ventral bar of the *Ligophorus* species is basically a broad inverted V-shaped bar with antero-median protuberances (or AMP) consisting of a median piece and two lateral membranous or non-membranous ear-like processes arising from the median piece (Fig. 1B). The AMP has also been referred to as anterior median expansions (Euzet & Suriano, 1977; Euzet & Sanfillipo, 1983), anterior protuberances (Gusev, 1955), digitiform antero-process with median knoll (Dmitrieva et al., 2009), membranous protuberance with median process (Rubtsova et al., 2006; Abdallah et al., 2009; Marcotegui & Martorelli, 2009) and membranous anterior medial processes (Sarabeev & Balbuena, 2004; Siquier & Otrowski de Nunez, 2009).

MATERIAL AND METHODS

Collection of hosts and parasites. — The mullet hosts, *L. subviridis* (49 specimens) and *V. buchanani* (6 specimens) were collected in the coastal waters off Carey Island (2°51'N, 101°22'E) and off Langkawi Island (6°21'N, 99°46'E) on the west coast of Peninsular Malaysia. Monogeneans were collected from freshly killed or frozen fish and prepared for taxonomic purposes as in Lim & Gibson (2010). Briefly, the monogeneans were removed from the gills and flattened to properly expose the hard parts and soft anatomical structures. Some specimens were fixed and cleared in modified ammonium-picrate-glycerin (Malmberg, 1957; Lim, 1991) for study under phase contrast microscopy. These ammonium-picrate-glycerin specimens were later washed and dehydrated through a graded alcohol series and mounted in Canada Balsam. Some specimens were fixed in AFA (acetic acid-formalin-alcohol), stained in Gomori's triple stain and mounted in Canada Balsam after dehydration. The stained and unstained specimens were studied under bright-field and phase contrast microscopy. Images of the hard and soft anatomical structures of the *Ligophorus* species were captured using a Leica digital camera and an image analysis software (QWin Plus) and illustrated using a digitizing tablet (WACOM) and Adobe Illustrator software. In this paper, two composite illustrations (*Ligophorus navjotsodhii*, new species and *L. chelatus*, new species) (Figs. 7i, 8i) are given. Type-specimens are deposited at the Museum of Natural History, London (NHMUK), Zoological Reference Collection, Raffles Museum of Biodiversity Research, National University of Singapore, Singapore (ZRC), and Zoological Museum University of Malaya, Kuala Lumpur (MZUM).

Morphometric measurements and analysis. — The sclerotised hard parts of the haptor (anchors, bars and marginal hooks) and the copulatory organ (copulatory tube and accessory piece) of 318 specimens belonging to the present *Ligophorus* species, which have been properly flattened (stained and unstained) are measured as shown in Fig.1. The mean values and the range (within parentheses)

Table 1. List of new and known *Ligophorus* species with description and re-description information only

***Ligophorus* species**	**Host species**	**Localities (Type)**	**References**
L. acuminatus Euzet & Suriano, 1977	*Liza saliens* Risso	Mediterranean Sea	Euzet & Suriano, 1977
L. angustus Euzet & Suriano, 1977	*Chelon labrosus* Risso	Mediterranean Sea	Euzet & Suriano, 1977
L. brasiliensis Abdallah et al., 2009	*Mugil liza* Valenciennes	Off Brazil	Abdallah et al., 2009
L. cephali Rubtsova et al., 2006	*Mugil cephalus* Linnaeus	Black Sea	Rubtsova et al., 2006
L. chabaudi Euzet & Suriano, 1977	*Mugil cephalus* Linnaeus	Mediterranean Sea	Euzet & Suriano, 1977; Rubtsova et al., 2006
L. cheleus Rubtsova et al., 2007	*Mugil cephalus* Linnaeus	Sea of Japan	Rubtsova et al., 2007
L. chenzhenensis Hu & Li, 1992	*Mugil cephalus* Linnaeus	Off Chongming Island, China	Hu & Li, 1992
L. chongmingensis Hu & Li, 1992	*Mugil cephalus* Linnaeus	Off Chongming Island, China	Hu & Li, 1992
L. confusus Euzet & Suriano, 1977	*Liza ramada* Risso	Mediterranean Sea	Euzet & Suriano, 1977
L. domnichi Rubtsova et al., 2007	*Mugil cephalus* Linnaeus	Sea of Japan	Rubtsova et al., 2007
L. ellochelon Zhang, 2001	*Liza vaigiensis* Quoy & Gaimard	South China Sea	In Zhang et al., 2001
L. euzeti Dmitrieva & Gerasev, 1996	*Liza saliens* Risso	Black Sea	Dmitrieva & Gerasev, 1996
L. fluviatilis (Bychowsky, 1949) Dmitrieva et al., 2012 (syn. *Ancyrocephalus fluviatilis* Bychowsky, 1949)	*Liza abu* Heckel	Off Iran	Bychowsky, 1949; Dmitrieva et al., 2012
L. guanduensis Abdallah et al., 2009	*Mugil liza* Valenciennes	Off Brazil	Abdallah et al., 2009
L. hamulosus Pan, 1999	*Liza macrolepis* Smith	Hainan Island, China	Pan, 1999
L. heteronchus Euzet & Suriano, 1977	*Liza saliens* Risso	Mediterranean Sea	Euzet & Suriano, 1977
L. huitrempe Fernandez-Bargiela, 1987	*Mugil cephalus* Linnaeus	Off Chile	Fernandez-Bargiela, 1987
L. imitans Euzet & Suriano, 1977	*Liza ramada* Risso	Mediterranean Sea	Euzet & Suriano, 1977
L. kaohsianghsieni (Gusev, 1962) Gusev, 1985 [syn. *Ancyrocephalus kaohsianghsieni* Gusev, 1962]	*Liza haematocheila* Temminck & Schlegel	Sea of Japan	Gusev, 1985
L. leporinus (Zhang & Ji, 1981) Gusev, 1985 [syn. *Ancyrocephalus leporinus* Zhang & Ji, 1981]	*Mugil cephalus* Linnaeus	East China Sea	Zhang & Ji, 1981, in Zhang et al., 2001; Gusev, 1985
L. lizae Abdallah et al., 2009	*Mugil liza* Valenciennes	Off Brazil	Abdallah et al., 2009
L. llewellyni Dmitrieva et al., 2007	*Liza haematocheila* Temminck & Schlegel	Black Sea	Dmitrieva et al., 2007
L. macrocolpos Euzet & Suriano, 1977	*Liza saliens* Risso	Mediterranean Sea	Euzet & Suriano, 1977
L. mediterraneus Sarabeev et al., 2005	*Mugil cephalus* Linnaeus	Mediterranean Sea	Sarabeev et al., 2005
L. minimus Euzet & Suriano, 1977	*Liza saliens* Risso	Mediterranean Sea	Euzet & Suriano, 1977
L. mugilinus (Hargis, 1955) Euzet & Suriano, 1977 [syn. *Pseudohaliotrema mugilinus* Hargis, 1955]	*Mugil cephalus* Linnaeus	Gulf of Mexico	Hargis, 1955; Euzet & Suriano, 1977
L. pacificus Rubtsova et al., 2007 [syn. *L. vanbenedenii* sensu Zhang, 2001]	*Mugil cephalus* Linnaeus	Sea of Japan	Rubtsova et al., 2007; in Zhang et al., 2001
L. parvicirrus Euzet & Sanfillipo, 1983	*Liza ramada* Risso	Gulf of Lion	Euzet & Sanfillipo, 1983

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L. brasiliensis Abdallah et al., 2009	*Mugil liza* Valenciennes	Off Brazil	Abdallah et al., 2009
L. cephali Rubtsova et al., 2006	*Mugil cephalus* Linnaeus	Black Sea	Rubtsova et al., 2006
L. chabaudi Euzet & Suriano, 1977	*Mugil cephalus* Linnaeus	Mediterranean Sea	Euzet & Suriano, 1977; Rubtsova et al., 2006
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L. chenzhenensis Hu & Li, 1992	*Mugil cephalus* Linnaeus	Off Chongming Island, China	Hu & Li, 1992
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L. confusus Euzet & Suriano, 1977	*Liza ramada* Risso	Mediterranean Sea	Euzet & Suriano, 1977
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L. ellochelon Zhang, 2001	*Liza vaigiensis* Quoy & Gaimard	South China Sea	In Zhang et al., 2001
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L. guanduensis Abdallah et al., 2009	*Mugil liza* Valenciennes	Off Brazil	Abdallah et al., 2009
L. hamulosus Pan, 1999	*Liza macrolepis* Smith	Hainan Island, China	Pan, 1999
L. heteronchus Euzet & Suriano, 1977	*Liza saliens* Risso	Mediterranean Sea	Euzet & Suriano, 1977
L. huitrempe Fernandez-Bargiela, 1987	*Mugil cephalus* Linnaeus	Off Chile	Fernandez-Bargiela, 1987
L. imitans Euzet & Suriano, 1977	*Liza ramada* Risso	Mediterranean Sea	Euzet & Suriano, 1977
L. kaohsianghsieni (Gusev, 1962) Gusev, 1985 [syn. *Ancyrocephalus kaohsianghsieni* Gusev, 1962]	*Liza haematocheila* Temminck & Schlegel	Sea of Japan	Gusev, 1985
L. leporinus (Zhang & Ji, 1981) Gusev, 1985 [syn. *Ancyrocephalus leporinus* Zhang & Ji, 1981]	*Mugil cephalus* Linnaeus	East China Sea	Zhang & Ji, 1981; Zhang et al., 2001
L. lizae Abdallah et al., 2009	*Mugil liza* Valenciennes	Off Brazil	Abdallah et al., 2009

of these measurements are used in the descriptions of the new species.

Principle Component Analysis (PCA) (Pearson, 1901) – Morphometric data from these 318 specimens are statistically analysed using PCA in R (version 2.12.1; R Core Development Team, 2008). The morphometric data are analysed to narrow down the dimension of the data set and to view the important distinguishing characters as a two-dimensional PCA plot (Fig. 2).

Numerical Taxonomy (NT) analysis (Sneath & Sokal, 1973): Metric and morphological categorisation, species characterisation, similarity indices and cluster analysis. —

Metric categorisation. — The first step in NT analysis is to categorise the sclerotised hard parts of the haptors and the copulatory organs of the 8 new and 42 known *Ligophorus* species according to their size (metric) and shape into different character states and coded (table available upon request). A total of 60 character states representing all the hard parts (haptoral and copulatory organs) have been identified and categorised from the 50 *Ligophorus* species and tabulated (Table 3).

Characterisation. — The 8 new and 42 known species are next characterised on the basis of the presence (marked as '1') or absence (marked as '0') of the categorised character states.

Index of similarity. — Jaccard's Index of Similarity (Dunn & Everitt, 2004) is calculated (pairwise) for all the 50 *Ligophorus* species characterised using 4 sets of characters viz., anchors, bars, accessory piece of copulatory organs and AMP of ventral bars.

Jaccard's Index of Similarity (S_J) = C / (A + B + C)

where A = Number of attributes present in operational taxonomic unit (OTU) A

B = Number of attributes present in OTU B

C = Number of attributes present in both OTU A and B

Clustering. — The neighbour-joining clustering method in R (version 2.12.1; R Core Development Team, 2008) is used to cluster the species based on the similarity indices generated. In this paper only 4 of 7 dendrograms of relationships are presented and used in the differential diagnoses. The 4 dendrograms group the 50 *Ligophorus* species based on the anchors, bars, AMP of the ventral bar and accessory pieces (Figs. 3–6).

RESULTS

Results of the PCA of the morphometric data of the present eight *Ligophorus* species and the NT analyses of the morphologically characterised *Ligophorus* species will be discussed generally to avoid repetition prior to the descriptions of the new species. The results from these two analyses will be used in the differential diagnoses of the eight new species.

