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V. SARABEEV, N. RUBTSOVA,
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TAXONOMIC REVISION OF THE ATLANTIC AND PACIFIC SPECIES OF *LIGOPHORUS* (MONOGENEA, DACTYLOGYRIDAE) FROM MULLETS (TELEOSTEI, MUGILIDAE) WITH THE PROPOSAL OF A NEW GENUS AND DESCRIPTION OF FOUR NEW SPECIES

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V. SARABEEV, N. RUBTSOVA, T. YANG, J. A. BALBUENA

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KYIV–2013

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Sarabeev V.[1]*, Rubtsova N.[1], Yang T.[2], Balbuena J. A.[3] Taxonomic Revision of the Atlantic and Pacific Species of *Ligophorus* (Monogenea, Dactylogyridae) from Mullets (Teleostei, Mugilidae) with the Proposal of a New Genus and Description of Four New Species. — A revision of the Atlantic and Pacific species of *Ligophorus* Euzet et Suriano, 1977 based on abundant newly sampled material from mugilids of the Mediterranean Sea, Sea of Japan and South China Sea, as well as available type and voucher specimens, is presented. All 35 nominal species of *Ligophorus* known from the Atlantic and the Pacific waters are treated. Of them, 30 are considered valid, one incertae sedis (*L. leporinus*), one species inquirendae (*L. chongmingensis*), two junior synonyms (*L. euzeti* and *L. gussevi*) and one is transferred to another genus. Three new species of *Ligophorus* are described: *L. triangularis*, *L. miroshnichenki*, and *L. rectus*. An amended diagnosis of *Ligophorus* is given with critical comments on previous definition of key features of the genus. Description of the main morphological types for the copulatory organ, the accessory piece of the copulatory complex, the distal end of the vagina, the ventral bar and anchors are provided. The taxonomic importance of sclerotized parts is discussed in relation with their functional morphology. For each species, previous and present records on host and geographic distribution were compiled. A new genus of Dactylogyridae *Kriboetrema* is proposed for species morphologically similar to *Ligophorus* spp., but which differ from the latter in having a large dorsoventrally flattened body, a coiled copulatory organ with a bulbous base, two prostatic reservoirs, a subovate or piryform ovary and inconspicuous or poorly developed lateral flaps of the haptor. Two species are proposed for allocation within the new genus, *K. ellochelon* comb. n. and *K. rectangulus* sp. n., from *Liza vaigiensis* and *Valamugil cunnesius*, respectively, in the Pacific. A key to genera and valid species in the surveyed regions is provided.

Key words: Mediterranean, Black Sea, Sea of Azov, Japan Sea, South China Sea, sclerotized parts, morphology, specificity.

Сарабеев В.[1]*, Рубцова Н.[1], Янг Т.[2], Бальбуэна Х. А.[3] Таксономическая ревизия атлантических и тихоокеанских видов *Ligophorus* (Monogenea, Dactylogyridae) от кефалевых рыб (Teleostei, Mugilidae) с предложением нового рода и описанием четырех новых видов. — В работе представлена ревизия атлантических и тихоокеанских видов *Ligophorus* Euzet et Suriano, 1977 основанная на богатом свежесобранном материале от кефалевых рыб из Средиземного, Японского и Южно-Китайского морей, а также на доступных для исследования типовых и ваучерных коллекционных материалах. Все 35 номинальных видов *Ligophorus*, известных из бассейнов Атлантического и Тихого океанов, критически пересмотрены. Из них 30 признаны валидными, один incertae sedis (*L. leporinus*), один species inquirendae (*L. chongmingensis*), два младшими синонимами (*L. euzeti* и *L. gussevi*) и один вид перенесен в другой род. Описано три новых вида *Ligophorus*: *L. triangularis*, *L. miroshnichenki* и *L. rectus*. Предоставлен расширенный диагноз *Ligophorus*, критически пересмотрены предыдущие определяющие признаки рода. В работе приведены описания основных морфологических типов копуляторного органа, вспомогательного аппарата копулятивного комплекса, дистального конца вагины, вентральной пластинки и срединных крючьев. Обсуждена таксономическая значимость склеротизированных частей в соотношении с их функциональной морфологией. Для каждого вида указаны предыдущие и настоящие находки на хозяевах и их географическое распространение. Для видов, морфологически схожих с *Ligophorus* spp., но отличающихся большим, сплющеным в дорсовентральном направлении телом, скрученным копулятивным органом с шарообразным основанием, двумя простатическими пузырьками, грушевидным или субовальным яичником и малозаметными или слаборазвитыми боковыми выростами прикрепительного диска, предложен новый род *Kriboetrema*. Два вида из бассейна Тихого океана отнесены к новому роду — *K. ellochelon* comb. n. и *K. rectangulus* sp. n., от *Liza vaigiensis* и *Valamugil cunnesius* соответственно. Дана таблица для определения родов и валидных видов исследованных регионов.

Ключевые слова: Средиземное море, Черное море, Азовское море, Южно-Китайское море, склеротизированные структуры, морфология, специфичность.

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«L'amitié d'un grand homme est un bienfait des dieux»
Voltaire, Œdipe.

This monograph is fondly dedicated to Prof. Louis Euzet
for his immense contribution to helminthology in general,
and to the taxonomy of monogeneans in particular.
We would like express our gratitude for sharing your passion,
commitment and knowledge with us.

Introduction

The monogenean *Ligophorus* Euzet and Suriano, 1977 includes specific gill parasites of grey mullets (Teleostei, Mugilidae). This genus is characterized by the combination of the following features: vas deferens on the left side not encircling the intestinal caeca; one prostatic reservoir; copulatory complex comprising a copulatory organ with bilobed base and an accessory piece; a J- to U-shaped ovary, a vagina sclerotized or not; dorsal and ventral anchor/bar complex with seven pairs of hooks and bars dissimilar in shape, ventral bar with anteromedian protuberances (Euzet, Suriano, 1977; Euzet, Sanfilippo, 1983; Soo, Lim, 2012).

Euzet and Suriano (1977) proposed *Ligophorus* as a genus within the Ancyrocephalidae Bychowsky, 1937. However, numerous taxonomic revisions of Dactylogyrinea Bychowsky, 1937, based on both morphological and molecular data, indicate that Ancyrocephalidae contains poly- and paraphyletic features and this is therefore unnatural (Kritsky, Boeger, 1989; Šimková et al., 2003; Plaisance et al., 2005; Šimková et al., 2006, etc.). A recent study of the molecular phylogeny of 15 Mediterranean species revealed the affinities of *Ligophorus* with other genera of marine Ancyrocephalinae within the Dactylogyridae (Blasco-Costa et al., 2012). Therefore, *Ligophorus* as well as *Kriboetrema* gen. n., are considered herein as members of Dactylogyridae.

Species discrimination within the genus relies on the morphology and size of sclerotized elements of the haptor and genital structures. However, the most recent studies (Caltran et al., 1995 a; Sarabeev, Balbuena, 2004; Rubtsova et al., 2005; Sarabeev et al., 2005) suggest higher variation of metric characters than reported by Euzet and Suriano (1977). Sometimes, variation ranges widely overlap making species identification difficult. Therefore, a revision of important taxonomic characters for species identification within *Ligophorus* is needed.

Examination of host-parasite associations indicates that often one given host species harbours several species of *Ligophorus* (Euzet, Suriano, 1977; Euzet, Sanfilippo, 1983; Radujković, Raibaut, 1989; Abu Samak, Hassan, 1998, 1999; Caillot et al., 1999; Sarabeev, Balbuena, 2004; Sarabeev et al., 2005; Rubtsova et al., 2006 a; Rubtsova et al., 2007; Abdallah et al., 2009; Soo, Lim, 2012). In fact, Euzet and Suriano (1977) considered that the species of *Ligophorus* are oioxenous given that their occurrence on atypical hosts is rare and often limited to single specimens. However, a number of studies report species of *Ligophorus* on atypical hosts. For instance, *L. vanbenedenii*, whose specific host is the golden grey mullet *Liza aurata* (Risso), has also been reported on flathead mullet *Mugil cephalus* L. and eastern keelback mullet *Liza affinis* (Günther) (Zhang, Ji, 1981; Dmitrieva, Gerasev, 1996; Zhang, 2001). Likewise, *L. kaohsianghsieni*, common on the so-iuy mullet *Liza haematocheilus* (Temminck et Schlegel), has been recorded on *M. cephalus* and *Lz. aurata* (Ji et al., 1982; Dmitrieva, 1996; Miroshnichenko, Maltsev, 1998), and *L. macrocolpos*, specific to the leaping mullet *Liza saliens* (Risso), occurs also on *Lz. aurata* (Dmitrieva, Gerasev, 1996). Thus, a critical review and an assessment of these records are needed to comprehend or redefine the host specificity patterns within *Ligophorus*.

Since the erection of *Ligophorus*, the number of species has increased to include at least of 35 species on mullets distributed throughout the Atlantic and the Pacific region. However, the validity and taxonomic status of some of these species is unclear. Our ongoing studies of specimens of *Ligophorus* from various localities around the surveyed regions show that they are difficult to identify with certainty to species level using the existing literature due to the absence of a key to species and, in some instances, incomplete or erroneous descriptions and lack of precision in the differential diagnoses. However, there is growing interest in this genus. In fact, over the last decade, about 30 species of *Ligophorus* have been described in the world (Sarabeev, Balbuena, 2004; Sarabeev et al., 2005; Rubtsova, et al., 2006 a; Dmitrieva, et al., 2007; Rubtsova, et al., 2007; Failla Siquier, Ostrowski de Núñez, 2009; Abdallah, et al., 2009; Marcotegui, Martorelli, 2009; Dmitrieva et al., 2012; Soo, Lim, 2012; Dmitrieva et al., 2013).

This state of affairs and our abundant samples from the Mediterranean and the Sea of Japan prompted the present study in order to: i) establish the taxonomic identity of the Atlantic and Pacific species currently considered to belong to *Ligophorus*, ii) review the morphological traits used for their discrimination, iii) summarize data on species specificity, host records and geographic distribution, iv) provide additional voucher specimens for further studies and v) propose a key to species discrimination.

This paper represents the first taxonomic review of *Ligophorus* species known from Atlantic and Pacific mullet hosts. For the present effort, all mugilid species previously reported as hosts of *Ligophorus* were newly sampled from localities of the Mediterranean region (including the Azov and Black Seas) and the Sea of Japan. All those described and two new species were represented in these samples. In addition, examination of type and new specimens collected by one of us (Y. T.) in the South China Sea from three mullet hosts, *Liza vaigiensis* (Quoy and Gaimard), *Lz. tade* (Forsskel) and *Valamugil cunnesius* (Valenciennes), revealed the presence of a new genus of Dactylogyridae and two new species, one of those considered to be in the new genus, the other in *Ligophorus*. In the present paper, an amended diagnosis of *Ligophorus* is given with critical comments on previous definition of key features. In order to facilitate species identification, different morphological types of the copulatory organ, the accessory piece, the distal end of the vagina, and the ventral bar and anchors are

defined and described. The taxonomic importance of the sclerotized parts of the male copulatory complex is discussed in relation with its functional morphology. One species is synonymised, two considered as incertae sedis or species inquirendae, one transferred to another genus and 30 accepted as valid species of *Ligophorus*. Redescriptions of 23 species are provided. For each species, previous and present records on host and geographic distribution are presented. A key to genera and valid species in the surveyed regions is given.