Clustering of the new* Ligophorus *species based on morphometry. — The 318 specimens of present *Ligophorus* species are clustered into eight clusters which correspond to the eight *Ligophorus* species in the PCA scatterplot (Fig. 2). In the PCA scatterplot, 49 specimens are clustered as *Ligophorus navjotsodhii*, new species, 50 specimens as *L. chelatus*, new species, 28 specimens as *L. funnelus*, new species, 60 specimens as *L. parvicopulatrix*, new species, 17 specimens as *L. bantingensis*, new species, 20 specimens as

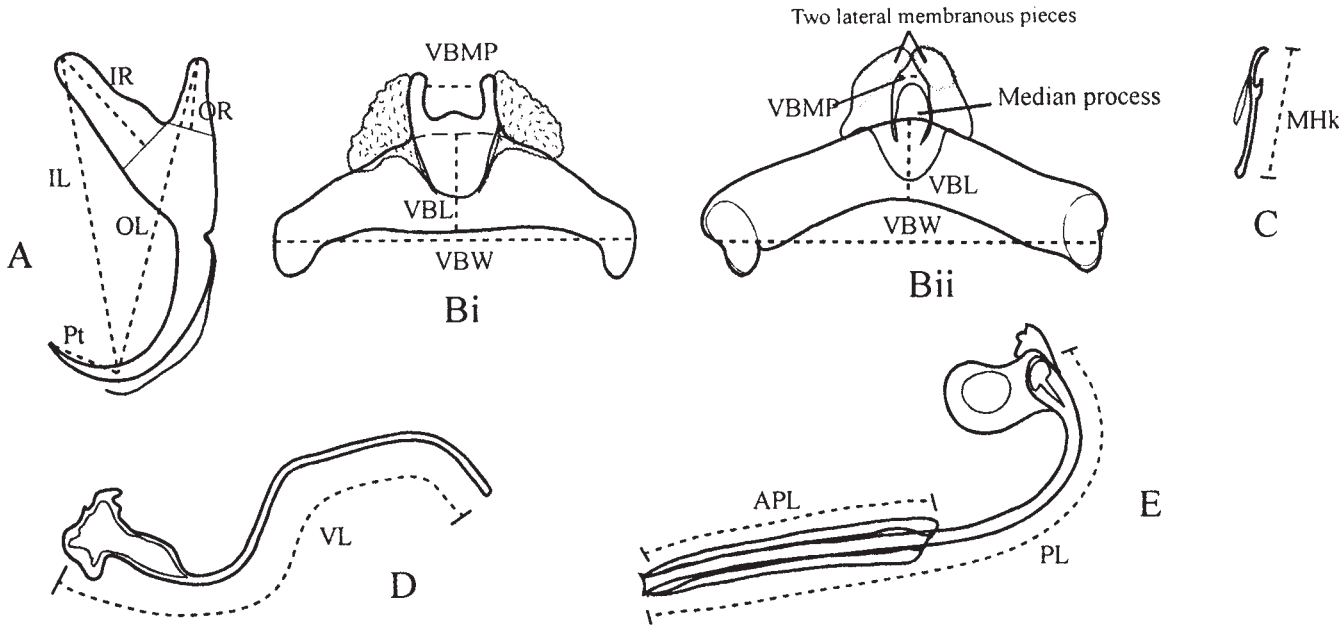

Fig. 1. Parameters measured: A, anchor; Bi, Bii, ventral bar; C, marginal hook; D, vagina; E, copulatory organ.

L. careyensis, new species, 67 specimens as *L. kedahensis*, new species and 27 specimens as *L. fenestrum*, new species (Fig. 2). Except for the latter two species which are from *V. buchanani*, the other six species are from *Liza subviridis*. *L. chelatus*, new species, *L. navjotsodhii*, new species, and *L. funnelus*, new species are grouped together, while the other five species, *L. parvicopulatrix*, new species, *L. bantingensis*, new species, *L. careyensis*, new species, *L. kedahensis*, new species, and *L. fenestrum*, new species, are grouped separately from each other (Fig. 2).

The first principle component axis (PC1, x-axis) which accounts for 44% of the total variations is an index of the overall size of all the hard parts and it separates the 318 individuals into three groups as shown in the horizontal bar plot (Fig. 2). The second principle component (PC2, y-axis) which explains 31% of the total variation, is an index that contrasts the copulatory tube length, outer length, inner root and outer root of ventral anchor, inner length and inner root of dorsal anchor, ventral and dorsal bar length against the other parameters, separating the *Ligophorus* specimens into four groups (Fig. 2). These diagnostic features will be used in the differential diagnosis of the eight species (see Descriptions and Figs. 7–14).

Clustering of the eight new and 42 known* Ligophorus *species on metric & morphological characters. — We have generated seven dendrograms based on their metric and morphological similarities but found that the information in them to be too repetitive and not effective in differential diagnosis. The dendrogram generated using all the character states together (anchors, bars, accessory pieces, and AMP) did not assist in reducing the comparative analyses, hence the decision to use the more variable morphological structures of anchors, bars, accessory pieces of the copulatory organs and AMP of the ventral bar, separately. We found that the dendrograms based on these four characters can provide us with better clusters for enough reliable information for comparison. To further facilitate differential diagnoses and to prevent excessive repetitions, we have summarised the results from the PCA and dendrograms resulting from separate analysis of the four characters (anchors, bars, accessory pieces, and AMP) (Table 2). In the differential diagnoses, comparisons are only made with species which shared at least two or more similar characters with the new species (Table 2). This way, we are able to limit our comparison to a manageable number of morphologically related species.

The 50 *Ligophorus* species are grouped into three main clusters at a distance level of 48% based on their anchors, bars, accessory pieces of the copulatory organ and AMP of the ventral bars (Figs. 3–6). At the 5% distance level (95% similarity level), 10 groups are generated when the anchors are used (Fig. 3), 13 groups are generated when the bars are used (Fig. 4), 15 groups are generated when the accessory piece is used (Fig. 5) and nine groups are generated when the AMP is used (Fig. 6). The present eight new species are found in association with different *Ligophorus* species in all four dendrograms generated (Figs. 3–6) indicating that these eight new species are different from the known species on the basis of their anchors, bars, accessory pieces, and AMP (see Descriptions of new species below).

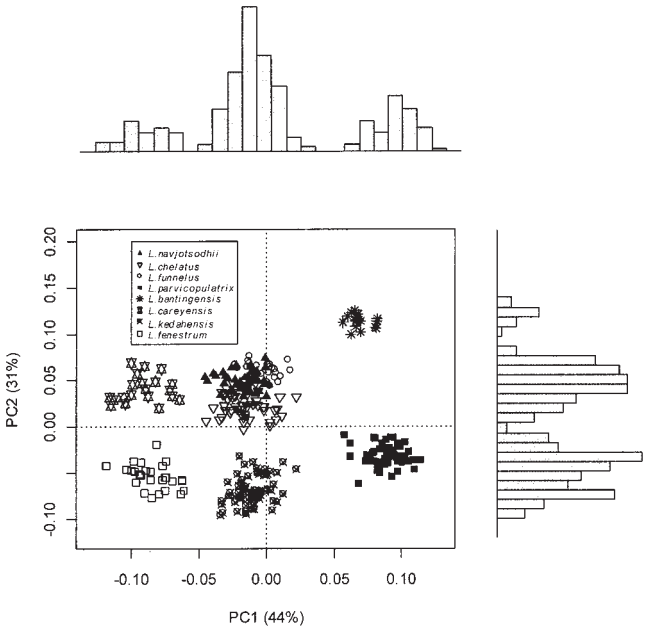

Fig. 2. Principle Component Analysis (PCA) scatterplot of 318 *Ligophorus* specimens. The vertical and horizontal bar plots indicate one-dimensional summary of the principle component axes.

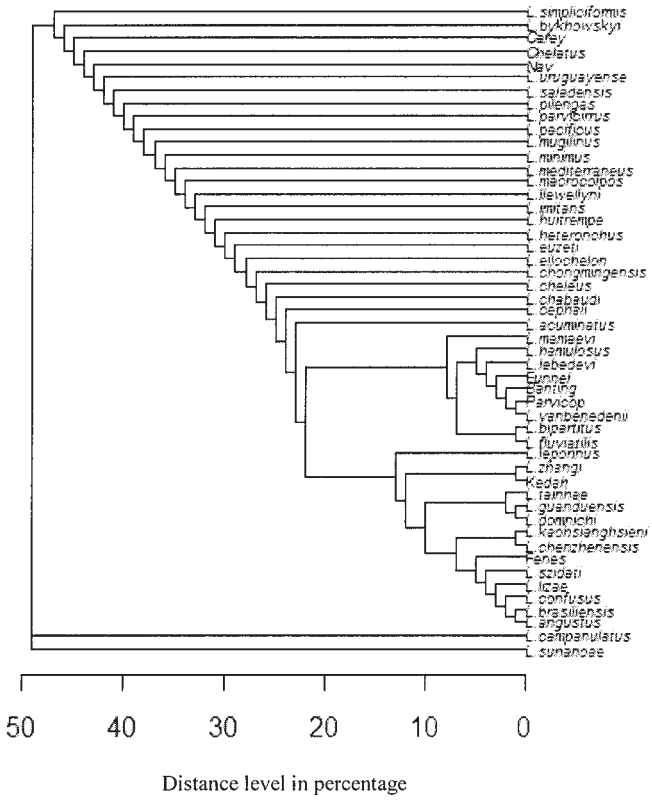

Fig. 3. Dendrogram of 50 *Ligophorus* species based on characteristics of the anchors [Nav = *L. navjotsodhii*, new species, Chelatus = *L. chelatus*, new species, Funnel = *L. funnelus*, new species, Parvicop = *L. parvicopulatrix*, new species, Banting = *L. bantingensis*, new species, Carey = *L. careyensis*, new species, Kedah = *L. kedahensis*, new species, and Fenes = *L. fenestrum*, new species].

Table 2. Clustering of the eight new *Ligophorus* species with known and new *Ligophorus* species based on PCA and numerical taxonomy (NT) analyses

New species	PCA (Fig. 2)	Dendrograms from Numerical Taxonomy Analyses				
		Anchors (Fig. 3)	**Bars** (Fig. 4)	**Accessory piece (AP)** (Fig. 5)	**AMP** (Fig. 6)	**Species occurring in 2 or more NT analyses**
L. navjotsodhii, new species	*L. chelatus*, new species *L. funnelus*, new species	*L. chelatus*, new species *L. careyensis*, new species *L. simpliciformis* *L. bykhowskyi* *L. uruguayense* *L. saladensis* *L. pilengas* *L. parvicirrus* *L. pacificus* *L. mugilinus* *L. minimus* *L. mediterraneus* *L. macrocolpos* *L. llewellyni* *L. imitans* *L. huitrempe* *L. heteronchus* *L. euzeti* *L. ellochelon* *L. cephali* *L. chongmingensis* *L. cheleus* *L. chabaudi* *L. acuminatus*	*L. zhangi* *L. llewellyni* *L. euzeti*	*L. careyensis*, new species *L. chelatus*, new species	*L. careyensis*, new species *L. funnelus*, new species *L. vanbenedenii* *L. zhangi* *L. surianoae* *L. uruguayense* *L. saladensis* *L. pilengas* *L. parvicirrus* *L. minimus* *L. mediterraneus* *L. macrocolpos* *L. llewellyni* *L. imitans* *L. heteronchus* *L. bipartitus*	*L. chelatus*, new species (Anchors & AP) *L. careyensis*, new species (Anchors, AP & AMP) *L. llewellyni* (Anchors, bars & AMP) *L. euzeti* (Anchors & Bars) *L. uruguayense* (Anchors & AMP) *L. saladensis* (Anchors & AMP) *L. pilengas* (Anchors & AMP) *L. parvicirrus* (Anchors & AMP) *L. minimus* (Anchors & AMP) *L. mediterraneus* (Anchors & AMP) *L. macrocolpos* (Anchors & AMP) *L. imitans* (Anchors & AMP) *L. heteronchus* (Anchors & AMP)
L. chelatus, new species	*L. navjotsodhii*, new species *L. funnelus*, new species	*L. navjotsodhii*, new species *L. careyensis*, new species *L. simpliciformis* *L. bykhowskyi* *L. uruguayense* *L. saladensis* *L. pilengas* *L. parvicirrus* *L. pacificus* *L. mugilinus* *L. minimus* *L. mediterraneus*	*L. careyensis*, new species *L. kaohsianghsieni* *L. parvicirrus* *L. minimus* *L. campanulatus*	*L. careyensis*, new species *L. navjotsodhii*, new species	*L. kedahensis*, new species *L. lebedevi* *L. mamaevi* *L. lizae* *L. campanulatus* *L. mugilinus* *L. guanduensis* *L. chabaudi* *L. cephali*	*L. navjotsodhii*, new species (Anchors & AP) *L. careyensis*, new species (Anchors, Bars & AP) *L. parvicirrus* (Anchors & Bars) *L. minimus* (Anchors & Bars) *L. mugilinus* (Anchors & AMP) *L. chabaudi* (Anchors & AMP) *L. cephali* (Anchors & AMP)

Table 2. Cont'd.