Material and metods

Fish hosts were collected by fishing rod, net or purchased at local fish markets from 18 localities during 2001–2009 (table 1). Collections of fish species differed among sites and seasons both in number and range due to collecting opportunity and differences in local fish fauna. Eight species of mullets were examined: flathead mullet *M. cephalus*; so-iuy mullet *Liza haematocheilus*; golden grey mullet *Lz. aurata*; thinlip mullet *Liza ramada* (Risso); leaping mullet *Lz. saliens*; thicklip grey mullet *Chelon labrosus* (Risso); tade mullet *Lz. tade*; and longarm mullet *V. cunnesius*. All host scientific names except one follow those provided in FishBase (Froese, Pauly, 2012), but the soiuy mullet is herein referred to as *Liza haematocheilus* instead of *Mugil soiuy* Basilewsky following Parin (2003); Chesalina, Chesalin (2003); Bogutskaya, Naseka (2004); Harrison (2004).

Fish were surveyed for parasites within a day of their capture or after freezing. Gills were removed and the surface of each gill arch was individually examined, scraped and rinsed in water. Dactylogyrids were collected from the surface or through rinsing of gills under a stereomicroscope. Over 54,700 specimens of *Ligophorus* were sampled from 1,649 infected of the 2,275 studied fish (table 1). Most specimens were mounted unstained directly in glycerin jelly (Gussev, 1983), but some were preserved in 70 % alcohol, stained in iron acetocarmine (Georgiev et al., 1986) or Delafield's haematoxylin (Humason, 1972), dehydrated through an ethanol series (from 70 to 100 %), cleared in dimethyl phthalate and mounted as whole mounts in Canada balsam to ascertain details of their soft internal anatomy. Likewise, after examination in glycerin jelly, some specimens were demounted, washed in warm distilled water and also stained. These specimens were not deposited in museums due to their partial destruction.

In addition to this newly sampled material, the following material was examined: four specimens of *L. mugilinus* Hargis, 1955 from Charleston, NW Atlantic; four paratypes of *L. ellochelon* Yang, 2001 from GDZJ; four paratypes of *L. huitrempe* Fernández, 1987 from MZUC; one paratype of *L. saladensis* Marcotegui and Martorelli, 2009 from MPIC; two syntypes of *L. uruguayense* Failla Siquier and Ostrowski de Núñez, 2009 from CHFC; three voucher specimens of *L. tainhae* Abdallah, Azevedo and Luque, 2009 *L. brasiliensis* Abdallah, Azevedo and Luque, 2009 from UFRRJ (see below for abbreviations); two paratypes of *L. bykhowskyi* Dmitrieva, Gerasev, Gibson, Pron'kina and Gally, 2012 from BMNH.

The following museum abbreviations appear in the text: BMNH, British Museum (Natural History), London, England; CHFC, Helminthological Collection of the Laboratorio de Zoología de Invertebrados, Facultad de Ciencias, Montevideo, Uruguay; CHIOC, Helminthological Collection of the Institute Oswaldo Cruz, Rio de Janeiro, Brazil; CZTNU, Chair of Zoology, Tavrichesky National University named after V. I. Vernadsky, Simferopol, Ukraine; DBHNU, Department of Biology, Hainan Normal University, Haikou City, Hainan Province, China; DBSTU, Department of Biology, Shanghai Teachers University (currently Shanghai Normal University), Shanghai, China; GDZJ, School of Life Science, Zhongshan (Sun Yat-sen) University, Guangzhou, China; IBSS, Institute of Biology of the Southern Seas of NASU, Sevastopol, Ukraine; IZAN, Schmalhausen Institute of Zoology, Kyiv, Ukraine; MLP, Museo de La Plata, Invertebrates Collection, La Plata, Argentina; MZUC, Museum of Zoology, University of Concepción, Concepción, Chile; NMNH, National Museum of Natural History, Paris, France; UFRRJ, Universidade Federal Rural de Rio de Janeiro, Departamento de Parasitologia Animal, Seropédica, Brazil; USNPC, U. S. National Parasite Collection, Beltsville, USA; ZIN, Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia; ZNUMZ, Zaporizhzhia National University, Museum of Zoology, Zaporizhzhia, Ukraine. Type and voucher specimens collected during the present study were deposited in the Collections of BMNH, IZAN and ZNUMZ.

Worms were examined using a compound photomicroscope Leica DM LB2 or Nikon Optiphot-2 equipped with phase contrast and differential interference contrast optics. Illustrations were prepared with the aid of a camera lucida. Photographs of sclerotized structures of the haptor and male copulative apparatus were made with an interference contrast and Leica DC150 digital camera.

Definition of measurements and terminology of sclerotized characters used in the present study are illustrated in figures 1–5. The following abbreviations for the characters are used throughout the text, drawings and tables: A, articulation of the secondary lobe with the main one of the accessory piece of copulatory organ; AMP, anteromedian process of ventral bar; AP, anterior protuberances of ventral bar; APCC, accessory piece of copulatory complex; APDL, copulatory complex accessory piece distal lobe length; APM, copulatory complex accessory piece main lobe; APML, copulatory complex accessory piece main lobe length; APMW, copulatory complex accessory piece distal portion of main lobe width; APPL, copulatory complex accessory piece proximal lobe length; APPW, copulatory complex accessory piece distal portion of proximal lobe width; APS, copulatory complex accessory piece secondary lobe; APSL, copulatory complex accessory piece secondary lobe length; APTL, copulatory complex accessory piece total length; B, bulb of copulatory organ base and distal end of vagina; BL, blade of anchor; COL, total length of copulatory organ; COW, copulatory organ width at mid-length; DBL, dorsal bar length; DBPMP, posteromedian process of dorsal bar; EDP, expansion of distal part of main lobe of accessory piece of copulatory complex; EOV, external opening of vagina; F, fibres tethering the acces-