New species	PCA (Fig. 2)	Dendrograms from Numerical Taxonomy Analyses				
		Anchors (Fig. 3)	**Bars** (Fig. 4)	**Accessory piece (AP)** (Fig. 5)	**AMP** (Fig. 6)	**Species occurring in 2 or more NT analyses**
		L. macrocolpos *L. llewellyni* *L. imitans* *L. huitrempe* *L. heteronchus* *L. euzeti* *L. ellochelon* *L. chongmingensis* *L. cheleus* *L. chabaudi* *L. cephali* *L. acuminatus*				
L. funnelus, new species	*L. navjotsodhii*, new species *L. chelatus*, new species	*L. bantingensis*, new species *L. parvicopulatrix*, new species *L. hamulosus* *L. lebedevi* *L. vanbenedenii*	*L. saladensis* *L. pilengas* *L. uruguayense* *L. acuminatus*	*L. bantingensis*, new species	*L. careyensis*, new species *L. navjotsodhii*, new species *L. vanbenedenii* *L. zhangi* *L. uruguayense* *L. saladensis* *L. pilengas* *L. parvicirrus* *L. minimus* *L. mediterraneus* *L. macrocolpos* *L. llewelyni* *L. imitans* *L. heteronchus* *L. bipartitus* *L. surianoae*	*L. bantingensis*, new species (Anchors & AP) *L. vanbenedenii* (Anchors & AMP) *L. saladensis* (Bars & AMP) *L. pilengas* (Bars & AMP) *L. uruguayense* (Bars & AMP)
L. parvicopulatrix, new species		*L. funnelus*, new species *L. bantingensis*, new species, *L. hamulosus* *L. lebedevi* *L. vanbenedenii*	*L. bantingensis*, new species *L. huitrempe*	*L. fenestrum*, new species *L. kedahensis*, new species *L. llewelynii* *L. lizae* *L. leporinus* *L. hamulosus*	*L. hamulosus*	*L. bantingensis*, new species (Anchors & Bars) *L. hamulosus* (Anchors, AP & AMP)
L. bantingensis, new species		*L. funnelus*, new species *L. parvicopulatrix*, new species *L. hamulosus* *L. lebedevi* *L. vanbenedenii*	*L. parvicopulatrix*, new species *L. huitrempe*	*L. funnelus*, new species	*L. szidati* *L. huitrempe* *L. confusus* *L. angustus* *L. fluviatilis*	*L. funnelus*, new species (Anchors & AP) *L. parvicopulatrix*, new species (Anchors & Bars) *L. huitrempe* (Bars & AMP)

Table 2. Cont'd.

New species	PCA (Fig. 2)	Dendrograms from Numerical Taxonomy Analyses				
		Anchors (Fig. 3)	**Bars** (Fig. 4)	**Accessory piece (AP)** (Fig. 5)	**AMP** (Fig. 6)	**Species occurring in 2 or more NT analyses**
L. careyensis, new species		*L. navjotsodhii*, new species *L. chelatus*, new species *L. simpliciformis* *L. bykhowskyi* *L. uruguayense* *L. saladensis* *L. pilengas* *L. parvicirrus* *L. pacificus* *L. mugilinus* *L. minimus* *L. mediterraneus* *L. macrocolpos* *L. llewellyni* *L. imitans* *L. huitrempe* *L. heteronchus* *L. euzeti* *L. ellochelon* *L. acuminatus* *L. chongmingensis* *L. cheleus* *L. chabaudi* *L. cephali*	*L. chelatus*, new species *L. kaohsianghsieni* *L. parvicirrus* *L. minimus* *L. campanulatus*	*L. navjotsodhii*, new species *L. chelatus*, new species	*L. funnelus*, new species *L. navjotsodhii*, new species *L. vanbenedenii* *L. zhangi* *L. surianoae* *L. uruguayense* *L. saladensis* *L. pilengas* *L. parvicirrus* *L. minimus* *L. llewelynii* *L. mediterraneus* *L. macrocolpos* *L. imitans* *L. heteronchus* *L. bipartitus*	*L. navjotsodhii*, new species (Anchors, AP & AMP) *L. chelatus*, new species (Anchors, Bars & AP) *L. parvicirrus* (Anchors, Bars & AMP) *L. minimus* (Anchors, Bars & AMP) *L. uruguayense* (Anchors & AMP) *L. saladensis* (Anchors & AMP) *L. pilengas* (Anchors & AMP) *L. mediterraneus* (Anchors & AMP) *L. macrocolpos* (Anchors & AMP) *L. llewellyni* (Anchors & AMP) *L. imitans* (Anchors & AMP) *L. heteronchus* (Anchors & AMP)
L. kedahensis, new species		*L. zhangi*		*L. fenestrum*, new species *L. parvicopulatrix*, new species *L. llewelynii* *L. lizae* *L. leporinus* *L. hamulosus*	*L. chelatus*, new species *L. mugilinus* *L. guanduensis* *L. chabaudi* *L. cephali*	
L. fenestrum, new species			*L. bykhowskyi* *L. ellochelon*	*L. kedahensis*, new species *L. parvicopulatrix*, new species *L. llewelynii* *L. lizae* *L. leporinus* *L. hamulosus*	*L. leporinus* *L. kaohsianghsieni* *L. chongmingensis*	*L. leporinus* (Bars, AP & AMP)

Table 3. List of metric and morphological characters used in the numerical taxonomy (NT) analyses.

Character	Character States
Copulatory tube: Length	Long: >150 μm Medium: 81–149 μm Short: <80 μm
Copulatory tube: Ornamentation of bilobed initial part	Absent Present
Accessory piece: Length	Long: >90 μm (91–102 μm) Medium: 21–89 μm Short: <20 μm (15–20 μm)
Accessory piece: Connection	Connected to initial part Not connected to initial part
Accessory piece: Shape	Simple grooved tube Grooved tube with expanded distal part Grooved tube with expanded proximal part Two opposing pieces Bifurcated ends with handle Bifurcated ends without handle Funnel-like Beak-like
Vagina:	Absent/Not observed Present
Vaginal tube: Length	Long (100–200 μm) Medium (30–99 μm) Short (15–29 μm)
Ventral bar: Width	Broad: >50 μm (51–78 μm) Narrow: ≤50 μm (9–50 μm)
Ventral bar: Shape	Inverted curved bar Straight horizontal bar
Ventral bar: Antero-median protuberance (AMP)	Raised median piece + non-membranous lateral pieces Raised elongate median piece + non-membranous lateral pieces Flat/depressed median piece + non-membranous lateral pieces Raised median piece + membranous lateral pieces Raised elongate median piece + membranous lateral pieces Flat/depressed median piece + membranous lateral pieces Bifurcated median piece + no lateral pieces Raised median piece + membranous lateral distal pieces Flat serrated median piece + no lateral pieces
Dorsal bar: Width	Broad: >50 μm (51–78 μm) Narrow: ≤50 μm (9–50 μm)
Dorsal bar: Shape	U-shape U-shape with shoulder V-shape V-shape with shoulder Broad V-shape Straight horizontal bar
Ventral anchor: Fenestration	Present Absent
Ventral anchor: Inner length	Long: ≥30 μm (30–49 μm) Short: <30 μm (14–29 μm)
Ventral anchor: Roots	Inner root longer than outer root Inner root shorter than outer root
Ventral anchor: Points	Long: ≥11 μm (11–18 μm) Short: ≤10 μm (1–10 μm)
Dorsal anchor: Fenestration	Present Absent
Dorsal anchor: Inner length	Long: ≥30 μm (30–49 μm) Short: <30 μm (14–29 μm)
Dorsal anchor: Roots	Inner root longer than outer root Inner root shorter than outer root
Dorsal anchor: Points	Long: ≥11 μm (11–18 μm) Short: ≤10 μm (1–10 μm)

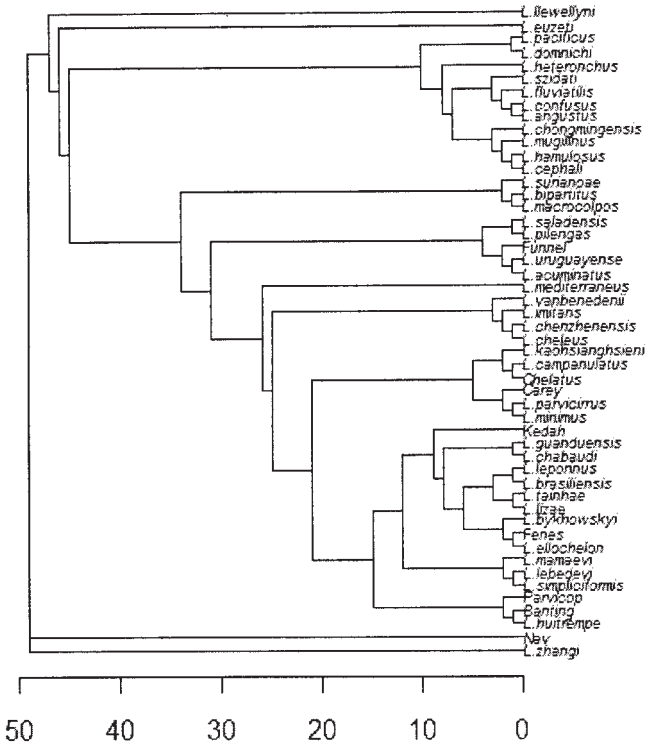

Fig. 4. Dendrogram of 50 *Ligophorus* species based on characteristics of the bars (abbreviations for new species as in Fig. 3).

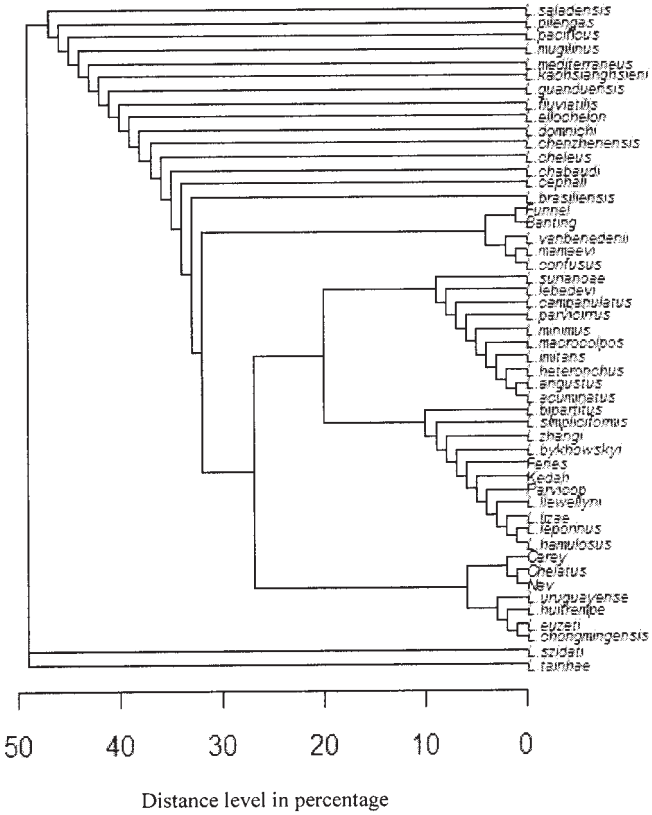

Fig. 5. Dendrogram of 50 *Ligophorus* species based on the accessory piece of the copulatory organs (abbreviations for new species as in Fig. 3).

TAXONOMY

Ligophorus navjotsodhii, new species

(Fig. 7i, 7A–F)

Type-host. — *Liza subviridis* Valenciennes

Type-locality. — Off Carey Island, Banting, Malaysia (2°51'N, 101°22'E)

Type specimens. — Holotype: NHMUK 2012.7.2.1

Paratypes: 6 paratypes NHMUK 2012.7.2.2–7 in the Natural History Museum, London; 1 paratype ZRC.PAR.02 in the Raffles Museum of Biodiversity Research, National University of Singapore; 41 paratypes MZUM(P)2012.444(P)–484(P) in the University of Malaya collection.

Material studied. — 49 specimens studied; 49 specimens measured.

Etymology. — This species is named in honour of the late Prof. Navjot S. Sodhi, National University of Singapore, Singapore for his contribution to Science.

Description. — Body elongate, 600 (382–801) × 97 (61–134) (n = 49), 3 pairs of head organs, 2 pairs pigmented eye spots, posterior with lenses and bigger than anterior pair. Mouth subterminal, ventral; pharynx ovoid, 31 (24–34) × 31 (24–35) (n = 49); intestine bifurcates posterior to pharynx, rejoins posterior to testis and anterior to peduncle forming cyclocoel. Haptor well demarcated; size 91 (59–136) × 109 (63–158) (n = 49); 14 larval type marginal hooks, similar,

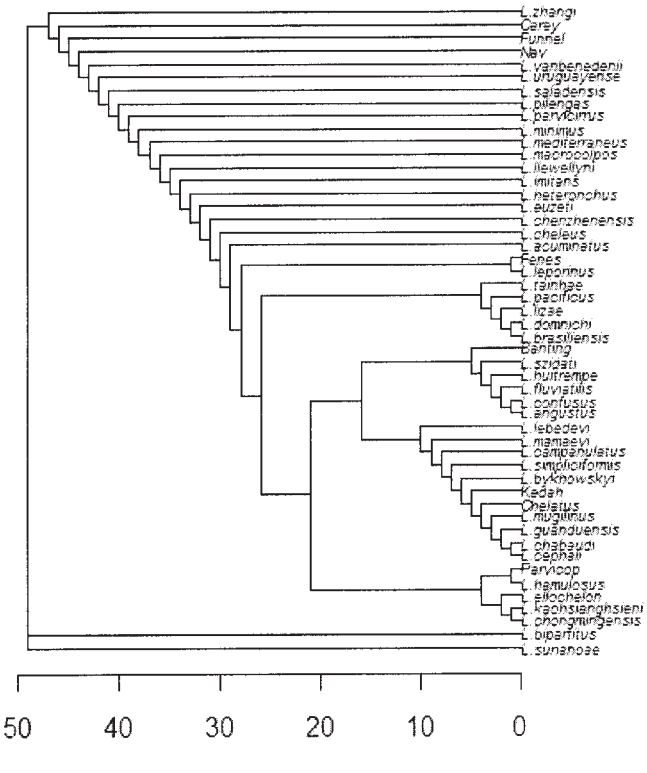

Fig. 6. Dendrogram of 50 *Ligophorus* species based on the AMP of the ventral bar (abbreviations for new species as in Fig. 3).

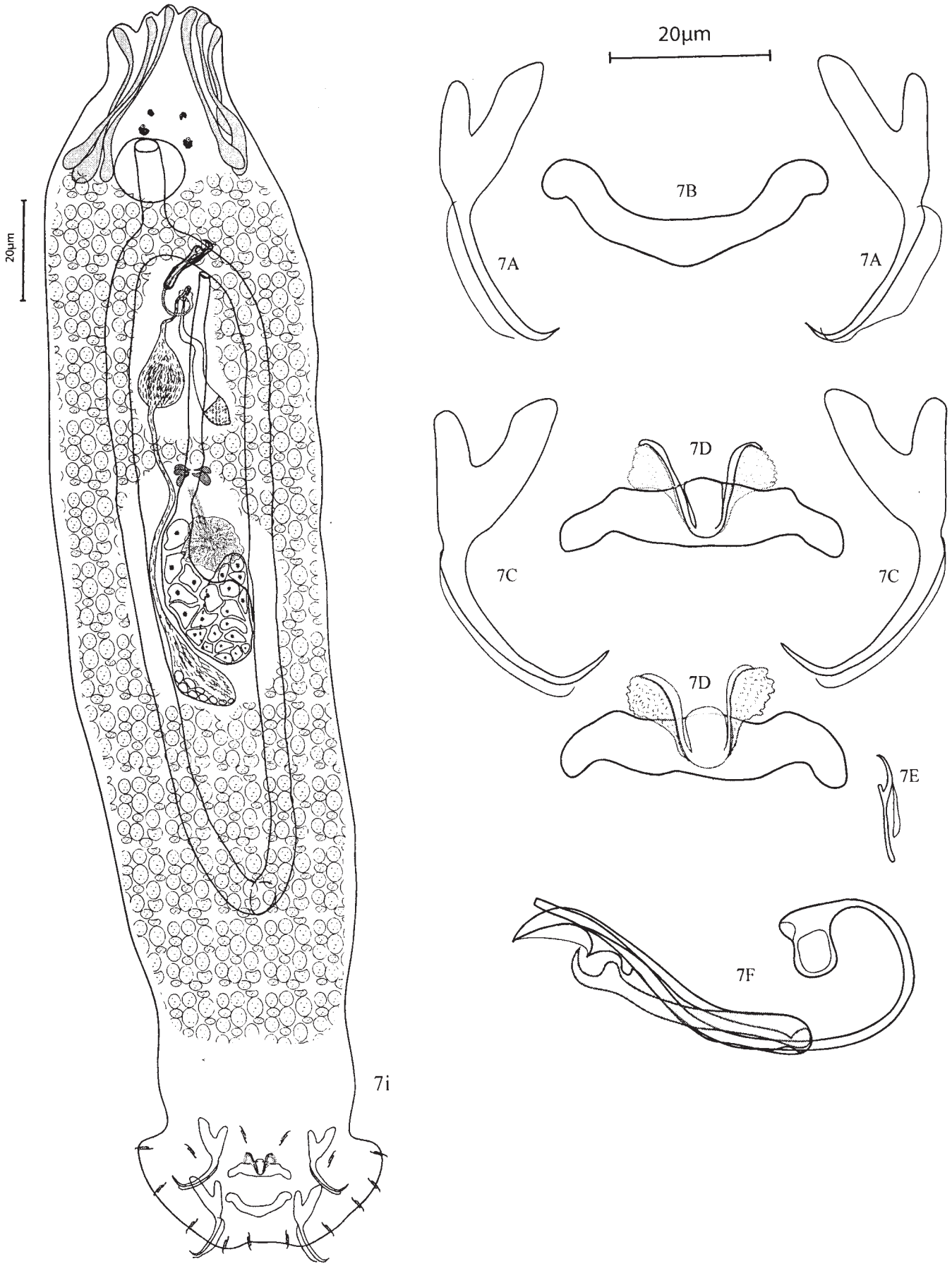

Fig. 7. *Ligophorus navjotsodhii*, new species. 7i, composite illustration of entire worm (dorsal view). 7A–F, sclerotised hard parts: A, dorsal anchors; B, dorsal bar; C, ventral anchors; D, ventral bar (two forms); E, marginal hook; F, male copulatory organ.

length 13 (11–15) (n = 49); two pairs of anchors; 2 dorsal anchors, inner length 36 (33–41) (n = 49), outer length 35 (31–38) (n = 49), inner root 14 (12–15) (n = 49), outer root 8 (6–9) (n = 49), point 6 (4–9) (n = 49); 2 ventral anchors, inner length 36 (32–39) (n = 49), outer length 37 (34–39) (n = 49), inner root 14 (11–16) (n = 49), outer root 9 (7–10) (n = 49), point 7 (5–8) (n = 49); 2 connecting bars: V-shaped dorsal bar, 33 (29–36) × 5 (4–6) (n = 49); ventral bar inverted V-shape, 33 (29–39) × 8 (5–9) (n = 49), AMP consisting of two membranous lateral pieces and a flattened median piece, distance between lateral pieces, 7 (6–10) (n = 49). Testis single, elongate ovoid, postero-dorsal to ovary; posterior region prominent, cells spermatozoa in anterior region, vas deferens leaves anterior region of testis, to sinistral-ventral side, ascends intercaecally, distending, forming seminal vesicle, narrows as vas efferens to enter into smaller lobe of bilobed initial part of copulatory tube. Single elongate gourd-shaped prostatic reservoir with prostatic duct leaving reservoir to enter bilobed initial of copulatory tube. Copulatory organ consists of copulatory tube, length 71 (63–96) (n = 49) with bilobed initial part and two opposing accessory pieces; an elongate groove piece, 27 (22–30) (n = 49) and similar length elongate non-groove piece with distal hook. Ovary elongate with recurved posterior region, J-shaped (Fig. 7i), anterior end narrows to form oviduct, continues anteriorly as oötype surrounded by Mehlis' gland; proceeds anteriorly as uterus to open near copulatory tube opening. Vagina and vaginal tube not observed, prominent sperm-filled seminal receptacle at midbody dorsal to ovary, duct from seminal receptacle to oviduct not observed in this species. Vitellarium in lateral fields approximately co-extensive with intestinal caeca, confluent just posterior to intestinal bifurcation, just anterior to ovary and just posterior to cyclocoel.

Differential diagnosis. — The scatterplot shows that the 49 specimens of *L. navjotsodhii*, new species are clustered together and closely associated with *L. chelatus*, new species and *L. funnelus*, new species (Fig. 2) in having metrically similar haptoral hard parts as well as copulatory tube. The NT analyses (Table 2) also indicate that *L. navjotsodhii*, new species is similar to *L. chelatus*, new species in having similar anchors and two opposing accessory pieces, but they differ in the distal end of the non-grooved part of the accessory piece; hook-like in *L. navjotsodhii*, new species and claw-like in *L. chelatus,* new species (Figs. 7F, 8F). *L. navjotsodhii*, new species differs from *L. funnelus*, new species in having two opposing accessory pieces compared to the single funnel-shaped accessory piece in *L. funnelus*, new species (Figs. 7F, 9F). The NT analyses (Table 2) also show that *L. navjotsodhii*, new species is similar to *L. careyensis*, new species in having similar types of anchors, accessory piece and AMP, to *L. llewellyni* in the structure of the anchors, bars and AMP, to *L. euzeti* in anchors and bars, to *L. zhangi* in bars and AMP and to *L. heteronchus*, *L. imitans*, *L. macrocolpos*, *L. minimus*, *L. mediterraneus*, *L. parvicirrus*, *L. pilengas*, *L. saladensis*, and *L. uruguayense* in the structure of the anchors and AMP (Table 2). *L. navjotsodhii*, new species however differs from all these abovementioned species mainly in possessing a hook-like distal end of the non-grooved piece of the accessory piece (Fig. 7F).

Ligophorus chelatus, new species
(Fig. 8i, 8A–G)

Type-host. — *Liza subviridis* Valenciennes

Type-locality. — Off Carey Island, Banting, Malaysia (2°51'N, 101°22'E)

Type specimens. — Holotype: NHMUK 2012.7.2.8

Paratypes: 5 paratypes NHMUK 2012.7.2.9–13 in the Natural History Museum, London; 3 paratypes (ZRC.PAR.05) and 2 paratypes (ZRC.PAR.08) in the Raffles Museum of Biodiversity Research, National University of Singapore; 39 paratypes MZUM(P)2012.278(P)–316(P) in the University of Malaya collection.

Material studied. — 50 specimens studied; 50 specimens measured.

Etymology. — This species is named after the claw-like accessory piece.

Description. — Body elongate, 610 (382–801) 95 (52–134) (n = 50), pharynx size 31 (24–37) × 31 (24–35) (n = 30). Head-organs, eye-spots and alimentary system as in *L. navjotsodhii*, new species. Haptor well demarcated; size 92 (55–148) × 115 (63–165) (n = 50); 14 larval type marginal hooks, length 13 (11–16) (n = 50); two pairs of anchors; 2 dorsal anchors, inner length 38 (33–41) (n = 50), outer length 37 (30–40) (n = 50), inner root 14 (12–17) (n = 50), outer root 8 (6–10) (n = 50), point 6 (4–8) (n = 50); 2 ventral anchors, inner length 36 (32–39) (n = 50), outer length 38 (30–41) (n = 50), inner root 14 (11–16) (n = 50), outer root 9 (7–11) (n = 50), point 7 (5–10) (n = 50); 2 connecting bars: V-shaped dorsal bar, 34 (29–41) × 5 (4–7) (n = 50); ventral bar inverted W, 35 (29–40) × 8 (6–10) (n = 50), AMP with two membranous lateral pieces and raised median piece, distance between lateral pieces, 7 (5–11) (n = 50). Soft anatomical male reproductive system as in *L. navjotsodhii,* new species. Copulatory organ consists of copulatory tube, length 70 (59–80) (n = 50) with bilobed initial part and two opposing accessory pieces; an elongate groove piece 26 (21–31) (n = 50) and similar length non-groove piece with distal claw. Soft anatomical female reproductive system as in *L. navjotsodhii,* new species except vagina is sclerotised, vaginal opening median at level of recurved portion of ovary, vaginal tube sclerotised, length 34 (30–37) (n = 10), leading to ovoid seminal receptacle.