Table 1. Results of mullet sampling with information on localities, host size and summary for total *Ligophorus* spp. infection parameters

Таблица 1. Места сбора кефалевых рыб с информацией о станциях сбора, размерах хозяев и показателях зараженности лигофорусами

Host	Locality*	Host total length (range, mm)	Number of fish examined/ infected	Total parasite intensity
Chelon labrosus	JE 39°09'41"N, 0°15'21"W	206–385	33/16	87
	ED 40°42'46"N, 0°43'00"W	370–473	11/5	60
Liza aurata	SPG 38°11'N, 0°34'W	293–480	102/87	1975
	JE 39°09'41"N, 0°15'21"W	107–308	6/4	99
	GV 38°25'N, 0°18'W	235–415	26/26	1287
	ED 40°42'46"N, 0°43'00"W	224–336	103/57	629
	SB 42°25'N, 27°41'E	189–448	65/40	706
	KC 45°20'N, 36°28'E	165–385	117/96	1836
	SL 46°07'N, 34°45'E	152–363	255/238	6043
	ME 46°26'N, 35°25'E	150–195	29/0	0
	BRB 46°43'N, 36°44'E	250–288	20/19	233
Liza saliens	JE 39°09'41"N, 0°15'21"W	221–258	3/3	252
	GV 38°25'N, 0°18'W	240–270	5/5	375
	ED 40°42'46"N, 0°43'00"W	224–358	71/27	332
	SB 42°25'N, 27°41'E	190–417	84/52	516
	KC 45°20'N, 36°28'E	271	1/1	1
	SL 46°07'N, 34°45'E	270–298	2/2	13
Liza ramada	SPG 38°11'N, 0°34'W	278–430	68/47	6910
	SPS 38°12'N, 0°36'W	331–420	48/42	2557
	JE 39°09'41"N, 0°15'21"W	315–355	3/3	105
	GV 38°25'N, 0°18'W	172–485	14/6	30
	ED 40°42'46"N, 0°43'00"W	285–665	53/28	316
Mugil cephalus	SPG 38°11'N, 0°34'W	339–560	90/62	2333
	SPS 38°12'N, 0°36'W	285–560	79/26	192
	JE 39°09'41"N, 0°15'21"W	445	1/1	16
	GV 38°25'N, 0°18'W	215–330	6/6	554
	ED 40°42'46"N, 0°43'00"W	210–470	131/103	2317
	SB 42°25'N, 27°41'E	384–470	12/4	19
	BB 44°29'N, 33°36'E	320–510	30/26	969
	KC 45°20'N, 36°28'E	343–650	99/47	1308
	UE 46°06'N, 34°54'E	405–505	35/32	947
	KB 42°51'N, 133°40'E	380–520	60/46	2254
	RD 43°20'56"N, 131°47'50"E	335–470	7/7	56
Liza haematocheilus	SB 42°25'N, 27°41'E	346–530	64/55	855
	KC 45°20'N, 36°28'E	300–640	132/116	2526
	SL 46°07'N, 34°45'E	200–444	135/119	2373
	UE 46°06'N, 34°54'E	290–680	67/35	593
	OB 46°24'N, 35°28'E	250–520	51/47	626
	ME 46°26' N, 35°25' E	30–120	34/5	10
	RD 43°20'56"N, 131°47'50"E	250–455	93/76	8018
	AD 43°19'03"N, 132°17'42"E	280–410	30/29	2219
	PB 42°34'N, 130°54'E	290–460	47/33	2763
Liza tade	ZH 21°2'N, 110°3'E	200–250	20/5	6
Valamugil cunnesius	ZH 21°2'N, 110°3'E	240	1/1	3

* Locality abbreviations: SPG, Santa Pola Gulf; SPS, Santa Pola Salt Marshes; JE, Júcar Estuary; GV, Gulf of Valencia; ED, Ebro Delta, Mediterranean Sea, Spain; SB, Sozopol Bay, Black Sea, Bulgaria; BB, Balaklava Bay; KC, Kerch Channel, Black Sea, Ukraine; SL, Sivash Lake; UE, Utlyuksky Estuary; OB, Obitochna Bay; ME, Molochny Estuary; BRB, Berdyansk Bay, Azov Sea, Ukraine; PB, Posiet Bay; RD, Razdol'naya Delta; AD, Artemovka Delta; KB, Kiyevka Bay, Sea of Japan, Russia; ZH, Zhanjiang, Guangdong Province, South China Sea, China.