Differential diagnosis. — Based on the PCA (Fig. 2) and NT analyses (Table 2), *L. chelatus*, new species is similar to *L. navjotsodhii*, new species in having anchors of similar shape and size and two opposing accessory pieces, but the two species are different in the distal end of the non-grooved part of the accessory piece; claw-like in *L. chelatus*, new species and hook-like in *L. navjotsodhii*, new species (Figs. 8F, 7F). *L. chelatus*, new species and *L. navjotsodhii*, new species are grouped with *L. funnelus*, new species in the PCA scatterplot (Fig. 2) based on similarities in measurements of their anchors, bars and copulatory tube but *L. chelatus*, new species differs from *L. funnelus*, new species in having

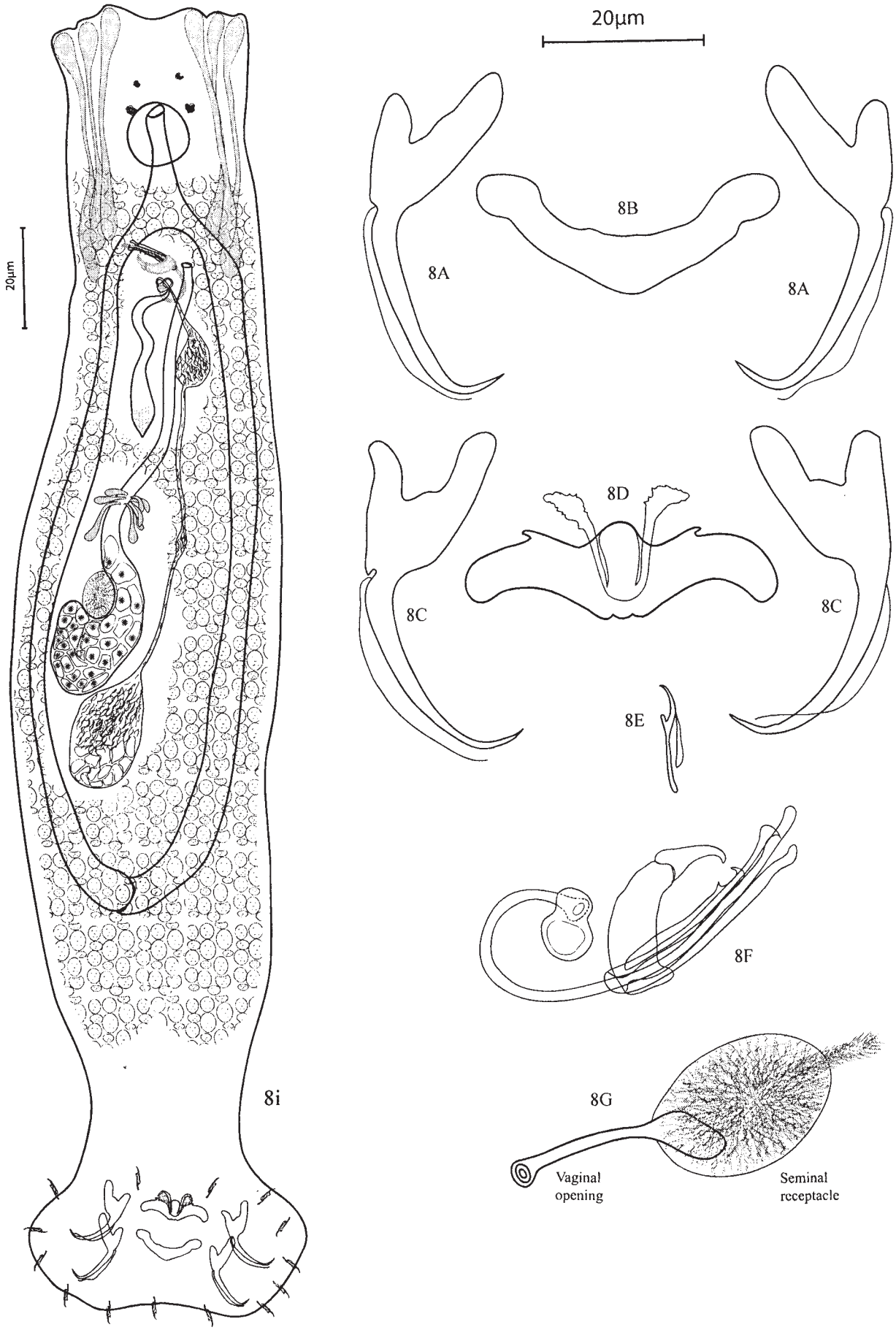

Fig. 8. *Ligophorus chelatus*, new species. 8i, composite illustration of entire worm (dorsal view). A–G, sclerotised hard parts: A, dorsal anchors; B, dorsal bar; C, ventral anchors; D, ventral bar (two forms); E, marginal hook; F, male copulatory organ; G, vaginal opening and seminal receptacle.

two opposing accessory pieces instead of the funnel-like accessory piece of *L. funnelus*, new species (Figs. 8F, 9F) and from *L. navjotsodhii*, new species in having a claw-like distal end instead of hook-like distal end of the non-grooved opposing accessory piece (Figs. 8F, 7F). The NT analyses grouped *L. chelatus,* new species with *L. careyensis,* new species based on similarities in the structure of the anchors, bars and accessory piece, with *L. parvicirrus* and *L. minimus* in the anchors and bars and with *L. cephali, L. chabaudi*, and *L. mugilinus* in the structure of the anchors and AMP (Table 2). However *L. chelatus*, new species differs from all these abovementioned species in having two opposing accessory pieces and from *L. careyensis*, new species in having the non-grooved opposing piece with a distal claw (Fig. 8F) instead of a distal fork (Fig. 12F).

Ligophorus funnelus, new species
(Fig. 9A–G)

Type-host. — *Liza subviridis* Valenciennes

Type-locality. — Off Carey Island, Banting, Malaysia (2°51'N, 101°22'E)

Type specimens. — Holotype: NHMUK 2012.7.2.14

Paratypes: 4 paratypes NHMUK 2012.7.2.15–18 in the Natural History Museum, London; 3 paratypes ZRC.PAR.01, ZRC.PAR.03 and ZRC.PAR.09 in the Raffles Museum of Biodiversity Research, National University of Singapore; 26 paratypes MZUM(P)2012.828(P)–853(P) in the University of Malaya collection.

Material studied. — 34 specimens studied; 28 specimens measured.

Etymology. — This species is named after its funnel-like accessory piece. Note that 'funnelus' is a noun in apposition.

Description. — Body elongate, 585 (381–790) × 95 (52–134) (n = 28), pharynx size 34 (29–39) × 34 (30–41) (n = 28). Head-organs, eye-spots, and alimentary system as in *L. navjotsodhii*, new species. Haptor well demarcated; size 86 (59–117) × 106 (46–162) (n = 28); 14 larval type marginal hooks, length 13 (9–15) (n = 28); two pairs of anchors; 2 dorsal anchors, inner length 25 (22–28) (n = 28), outer length 24 (23–25) (n = 28), inner root 12 (10–13) (n = 28), outer root 7 (5–8) (n = 28); point 6 (4–7) (n = 28); 2 ventral anchors, inner length 29 (24–32) (n = 28), outer length 34 (31–36) (n = 28), inner root 11 (9–13) (n = 28), outer root 9 (5–11) (n = 28), point 5 (4–7) (n = 28); 2 connecting bars: U-shaped dorsal bar, 38 (35–41) × 4 (3–6) (n = 28); ventral bar inverted V, 34 (30–36) × 7 (6–8) (n = 28), AMP with two membranous lateral pieces and flattened median piece, distance between lateral pieces, 6 (5–7) (n = 28). Soft anatomical male reproductive system as in *L. navjotsodhii*, new species. Copulatory organ consists of copulatory tube, length 77 (64–85) (n = 28) with bilobed initial part and funnel-like accessory piece, 24 (19–28) (n = 28). Soft anatomical female reproductive system as in *L. navjotsodhii*,

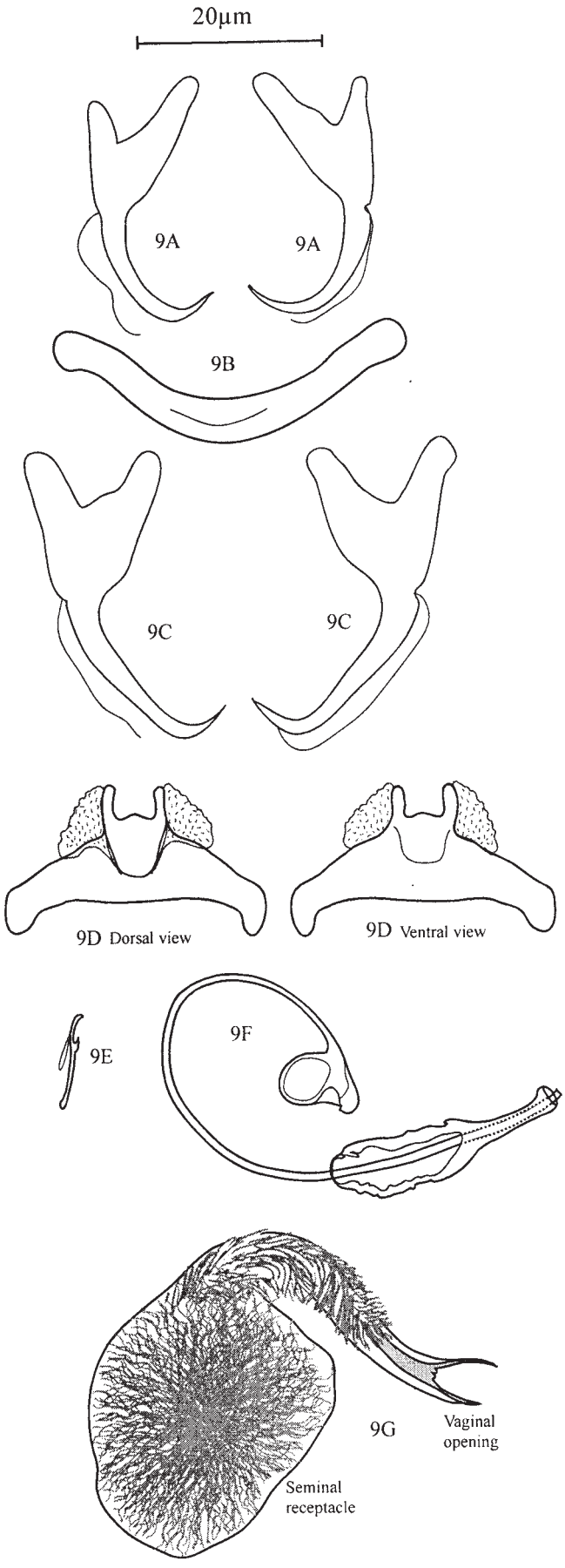

Fig. 9. *Ligophorus funnelus*, new species: A, dorsal anchors; B, dorsal bar; C, ventral anchors; D, ventral bar (two forms); E, marginal hook; F, male copulatory organ; G, vaginal opening and seminal receptacle.

new species except vagina sclerotised, sclerotised vaginal opening, sub-marginal, vaginal tube sclerotised, 37 (33–41) (n = 10), leading to ovoid seminal receptacle, sperm-filled duct from seminal receptacle to oviduct.

Differential diagnosis. — *L. funnelus*, new species is grouped with *L. navjotsodhii*, new species and *L. chelatus*, new species (Fig. 2) in the PCA scatterplot in having anchors, bars and copulatory tube of similar sizes. *L. funnelus*, new species differs in having a single funnel-shaped accessory piece compared to two opposing accessory pieces in *L. navjotsodhii*, new species and *L. chelatus*, new species (Figs. 9F, 7F, 8F). The NT analyses show that *L. funnelus,* new species is similar to *L. bantingensis,* new species in the structure of the anchors and accessory piece, to *L. vanbenedenii* in the anchors and AMP and to *L. uruguayense*, *L. pilengas*, and *L. saladensis* in the structure of the bars and AMP (Table 2). However *L. funnelus*, new species differs from these abovementioned species in having a single funnel-shaped accessory piece (Fig. 9F). *L. funnelus*, new species is similar to *L. bantingensis*, new species in the structure of the anchors and in having a funnel-like accessory piece (Figs. 9F, 11F) but the two species differ in the detailed structure of the accessory piece, where in *L. funnelus*, new species, the proximal opening is larger compared to the smaller opening in *L. bantingensis*, new species; in the detailed structures of the AMP where *L. funnelus*, new species has a depressed-flat median piece while *L. bantingensis*, new species has a slight raised median piece (Figs. 9D, 11D) and *L. bantingensis*, new species is smaller in terms of size of anchors, bars and copulatory tube as shown in the scatterplot (Fig. 2).

Ligophorus parvicopulatrix, new species
(Fig. 10A–F)

Type-host. — *Liza subviridis* Valenciennes

Type-locality. — Off Carey Island, Banting, Malaysia (2°51'N, 101°22'E)

Type specimens. — Holotype: NHMUK 2012.7.2.19

Paratypes: 6 paratypes NHMUK 2012.7.2.20–25 in the Natural History Museum, London; 1 paratype ZRC.PAR.04 in the Raffles Museum of Biodiversity Research, National University of Singapore; 61 paratypes MZUM(P)2012.22(P)–82(P) in the University of Malaya collection.

Material studied. — 69 specimens studied; 60 specimens measured.

Etymology. — This species is named after its small copulatory organ.

Description. — Body elongate, 1078 (642–1454) × 166 (73–231) (n = 60), pharynx ovoid, 53 (46–59) × 53 (46–59) (n = 30). Head-organs, eye-spots and alimentary system as in *L. navjotsodhii*, new species. Haptor well demarcated, size 122 (85–175) × 150 (71–208) (n = 60); 14 larval type marginal hooks, similar, length 11 (9–13) (n = 60); two pairs

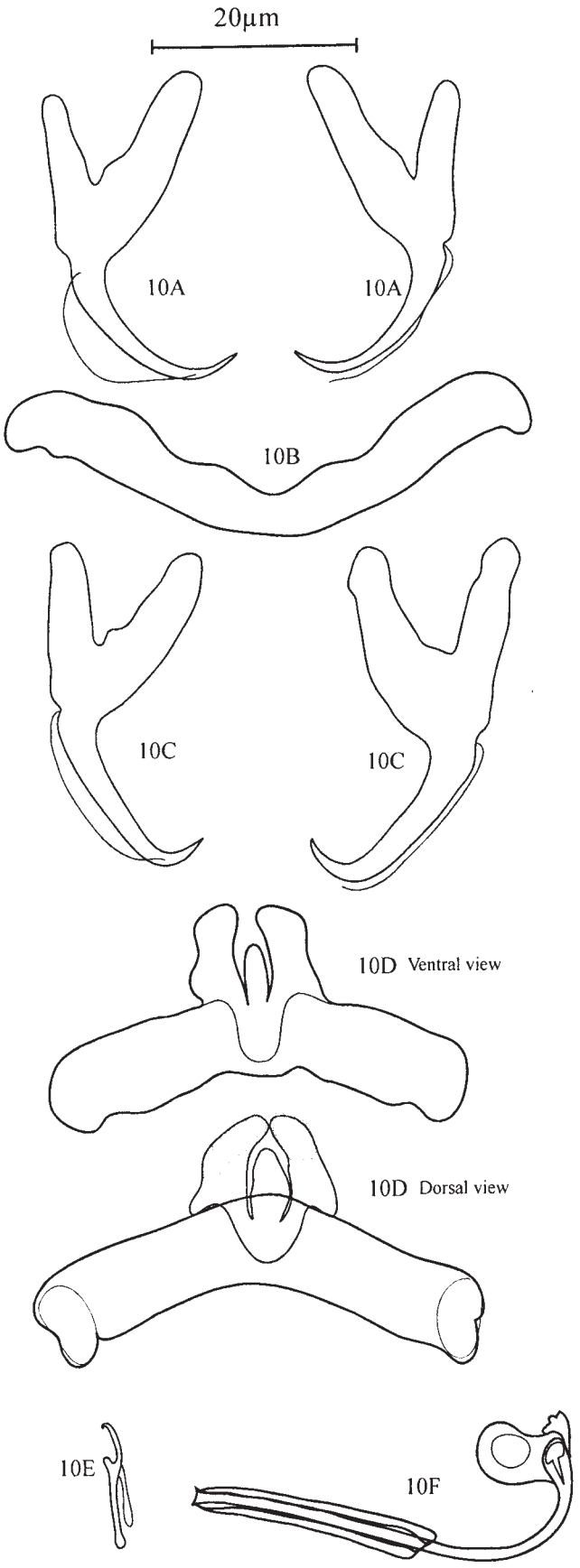

Fig. 10. *Ligophorus parvicopulatrix*, new species: A, dorsal anchors; B, dorsal bar; C, ventral anchors; D, ventral bar (two forms); E, marginal hook; F, male copulatory organ.

of anchors; 2 dorsal anchors, inner length 27 (23–30) (n = 60), outer length 29 (24–33) (n = 60), inner root 13 (10–15) (n = 60), outer root 10 (8–12) (n = 60), point 5 (3–8) (n = 60); 2 ventral anchors, inner length 29 (26–32) (n = 60), outer length 34 (32–36) (n = 60), inner root 13 (11–15) (n = 60), outer root 12 (10–14) (n = 60), point 5 (4–6) (n = 60); 2 connecting bars: dorsal bar slightly bent, 49 (38–59) × 5 (3–6) (n = 60); ventral bar broad inverted U, 39 (36–46) × 8 (7–9) (n = 60), AMP with two non-membranous lateral pieces and a raised median piece, distance between lateral pieces, 2 (1–4) (n = 60). Soft anatomical male reproductive system as in *L. navjotsodhii*, new species. Copulatory organ consists of copulatory tube, length 48 (41–71) (n = 60) with bilobed initial part, ornamentation on smaller lobe and simple tubular grooved accessory piece, 21 (17–26) (n = 60). Soft anatomical female reproductive system as in *L. navjotsodhii*, new species, sclerotised vaginal opening, median, at level of recurved portion of ovary, vaginal tube not observed, ovoid sperm-filled seminal receptacle, seminal receptacle tube to oviduct not observed.

Differential diagnosis. — *L. parvicopulatrix*, new species is well separated in the PCA scatterplot (Fig. 2) from the other seven new species and is characterised by having the shortest simple grooved accessory piece and copulatory tube and also in having a raised elongate median piece with two lateral non-membranous pieces. Raised elongated median pieces can be found in *L. pacificus*, *L. domnichi*, *L. brasiliensis*, *L. tainhae*, and *L. lizae*, but these species differ from *L. parvicopulatrix*, new species in having membranous lateral pieces. Based on NT analyses, *L. parvicopulatrix*, new species is grouped with *L. bantingensis*, new species in having anchors and bars of similar size and with *L. hamulosus* in the structure of the anchors, accessory piece and AMP (Table 2). However, *L. parvicopulatrix*, new species differs from *L. bantingensis*, new species in having a simple grooved accessory piece (Fig. 10F) compared to funnel-like in *L. bantingensis*, new species (Fig. 11F). *L. parvicopulatrix*, new species is similar to *L. hamulosus* in the structure of the anchors, in having a grooved accessory piece and two lateral non-membranous pieces in the AMP (Table 2) but the two species differ in the structure of the median piece of the AMP; a raised elongate median piece in *L. parvicopulatrix*, new species (Fig. 10D) compared to the flat median piece in *L. hamulosus*.

Ligophorus bantingensis, new species
(Fig. 11A–F)

Type-host. — *Liza subviridis* Valenciennes

Type-locality. — Off Carey Island, Banting, Malaysia (2°51'N, 101°22'E)

Type specimens. — Holotype: NHMUK 2012.7.2.26

Paratypes: 1 paratype NHMUK 2012.7.2.27 in the Natural History Museum, London; 2 paratypes ZRC.PAR.06 and ZRC.PAR.10 in the Raffles Museum of Biodiversity Research, National University of Singapore; 14 paratypes MZUM(P)2012.222(P)–235(P) in the University of Malaya collection.

Material studied. — 18 specimens studied; 17 specimens measured.

Etymology. — This species is named after the type locality.

Description. — Body elongate, 631 (418–804) × 103 (54–148) (n = 17), pharynx ovoid, size 35 (26–41) × 33 (24–39) (n = 17). Head-organs, eye-spots and alimentary system as in *L. navjotsodhii*, new species. Haptor well demarcated, size 74 (59–98) × 78 (50–105) (n = 17); 14 larval type marginal hooks, similar, length 11 (8–13) (n = 17); two pairs of anchors; 2 dorsal anchors, inner length 22 (20–24) (n = 17), outer length 22 (20–24) (n = 17), inner root 8 (7–10) (n = 17), outer root 4 (3–5) (n = 17), point 9 (7–10) (n = 17); 2 smaller ventral anchors, inner length 14 (12–19) (n = 17), outer length 14 (10–15) (n = 17), inner root 8 (5–10) (n = 17), outer root 4 (2–5) (n = 17), point 6 (4–8) (n = 17); 2 connecting bars: dorsal bar broad, inverted U, 28 (26–32) × 4 (2–5) (n = 17); ventral bar compact, inverted V, 29 (26–31) × 3 (2–4) (n = 17), AMP with two small, compact non-membranous lateral pieces and slightly raised median piece, distance between lateral pieces, 7 (6–8) (n = 17). Soft anatomical male reproductive system as in *L. navjotsodhii*, new species. Copulatory organ consists of copulatory tube, length 69 (59–97) (n = 17) with bilobed initial part, ornamented on smaller lobe and simple funnel-shaped accessory piece, 23 (18–28) (n = 17). Soft anatomical female reproductive system as in *L. navjotsodhii*, new species except vagina present. Vaginal opening heavily sclerotised, median at level of recurved portion of ovary, vaginal tube thin, sclerotised, 37 (33–42) (n = 10), leading to ovoid sperm-filled seminal receptacle.

Differential diagnosis. — *L. bantingensis*, new species, is unique in possessing the smallest and shortest anchors and bars and having a slender, small funnel-shaped accessory piece compared to all the present new species (Fig. 11F) and hence is distinctly grouped from the present seven species in the PCA scatterplot (Fig. 2). The NT analyses shows that *L. bantingensis*, new species is similar to *L. funnelus*, new species in the structure of the anchors and in having a funnel-like accessory piece but the two species differ in *L. bantingensis*, new species having the smaller anchors and bars and also in the detailed structure of the ventral bar and AMP; small ventral bar with slightly raised median piece in *L. bantingensis*, new species compared to a bigger ventral bar with a flat median piece in *L. funnelus*, new species (Figs. 11D, 9D) as well as in the smaller proximal opening of the funnel in *L. bantingensis*, new species compared to the larger proximal opening in *L. funnelus*, new species (Figs. 11F, 9F). Based on NT analyses, *L. bantingensis*, new species and *L. parvicopulatrix*, new species have morphologically similar anchors and bars but in *L. bantingensis*, new species, the anchors and bars are comparatively smaller. *L. bantingensis*, new species is similar to *L. huitrempe* in the structure of the bars and AMP (Table 2) but differs in the structure of the accessory piece; *L. bantingensis*, new species has a small slender funnel-like accessory piece (Fig. 11F) compared to a bifurcated accessory piece in *L. huitrempe*.

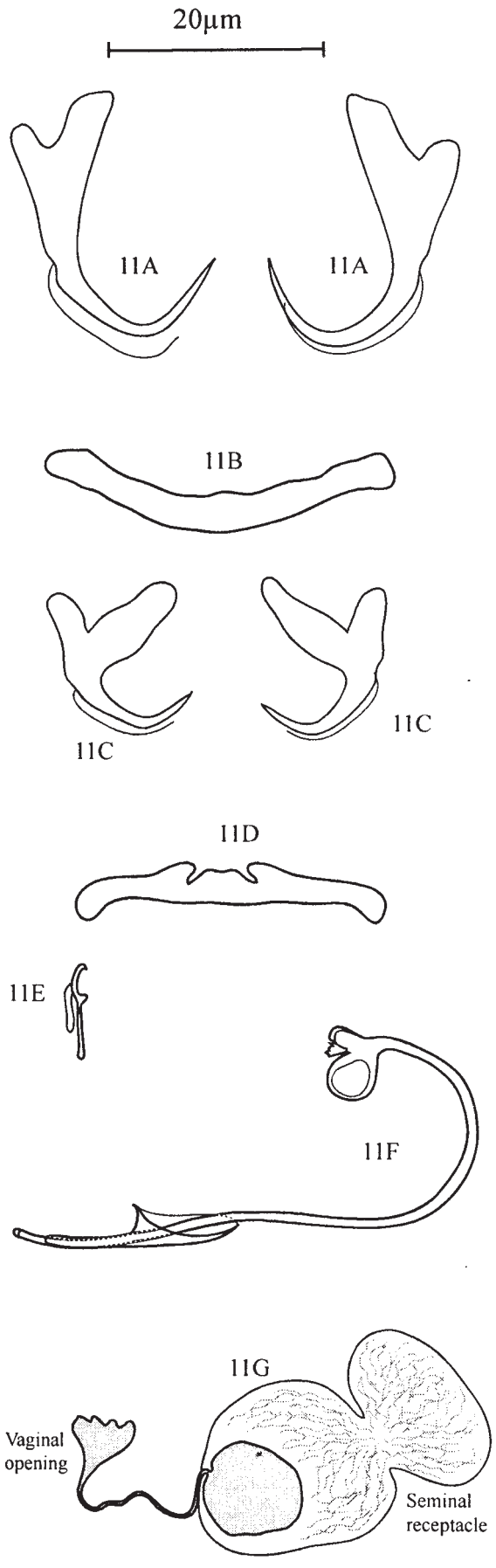

Fig. 11. *Ligophorus bantingensis*, new species: A, dorsal anchors; B, dorsal bar; C, ventral anchors; D, ventral bar; E, marginal hook; F, male copulatory organ; G, vaginal opening and seminal receptacle.

***Ligophorus careyensis*, new species**
(Fig. 12A–G)

Type-host. — *Liza subviridis* Valenciennes

Type-locality. — Off Carey Island, Banting, Malaysia (2°51'N, 101°22'E)

Type-specimens. — Holotype: NHMUK 2012.7.2.28

Paratypes: 1 paratype NHMUK 2012.7.2.29 in the Natural History Museum, London; 1 paratype ZRC.PAR.07 in the Raffles Museum of Biodiversity Research, National University of Singapore; 25 paratypes MZUM(P)2012.944(P)–968(P) in the University of Malaya collection.

Material studied. — 28 specimens studied; 20 specimens measured.

Etymology. — This species is named after Carey Island, the type locality.