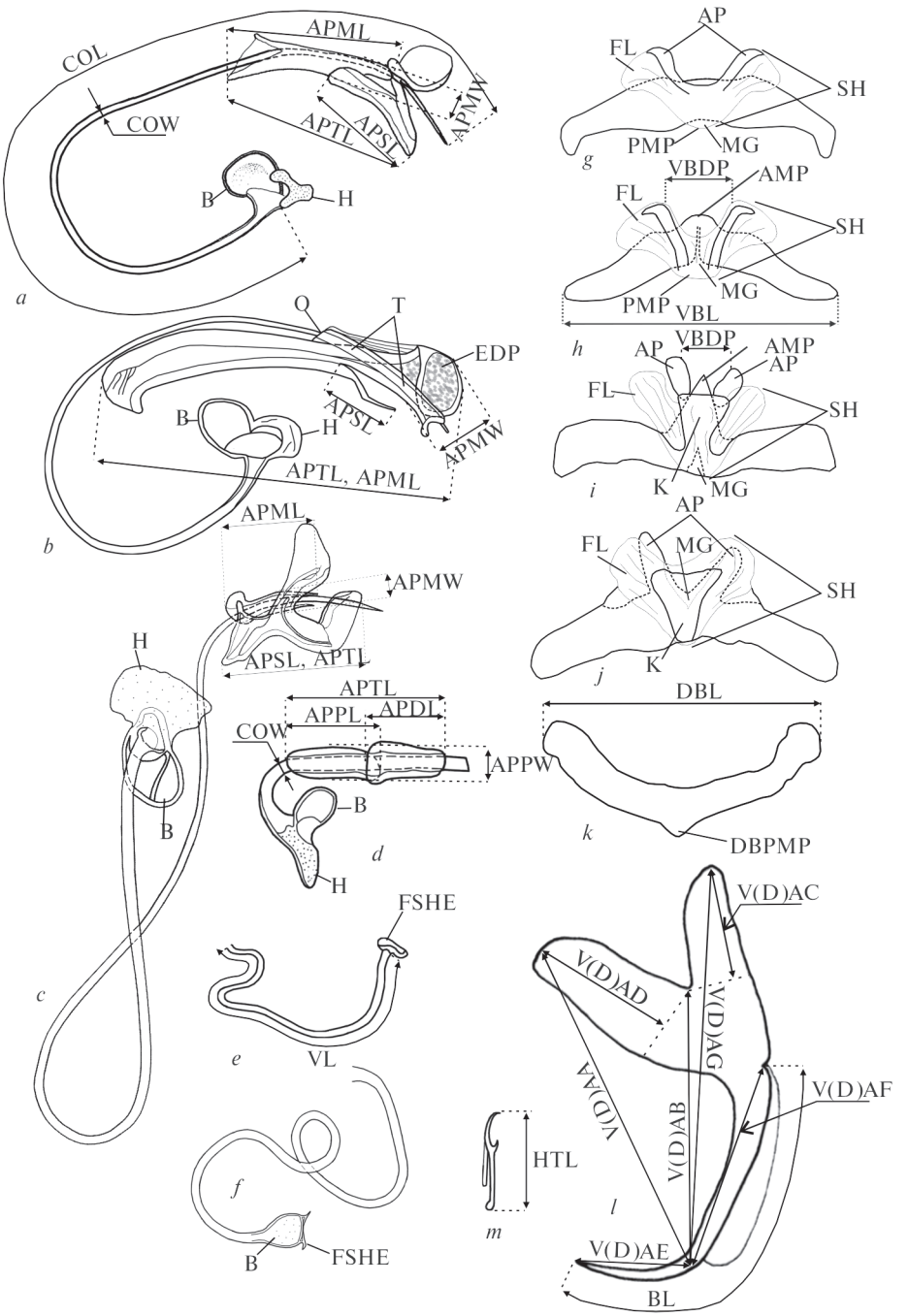

Fig. 1. Schematic drawing of the main morphological forms of genital and haptoral sclerotized structures with associated measurements and terminology used herein.

Рис. 1. Схематическое изображение основных форм половых и гапторальных склеротизированных структур с обозначением схемы промеров и используемой в работе терминологии.

sory piece or the distal end of the vagina to the tegument; FL, flaps of shield of ventral bar; FSHE, funnel-shaped extinction of the distal end of the vagina; GM, muscle guiding of the accessory piece; H, heel of base of copulatory organ; HTL, hook total length; K, knot of ventral bar; MG, median groove of ventral bar; O, funnel-shaped opening on top of distal part of main lobe of accessory piece of copulatory organ; PM, protractor muscle of the copulatory organ; PMP, posteromedian prolongation of shield of ventral bar; R, distal ring of main lobe of accessory piece of copulatory complex; SH, shield of ventral bar; T, tunnel perforates main lobe of accessory piece of copulatory complex; V(D)AA, ventral (dorsal) anchor inner length; V(D)AB, ventral (dorsal) anchor main part length; V(D)AC, ventral (dorsal) anchor outer root length; V(D)AD, ventral (dorsal) anchor inner root length; V(D)AE, ventral (dorsal) anchor point length; V(D)AF, ventral (dorsal) anchor shaft length; V(D)AG, ventral (dorsal) anchor outer length; VBDP, distance between anterior protuberances of ventral bar; VBL, ventral bar length; VL, vagina length. Metric characters (dimensions of the body, pharynx, testis, ovary, haptor, anchors, hooks, bars, male copulatory complex and vagina) of the specimens studied herein are presented in tables 2–15.

Descriptions

Dactylogyridae Bychowsky, 1933

Ligophorus Euzet et Suriano, 1977

Type species: *L. vanbenedenii* (Parona et Perugia, 1890)

Species transferred to another genus: *L. ellochelon* Zhang, 2001.

Other valid species: *L. abditus* Dmitrieva, Gerasev et Gibson, 2013; *L. acuminatus* Euzet et Suriano, 1977; *L. angustus* Euzet et Suriano, 1977; *L. bantingensis* Soo et Lim, 2012; *L. bipartitus* Dmitrieva, Gerasev, Gibson, Pron'kina et Gally, 2012; *L. brasiliensis* Abdallah, Azevedo Luque, 2009; *L. bykhowskyi* Dmitrieva, Gerasev, Gibson, Pron'kina et Gally, 2012; *L. campanulatus* Dmitrieva, Gerasev, Gibson, Pron'kina