Description. — Body elongate, 612 (353–825) × 118 (70–218) (n = 20), pharynx size, 37 (33–45) × 37 (30–49) (n = 20). Head-organs, eye-spots and alimentary system as in *L. navjotsodhii*, new species. Haptor well demarcated, size 93 (62–136) × 118 (73–184) (n = 20); 14 larval type marginal hooks, similar, length 11 (9–13) (n = 20); two pairs of anchors; 2 dorsal anchors, inner length 35 (31–39) (n = 20), outer length 33 (27–37) (n = 20), inner root 14 (11–18) (n = 20), outer root 7 (5–12) (n = 20), point 6 (3–10) (n = 20); 2 ventral anchors, inner length 36 (30–39) (n = 20), outer length 40 (32–44) (n = 20), inner root 14 (10–17) (n = 20), outer root 10 (6–13) (n = 20), point 7 (5–9) (n = 20); 2 connecting bars: V-shaped dorsal bar, 37 (33–42) × 5 (3–6) (n = 20); ventral bar inverted V, 41 (34–45) × 8 (6–10) (n = 20), AMP consists of two membranous lateral pieces and flat median piece, distance between membranous lateral pieces, 9 (6–11) (n = 20). Soft anatomical male reproductive system as in *L. navjotsodhii*, new species. Copulatory organ consists of copulatory tube, length 94 (78–111) (n = 20) with bilobed initial part, ornamented on bigger lobe, two opposing accessory pieces; an elongate groove piece, 25 (20–31) (n = 20) and similar length non-groove piece with distal fork. Soft anatomical female reproductive system as in *L. navjotsodhii*, new species, sclerotised vaginal opening, median, at level of recurved portion of ovary, vaginal tube thin, sclerotised, 36 (32–40) (n = 10), leading to ovoid seminal receptacle.

Differential diagnosis. — *L. careyensis*, new species is distinctly grouped from the other seven species in the PCA scatterplot (Fig. 2) in having the longest copulatory tube and ornamented bilobed initial part (Fig. 12F). From the NT analyses, *L. careyensis*, new species is similar to *L. navjotsodhii*, new species in the structure of the anchors, accessory piece and AMP, to *L. chelatus*, new species in the anchors, bars and accessory piece, to *L. minimus* and *L. parvicirrus* in the anchors, bars and AMP and to *L. heteronchus*, *L. imitans*, *L. llewellyni*, *L. macrocolpos*, *L. mediterraneus*, *L. pilengas*, *L. saladensis*, and *L. uruguayense* in the structure of the anchors and AMP (Table 2). However *L. careyensis*, new species differs from all the aforementioned

species in having two opposing accessory pieces with a fork-like distal end on its non-grooved piece and a long copulatory tube with an ornamented bilobed initial part (Fig. 12F).

Ligophorus kedahensis, new species
(Fig. 13A–F)

Type-host. — *Valamugil buchanani* Bleeker

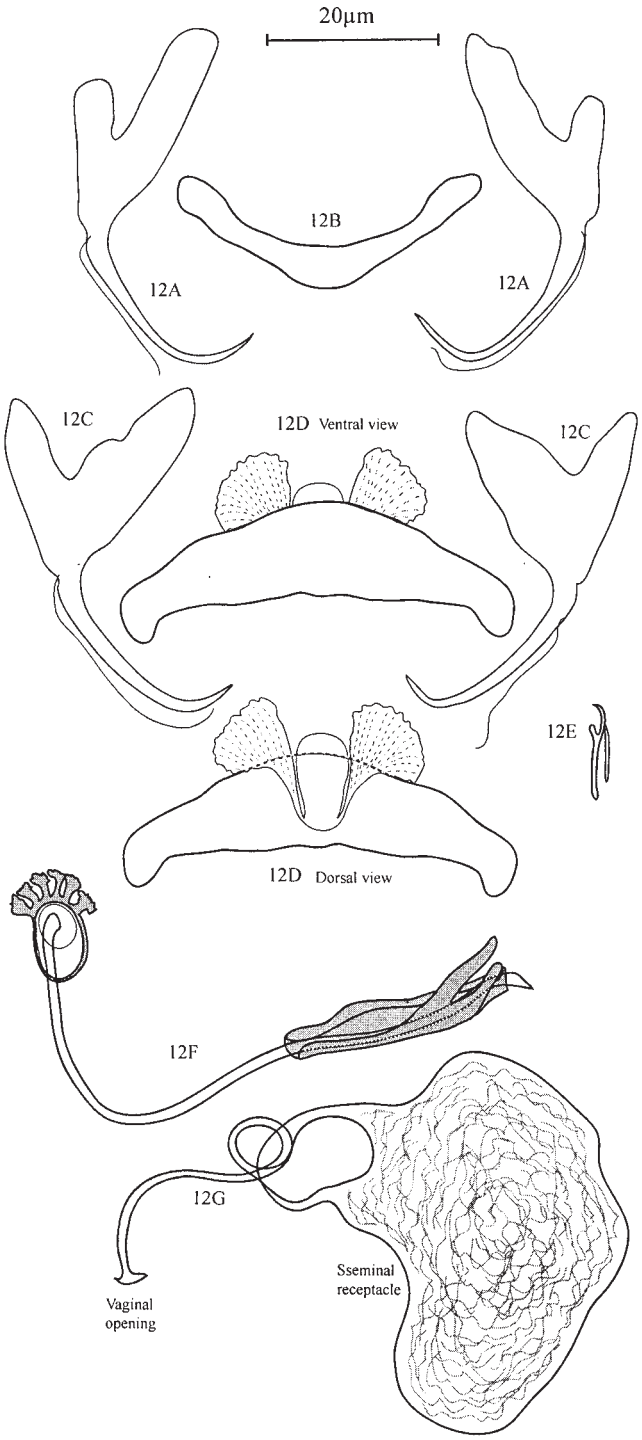

Fig. 12. *Ligophorus careyensis*, new species: A, dorsal anchors; B, dorsal bar; C, ventral anchors; D, ventral bar (two forms); E, marginal hook; F, male copulatory organ; G, vaginal opening and seminal receptacle.

Type-locality. — Off Langkawi Island, Kedah, Malaysia (6°21'N, 99°46'E)

Type-specimens. — Holotype: NHMUK 2012.7.2.30

Paratypes: 5 paratypes NHMUK 2012.7.2.31–35 in the Natural History Museum, London; 2 paratypes (ZRC.PAR.11) in the Raffles Museum of Biodiversity Research, National University of Singapore; 59 paratypes MZUM(P)2012.969(P)–1027(P) in the University of Malaya collection.

Material studied. — 67 specimens studied; 67 specimens measured.

Etymology. — This species is named after the state of Kedah.

Description. — Body elongate, 1181 (567–1455) × 199 (103–278) (n = 67), pharynx size 59 (44–71) × 60 (48–71) (n = 30). Head-organs, eye-spots and alimentary system as in *L. navjotsodhii*, new species. Haptor well demarcated, size 141 (74–169) × 139 (81–201) (n = 67); 14 larval type marginal hooks, similar, length 11 (10–13) (n = 67); two pairs of anchors; 2 dorsal anchors, inner length 35 (31–41) (n = 67), outer length 32 (27–37) (n = 67), inner root 16 (12–21) (n = 67), outer root 8 (6–11) (n = 67), point 11 (6–14) (n = 67); 2 ventral anchors, inner length 34 (27–38) (n = 67), outer length 32 (27–35) (n = 67), inner root 17 (12–22) (n = 67), outer root 11 (6–15) (n = 67), point 7 (5–12) (n = 67); 2 connecting bars: dorsal bar broad inverted U, 51 (43–58) × 6 (4–8) (n = 67); ventral bar inverted V, 51 (44–57) × 8 (5–10) (n = 67), AMP consists of two membranous lateral pieces and a raised median piece, distance between lateral pieces, 12 (7–15) (n = 67). Copulatory organ consists of copulatory tube, length 65 (57–75) (n = 67) with bilobed initial part and a boat-like simple grooved accessory piece, 33 (25–40) (n = 67). Vaginal opening and tube not observed.

Differential diagnosis. — *L. kedahensis*, new species is distinctly grouped from the other seven species in the PCA scatterplot (Fig. 2). This species is the second largest of the present new species. The lateral pieces of the AMP are set far apart as in *L. zhangi* except that in the present species, the median piece is raised while in *L. zhangi* the median piece is flat. *L. kedahensis*, new species differs from the present species in having a simple grooved accessory piece which is boat-like (Fig. 13F) compared to *L. parvicopulatrix*, new species which has a simple grooved accessory piece (Fig. 10F). This species is not grouped with any previous or present species twice for any characters used in the NT analyses. However it is morphologically similar to *L. fenestrum*, new species based on the copulatory organ (copulatory tube and accessory piece) but differs in *L. fenestrum*, new species having fenestrated anchors (Fig. 14A, C) and *L. kedahensis*, new species lack the fenestration (Fig. 13A, C).

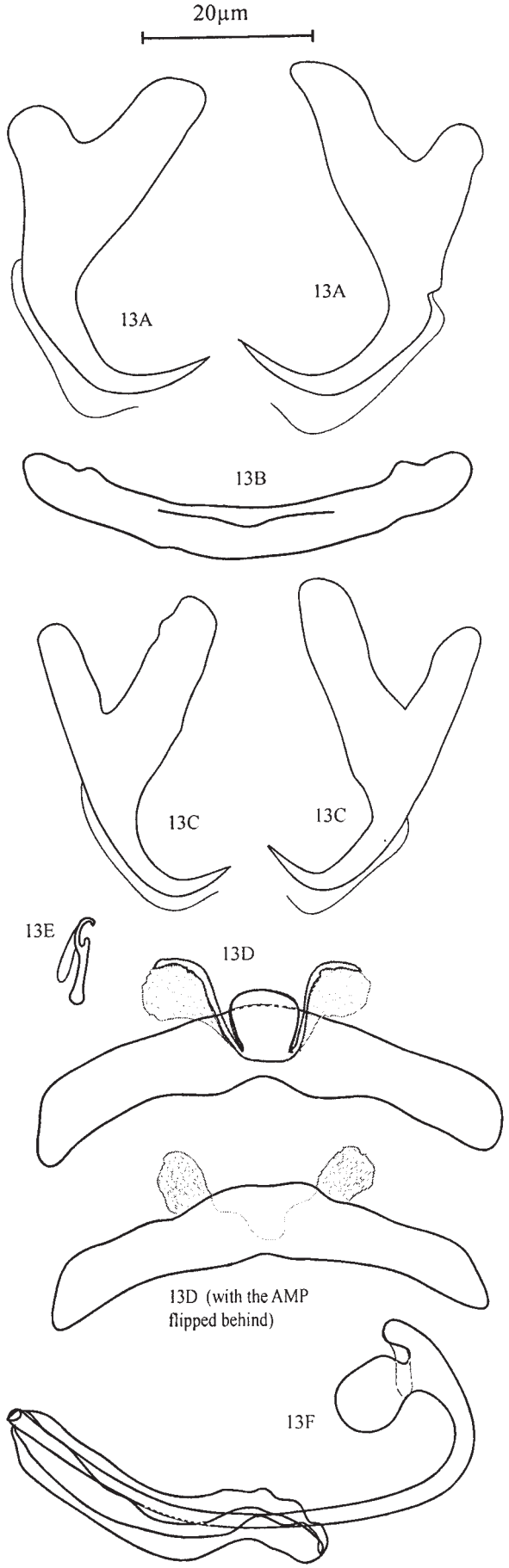

Fig. 13. *Ligophorus kedahensis*, new species: A, dorsal anchors; B, dorsal bar; C, ventral anchors; D, ventral bar; E, marginal hook; F, male copulatory organ.

***Ligophorus fenestrum*, new species**
(Fig. 14A–F)

Type-host. — *Valamugil buchanani* Bleeker

Type-locality. — Off Langkawi Island, Kedah, Malaysia (6°21'N, 99°46'E)

Type-specimens. — Holotype: NHMUK 2012.7.2.36

Paratypes: 3 paratypes NHMUK 2012.7.2.37–39 in the Natural History Museum, London; 2 paratypes (ZRC.PAR.12) in the Raffles Museum of Biodiversity Research, National University of Singapore; 21 paratypes MZUM(P)2012.1050(P)–1070(P) in the University of Malaya collection.

Materials studied. — 27 specimens studied; 27 specimens measured.

Etymology. — This species is named after the fenestration or windows on the anchors. Note that 'fenestrum' is a noun in apposition.

Description. — Body elongate, 1727 (1418–2027) × 270 (210–361) (n = 27), pharynx size 92 (77–105) × 94 (75–106) (n = 27). Head-organs, eye-spots and alimentary system as in *L. navjotsodhii*, new species. Haptor well demarcated, size 141 (104–192) × 129 (84–171) (n = 27); 14 larval type marginal hooks, similar, length 12 (11–14) (n = 27); two pairs of anchors; 2 dorsal anchors, inner length 38 (33–41) (n = 27), outer length 35 (31–37) (n = 27), inner root 19 (16–23) (n = 27), outer root 12 (8–16) (n = 27), point 11 (8–14) (n = 27); 2 ventral anchors, inner length 38 (34–40) (n = 27), outer length 36 (32–39) (n = 27), inner root 19 (14–22) (n = 27), outer root 13 (8–16) (n = 27), point 11 (9–13) (n = 27); 2 connecting bars: dorsal bar broad inverted U, 50 (41–57) × 7 (5–10) (n = 27); ventral bar horizontally straight 47 (43–52) × 8 (6–10) (n = 27), bifurcated median piece with no lateral pieces, distance between bifurcated piece, 4 (2–6) (n = 27). Copulatory organ consists of copulatory tube, length 86 (73–95) (n = 27) with bilobed initial part, ornamented on smaller lobe and boat-like simple grooved accessory piece, 34 (29–38) (n = 27). Vaginal opening and tube not observed.