Fig. 1. Schematic drawing of the main morphological forms of genital and haptoral sclerotized structures with associated measurements and terminology used herein: *a-d* — male copulatory complex; *e, f* — sclerotized vagina; *g-j* — ventral bar in ventral view; *k* — dorsal bar; *l* —anchor; *m* — hook. C-shaped (*a, b*), winding (*c*) and J-shaped (*d*) copulatory organ enters proximally (*a*, *c*, *d*) or distally (*b*) a claw-shaped (*a*, *b*), cross-shaped (*c*) or rod-shaped (*d*) accessory piece. The sclerotized vagina with a funnel-shaped (*e*) and scyphoid (*f*) distal end. Figure 1 *g* represents the simplest structure of the ventral bar with shield, anterior protuberances and lateral flaps; all these structures occupy ventral position in relation to a "body" of the bar; the anteromedian process and median knot is absent, dorsal median groove covered by ventral shield. On figure *h* ventral bar is complicated by presence of a small hill-shaped anteromedian process. Figure *i* depicts the most complicated structure of the ventral bar that has the ventral shield with a T-shaped knot attached to a Λ-shaped dorsal anteromedian process; the finger-like anterior protuberances extend to or beyond the level of the dorsal side of the bar, where they are reduced to a pair of small plates. The ventral bar presented on figure *j* differs from those previous by the position of the finger-like anterior protuberances that occupy dorsal side of the ventral bar to form a V-shaped structure, the anteromedian process on the dorsal side of the bar absent; instead, median groove is present that is formed by protuberances, knot massive, V-shaped. See Material and methods section for abbreviations of sclerotized structures.

Рис. 1. Схематическое изображение основных форм половых и гаптоpальных склеротизированных структур с обозначением схемы промеров и используемой в работе терминологии: *a-d* — мужской копулятивный комплекс; *e, f* — склеротизированная вагина; *g-j* — вентральная пластинка, вентральный вид; *k* — дорсальная пластинка; *l* —срединный крючок; *m* —краевой крючок. С-образный (*a*, *b*), извитой (*c*) и J-образный (*d*) копулятивный орган входит во вспомогательный аппарат проксимально (*a*, *c*, *d*) или дистально (*b*) в клешнеобразный (*a*, *b*), крестообразный (*c*) или палочковидный вспомогательный аппарат (*d*). Склеротизированная вагина с воронкообразным (*e*) и чашевидным (*f*) дистальным концом. Рисунок 1, *g* представляет собой простейшую структуру вентральной пластинки с щитком, передними протуберанцами и крыловидными латеральными выростами, все эти структуры расположены вентрально по отношению к «телу» пластинки; антеромедиальный отросток и медиальный узел отсутствуют, дорсальная срединная канавка покрыта вентральным щитком. На позиции *h* вентральная пластинка усложнена присутствием небольшого антеромедиального отростка в виде бугорка. Позиция *i* иллюстрирует самую сложную форму ветральной пластинки, последняя имеет вентральный щиток с Т-образным узлом, который соединен с Λ-образным дорсальным антеромедиальным отростком; пальцевидные передние протуберанцы, которые достигают или выступают за уровень спинной стороны срединной пластинки, где они редуцируются в пару небольших пластин. Вентральная пластинка представленная на позиции *j* отличается от всех предыдущих положением пальцеобразных передних протуберанцев, которые расположены на дорсальной стороне вентральной пластинки, образуя V-подобную структуру, антеромедиальный вырост на дорсальной пластинке отсутствует, вместо него имеется срединная бороздка, образованная передними протуберанцами, узел массивный, V-образный. Аббревиатуры промеров и названий склеротизированных структур см. в гл. Материал и методы.

et Gally, 2012; *L. careyensis* Soo et Lim, 2012; *L. cephali* Rubtsova, Balbuena, Sarabeev, Blasco-Costa et Euzet, 2006; *L. chabaudi* Euzet and Suriano, 1977; *L. chelatus* Soo et Lim, 2012; *L. cheleus* Rubtsova, Balbuena et Sarabeev, 2007; *L. chenzhenensis* Hu et Li, 1992; *L. confusus* Euzet et Suriano, 1977; *L. domnichi* Rubtsova, Balbuena et Sarabeev, 2007; *L. fenestrum* Soo et Lim, 2012; *L. fluviatilis* (Bychowsky, 1949) Pan, 1999; *L. funnelus* Soo et Lim, 2012; *L. guanduensis* Abdallah, Azevedo et Luque, 2009; *L. hamulosus* Pan et Zhang, 1999; *L. heteronchus* Euzet et Suriano, 1977; *L. huitrempe* Fernández, 1987; *L. imitans* Euzet et Suriano, 1977; *L. kaohsianghsieni* (Gussev, 1962); *L. kedahensis* Soo et Lim, 2012; *L. lebedevi* Dmitrieva, Gerasev, Gibson, Pron'kina et Gally, 2012; *L. lizae* Abdallah, Azevedo et Luque, 2009; *L. llewellyni* Dmitrieva, Gerasev et Pron'kina, 2007; *L. macrocolpos* Euzet et Suriano, 1977; *L. mamaevi* Dmitrieva, Gerasev, Gibson, Pron'kina et Gally, 2012; *L. mediterraneus* Sarabeev, Balbuena et Euzet, 2005; *L. minimus* Euzet et Suriano, 1977; *L. miroshnichenki* sp. n.; *L. mugilinus* (Hargis, 1955); *L. navjotsodhii* Soo et Lim, 2012; *L. pacificus* Rubtsova, Balbuena et Sarabeev, 2007; *L. parvicirrus* Euzet et Sanfilippo, 1983; *L. parvicopulatrix* Soo et Lim, 2012; *L. pilengas* Sarabeev et Balbuena, 2004; *L. rectus* sp. n.; *L. saladensis* Marcotegui and Martorelli, 2009; *L. simpliciformis* Dmitrieva, Gerasev, Gibson, Pron'kina et Gally, 2012; *L. surianoae* Dmitrieva, Gerasev, Gibson, Pron'kina et Gally, 2012; *L. szidati* Euzet et Suriano, 1977; *L. tainhae* Abdallah, Azevedo et Luque, 2009; *L. triangularis* sp. n.; *L. uruguayense* Failla Siquier et Ostrowski de Núñez, 2009 et *L. zhangi* Dmitrieva, Gerasev, Gibson, Pron'kina et Gally, 2012.