Differential diagnosis. — *L. fenestrum*, new species is different from the other seven species as indicated by the PCA scatterplot (Fig. 2). It is larger than *L. kedahensis*, new species, and in fact is the largest of the present *Ligophorus* species. This species is unique in possessing anchors with fenestrations, AMP is composed only of a bifurcated median piece without lateral pieces, a boat-like accessory piece and having the longest dorsal bar among all eight species (Fig. 14A–D, F). The NT analyses indicate that *L. fenestrum*, new species is similar to *L. leporinus* in the structure of the bars, grooved accessory piece and an AMP with bifurcated median piece without lateral pieces but *L. leporinus* lacks fenestrated anchors as in *L. fenestrum*, new species (Fig. 14A, C).

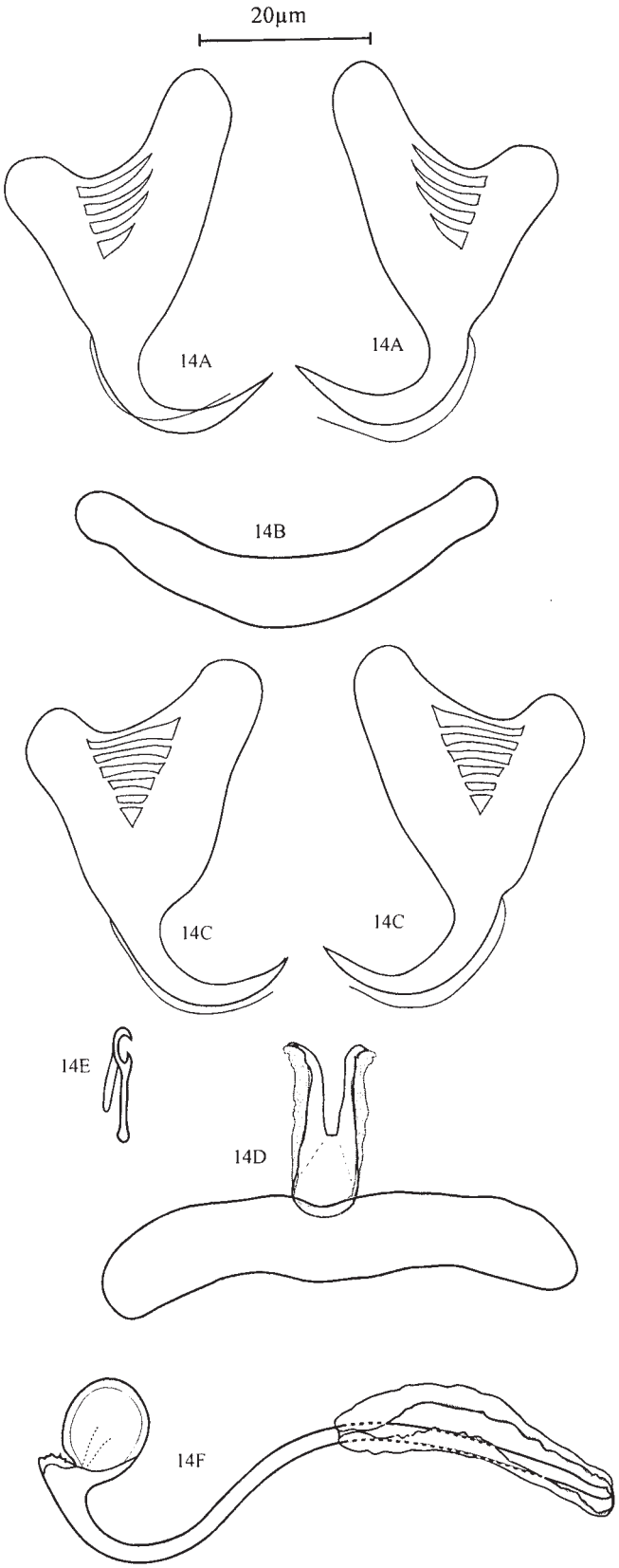

Fig. 14. *Ligophorus fenestrum*, new species: A, dorsal anchors; B, dorsal bar; C, ventral anchors; D, ventral bar; E, marginal hook; F, male copulatory organ.

DISCUSSION

With the present eight species, there are now 50 *Ligophorus* species found on members of the Mugilidae (Table 1). This is the first time that *Ligophorus* are described from *L. subviridis* and *V. buchanani*, off Peninsular Malaysia. The eight new species are different from the previously described *Ligophorus* species and from each other on the metric and morphological characteristics of their anchors, bars, accessory pieces of their copulatory organs, and AMP of the ventral bars as indicated by the way they are associated in the dendrograms generated (Figs. 3–6) and summarised in Table 2. PCA and NT analyses indicate that sclerotised hard parts of the haptors, in particular the AMP of the ventral bar and accessory piece of the copulatory organs are good diagnostic characters for *Ligophorus*. However there are difficulties in deciphering the morphologies of the accessory piece from previous published works due to unclear and incomplete illustrations.

To generate groupings in PCA, morphometric data from large numbers of specimens are essential (Costello & Osbourne, 2005; Tan et al., 2010). In this study, 318 specimens of *Ligophorus* species are used and all the *Ligophorus* species are well represented with *L. bantingensis*, new species being represented by 17 specimens, the lowest number of specimens in the analysis and the highest is *L. kedahensis*, new species with 67 specimens. Tan et al. (2010) used PCA to cluster 448 specimens belonging to four *Trianchoratus* species to detect the presence of morphovariants with 25–113 specimens per monogenean species being used. In comparison, Mariniello et al. (2004) used 107 specimens belonging to 12 *Ligophorus* species, which worked out to be 3–12 specimens per monogenean species for PCA; Rubtsova et al. (2006) used PCA to cluster two *Ligophorus* species according to localities using 6–20 specimens per monogenean species and later in 2007, clustered three *Ligophorus* species with 25–31 specimens per species for species discrimination, whilst Dmitrieva et al. (2007, 2009, 2012) used 2–27 specimens per species to generate PCA scatterplots for species discrimination.

NT analysis has been used to group dactylogyrid species (Lim & Furtado, 1987) and spiders (Agnarsson, 2004) based on their descriptive data. In this study, we used this method to group *Ligophorus* species using descriptive character states with or without metric data. The NT analysis indicates that haptoral hard parts (anchors and bars) and copulatory organs can be used to differentiate between *Ligophorus* species.

The marginal hooks of the new and known *Ligophorus* species are of larval type and metrically similar in size (9–15 µm). Morphologically the anchors are similar with roots, broad bases, thin shafts and short recurving points but can be differentiated based on length of the inner and outer length, inner and outer roots and anchor points. Only in the case of *L. fenestrum*, new species, are the anchors morphologically different in possessing horizontal fenestrations on the base of both ventral and dorsal anchors (Fig. 14A, C).

The dorsal and ventral bars vary from V- to U-shape with or without shoulders (Figs. 7B, 9B, 10B). The ventral bar is an inverted V-shape with AMP. Basically, the AMP consists of a median piece with two lateral ear-like projections, which can be membranous or non-membranous. The AMP is variable, with the median piece varying from a simple raised mound in *L. bantingensis*, new species (Fig. 11D) to a depression in *L. funnelus*, new species (Fig. 9D) to a raised elongate structure in *L. parvicopulatrix*, new species (Fig. 10D) and with the two lateral processes varying from membranous in *L. chelatus*, new species (Fig. 8D) to non-membranous in *L. parvicopulatrix*, new species (Fig. 11D). *L. fenestrum*, new species is the most unique in having a raised elongate bifurcating median piece without lateral pieces (Fig. 14D).

The copulatory organ of *Ligophorus* species usually consists of a simple tube with a bilobed initial part and accessory piece. The bilobed initial part is of unequal sizes, smaller lobe surrounding the opening of the tube and a larger lateral lobe. The smaller lobe can be ornamented (serrated) as in *L. careyensis*, new species (Fig. 12D) or unornamented. We observed the vas efferens entering the smaller sclerotised lobe, while the prostatic reservoir duct seems to enter the copulatory tube from the larger lobe (Figs. 7i, 8i). Two types of accessory pieces are observed for the present and known *Ligophorus* species: (1) a single grooved piece as in *L. parvicopulatrix*, new species (Fig. 10F), and (2) two opposing attached sclerotised pieces consisting of a grooved tube and a non-grooved piece with distal hook, claw or fork as in *L. navjotsodhii*, new species, *L. chelatus*, new species and *L. careyensis*, new species, respectively (Figs. 7F, 8F, 12F). The accessory pieces are either attached to the initial part of the copulatory tube as illustrated in *L. angustus*, *L. cephali*, *L. confusus*, *L. ellochelon*, *L. heteronchus*, and *L. szidati* or not attached as in the other 36 previously described species as well as in the present eight new species.

In the present species, the ovary is observed to be J-shape (elongate with recurved posterior region) (Figs. 7i, 8i). The ovary of *Ligophorus* has been illustrated and described as U-shaped by Rubtsova et al. (2007), Abdallah et al. (2009), and Marcotegui & Martorelli (2009), and as recurved by Euzet & Suriano (1977), Fernandez-Bargiela (1987), and Hu & Li (1992) as well as ovoid in the majority of the descriptions for *Ligophorus* species.

According to the generic diagnosis of *Ligophorus*, the vagina is sclerotised but this is not the case for all *Ligophorus* species. In fact only 35 of the 42 previously described species and four of the present species (*L. chelatus*, new species, *L. funnelus*, new species, *L. bantingensis*, new species, and *L. careyensis*, new species) have obvious sclerotised vaginal openings and tubes. In *L. parvicopulatrix*, new species, only a round sclerotised opening without the sclerotised vaginal tube is observed. No obvious vaginal openings or tubes are observed in the other three new species (*L. navjotsodhii*, new species, *L. kedahensis*, new species, and *L. fenestrum*, new species). It is possible that in these species (three new and seven previously described species), the vaginal openings and tubes are not sclerotised or lightly sclerotised and short. In most of the cases where the vagina is observed and described, the opening is median or sub-marginal on the dextral side. The seminal receptacle is observed as a large sperm-filled ovoid body in all the presently described new species (Figs. 7i, 8i, 9G, 11G, 12G) and also well-depicted in previously described species. The seminal receptacle is located in mid-body ventral to the median ovary while the vaginal system (when observed) is usually found to enter the seminal receptacle posteriorly. The seminal receptacle tube leading into the oviduct is not obvious, probably because it is not sclerotised and in some cases it can be observed as a non-sclerotised sperm-filled tube.

The generic diagnosis of *Ligophorus* is emended to include the fact that the ovary is J-shaped and that the vaginal system is not obvious in all species of *Ligophorus.*

***Ligophorus* Euzet & Suriano, 1977** (emended)

Ancyrocephalidae, Bychowsky, 1937. 3 pairs of head organs, 4 eye-spots. Subterminal mouth, intestine bifurcating just posterior to pharyngeal bulb, intestinal caeca reuniting just anterior to haptor. Haptor set off from body, with 14 marginal hooks and two pairs of anchors, two connective bars, ventral bar inverted V-shape with antero-median protuberance (AMP) of one median piece with or without lateral processes which can be membranous or non-membranous. Testis median, vas deferens leaving anterior part of testis to left side of body, does not overlap sinistral caecum, continues anteriorly, extending forming seminal vesicle, narrows as vas efferens to open into smaller lobe of the bilobed initial of copulatory tube. One prostatic reservoir draining into bilobed initial part. Copulatory organ consists of tube with bilobed initial part and accessory piece which is either simple groove piece or two opposing pieces of which one is grooved. Ovary J- to U-shape, median, pre-testicular, oviduct receives tube from seminal receptacle, continues as oötype receiving Mehlis' gland, continues as uterus to open near copulatory organ. Vagina can be non-sclerotised (not observed) or sclerotised, dextro-ventral, sub-median to sublateral; sclerotised vaginal tube if present enters into ovoid sperm-filled seminal receptacle located near bend of J-shaped ovary. Egg operculate, ovoid, with short filament. Parasites of Mugilidae.

Type-species. — *Ligophorus vanbenedenii* (Parona & Perugia, 1890) Euzet & Suriano, 1977 [syns. *Tetraonchus vanbenedenii* Parona & Perugia, 1890, *Ancyrocephalus vanbenedenii* Johnston & Tiegs (1922), *Haplocleidus vanbenedenii* Palombi (1949), *Haliotrema vanbenedenii* Young (1968)].

Type-locality. — Gulf of Genoa, Italy

Type-host. — *Mugil auratus* (now known as *Liza aurata*)

Other species. — As in Table 1

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