Junior synonyms: *L. euzeti* Dmitrieva et Gerasev, 1996 and *L. gussevi* Miroshnichenko et Maltsev, 2004

Species inquirendae: *L. leporinus* (Zhang et Ji, 1981) Gussev, 1985 and *L. chongmingensis* Hu et Li, 1992.

Emended diagnosis

Body fusiform, comprising cephalic region, trunk, peduncle and haptor. Tegument smooth. One or two terminal cephalic lobes and two bilateral cephalic lobes; cephalic glands unicellular, lateral or posterolateral to pharynx, opening anterolaterally via three pairs of clusters of ducts on lateral margins of cephalic region. Mouth subterminal, midventral; pharynx muscular, glandular bulb; oesophagus short; intestinal caeca two, simple, confluent posterior to gonads, lacking diverticula. Eyes two pairs, each with small lens. Anterior pair closer together and smaller than posterior pair. Gonads intercaecal, tandem or slightly overlapping; testis postovarian, medial, ovate or subspherical; vas deferens on left side not encircling intestinal caeca, runs anterosinistrally, entering laterally pyriform seminal vesicle. One pyriform prostatic reservoir. Copulatory complex comprising tubular sclerotized, uncoiled copulatory organ and non-articulated accessory piece; base of copulatory organ expanded into complex structure comprising heel and bulb. Accessory piece serving as guide for distal portion of copulatory organ, comprises either simple concave to tube-like or bilobed structure; when accessory piece bilobed, one tube-like lobe directly serving copulatory organ, while other lobe, highly variable in shape, adjoins the first one and usually unconnected with copulatory organ (below referred to as main and secondary lobe, respectively). Ovary medial, elongated, U- or J-shaped, proximal limb ventral, shorter than distal one. Seminal receptacle at ovary level, between its limbs; vaginal aperture submidventral or dextroventral, vagina sclerotized or not, distal end of vagina funnel-shaped or scyphoid. Common genital pore midventral, near level of intestinal bifurcation. Vitellaria in trunk. Haptor globose with well developed lateral flaps, dorsal and ventral anchor/bar complexes and seven pairs of hooks subequal in shape and size. Hook distribution normal; hook with upright acute thumb, slender shank comprised one subunit. Both ventral and dorsal anchors with filament, inner and outer roots, base and

blade; base markedly thicker than blade, separated by external (or outer) notch; blade comprising shaft and point. Bars dissimilar in shape, transverse ventral bar inverted V-shaped, with shield on ventral side reaching in anterior pair of protuberances. Dorsal bar relatively simple, V or yoke-shaped, shield absent. Parasites on gills of mugilid fishes.

Remarks

The generic diagnosis proposed by Euzet and Suriano (1977) included the following features: haptor armed with 14 hooks, two anchor pairs and two transverse bars; three pairs of clusters of ducts of cephalic glands; intestinal caeca simple, united posteriorly; testis median, vas deferens on left side, seminal vesicle present; one prostatic reservoir; tubular copulatory organ long and thin with accessory piece; ovary intercaecal; sclerotized vagina submidventral; seminal receptacle spherical preovarial. A few years later, Euzet and Sanfilippo (1983), after describing a new species of *Ligophorus* from *Lz. ramada*, found some differences with the previously described species that led them to amend the generic diagnosis. The proposed changes concerned the traits of genital structures, namely, "Tubular copulatory organ thin..." instead of "Tubular copulatory organ long and thin..." and "Vagina sclerotized or not..." instead of "Vagina sclerotized...". Sarabeev and Balbuena (2004) based on the comparative morphology of two studied species suggested: "the following feature should be considered in revised generic diagnosis: ventral transversal bar can have two membranous anterior processes flanking and a nonmembranous median process between them". Rubtsova et al. (2007) described new species from flathead mullet *M. cephalus* in the Sea of Japan and found elongated U-shaped ovary in all three new species, as well as in additionally studied species from the Mediterranean region. It was supposed that this feature is shared by all other species (Rubtsova et al., 2007). Dmitrieva et al. (2009 a, b) considered details of morphology of the ventral bar and the accessory piece of the male copulatory complex. They proposed the conception of the different morphology for the ventral and dorsal side of the ventral bar and a grooved accessory piece of the copulatory organ. Soo and Lim (2012) described eight new species from Malaysian mullets and emended generic diagnosis to include the following new features: the ventral bar inverted V-shape with the anteromedian protuberance of one median piece with or without lateral processes; the base of the copulatory organ bilobed, the accessory piece represents a simple groove piece or two opposing pieces of which one is grooved; the ovary J to U-shaped, the vaginal aperture dextroventral, sub-median to sublateral.

The present amended diagnosis of *Ligophorus* replaces that of Euzet and Suriano (1977), supplemented by Euzet and Sanfilippo (1983), Sarabeev and Balbuena (2004) and Soo and Lim (2012). The main new features are the following: i) copulatory organ uncoiled, non-articulated accessory piece; ii) base of copulatory organ expanded to form bulb and heel; iii) accessory piece is either simple concave to tube-like or bilobed structure; when accessory piece bilobed, one tube-like lobe immediately serving for copulatory organ and other lobe, highly variable in shape, serving for copulatory organ mediately through the first one; iv) haptor globose with well developed lateral flaps; v) hooks subequal in shape and size, each hook with upright acute thumb, domus, shank comprised of one subunit; vi) both ventral and dorsal anchors with filament, inner and outer roots, base and blade; base markedly thicker than blade, separated by an external (or outer) notch; blade comprising shaft and point; vii) bars dissimilar in shape, transverse ventral bar with shield on ventral side and anterior pair of protuberances; viii) dorsal bar V or yoke-shaped, shield absent. These features are shared by all valid species from the Atlantic and Pacific region examined in the present study, as well as by 16 recently described species from the Indian region (Dmitrieva et al., 2012; Soo, Lim, 2012).

The first feature describes the shape of the copulatory organ, which is uncoiled (C-, J-shaped or winding) and non-articulated with the accessory piece in *Ligophorus* spp. as

opposed to coiled or articulated with the accessory piece (as, for example, in some species of *Euryhaliotrema* (Kritsky, Boeger, 2002; Kritsky, 2012).

The second feature specifies the structure of the base of the copulatory organ that was defined by Soo and Lim (2012) as bilobed with one lobe smaller than the other one. However, as it was described correctly by Llewellyn and Anderson (1984), the copulatory organ of *Ligophorus* expanded into a complex structure. On one side there is a hollow thin-walled vesicle, which appears to be a semi-circular rod or plate due to an optical effect and, probably, peculiarities of fixation. On the other side the expanded base of the copulatory organ usually represents a thick-walled vesicle, which receives a duct from the seminal vesicle that communicates with the lumen of the copulatory organ; the outer surface of the vesicle serves for the muscle attachment. These structures are proposed to be named herein as bulb and heel, respectively, to distinguish *Ligophorus* from other morphologically similar dactylogyrids genera, e. g. *Haliotrema* and *Euryhaliotrema*, which have a plate-like or bulbous base of the copulatory organ. All valid species of *Ligophorus* examined in the present study from the surveyed regions possess a thick-walled heel (fig. 2, *a-c*, *e*, *g*) except *L. parvicirrus*, which exhibits a thin-walled heel (fig. 2, *f*). The shape of this structure in most species varies from heel-shaped (fig. 2, *a*) to semilunar (fig. 2, *c*, *e*) or to auriculate, as for example in *L. kaohsianghsieni* (fig. 2, *b*). Our observation of specimens of *L. kaohsianghsieni* revealed that the shape and size of the heel depend on worm age. Specimens were categorized as juvenile or adult based on their body size and development of the male and female genital systems. Adult worms were characterized by a large heel (with shape variation from auriculate (fig. 2, *b*) to semilunar (fig. 2, *c*)), while juveniles showed a small heel (fig. 2, *g*). At the same time the bulb remains invariable in size compared with the heel (fig. 2, *a*, *e*, *c*, *g*). Therefore, the generic definition of the copulatory organ of *Ligophorus* as bilobed with one lobe smaller than the other one by Soo and Lim (2012) is erroneous.

The only exception to the morphology of the base of the copulatory organ is the description of *L. bykhowskyi* and *L. zhangi* by Dmitrieva et al. (2012), where the base was characterized as a single-chambered structure. However, reinvestigation of two of the four type specimens of *L. bykhowskyi* from BMNH (N 2011.11.17.1–4) revealed the presence of bilobed base in this species (fig. 2, *d*, *h*). The texture of the sclerotization of the different portions of the base is almost equal, which complicates their differentiation on a bilobed structure with a bulb and a heel. The line drawings and microphotographs provided by Dmitrieva et al. (2012) for *L. zhangi* clearly indicate the presence of a bilobed base of the copulatory organ in this species (fig. 4, *c* and 5, *e* in Dmitrieva et al.

Fig. 2. Microphotographs of the copulatory complex of *L. confusus* (*a* and *e*), *L. kaohsianghsieni* (*b*, *c*, *g*), *L. parvicirrus* (*f*) and *L. bykhowskyi* (*d* and *h*, both examined type specimens are presented, which exhibit the base obtained from different views) with illustration of morphological variations in the base of the copulatory organ. As example, the texture of a sclerotization of different portions of the base of the copulatory organ is unequal in *L. confusus* and *L. kaohsianghsieni* (*a-c, e*, *g*), with a thick-walled heel and a thin-walled bulb, and almost equal, thin-walled in *L. parvicirrus* and *L. bykhowskyi* (*f*, *d*, *h*). *a-c* and *e-g* illustrate variations in the shape and texture of the heel of species reviewed in the present study indicating a difference between adult (*a-c*, *e*, *f*) and juvenile specimens (*g*): *a* and *g* represent a thick-walled small heel; *b*, a thick-walled large auriculate heel; *c* and *e*, a thick-walled large semilunar heel; *f*, a thin-walled heel. See Material and methods section for abbreviations of sclerotized structures.

Рис. 2. Микрофотографии копулятивного комплекса *L. confusus* (*a* и *e*), *L. kaohsianghsieni* (*b*, *c*, *g*), *L. parvicirrus* (*f*) и *L. bykhowskyi* (*d* и *h*, исследованы оба типовых экземпляров, показано основание в разных ракурсах) с иллюстрацией морфологических вариаций строения основания копулятивного органа. В качестве примера, у *L. confusus* и *L. kaohsianghsieni* (*a-c*, *e*, *g*) степень склеротизации разных частей основания копулятивного органа различна (толстостенная пятка и тонкостенное шарообразное расширение), и почти одинаковая, тонкостенная у *L. parvicirrus* и *L. bykhowskyi* (*f*, *d*, *h*). *a-c* и *e-g* показывают вариации формы и степени склеротизации пятки рассмотренных в данной работе видов, с указанием различий у половозрелых (*a-c*, *e*, *f*) и ювенильных экземпляров (*g*): *a* и *g* илюстрируют толстостенную маленькую пятку; *b* — толстостенную большую ухообразную пятку; *c* и *e*— толстостенную большую полулунную пятку; и *f* — тонкостенную пятку. Аббревиатуры названий склеротизированных структур см. в гл. Материл и методы.

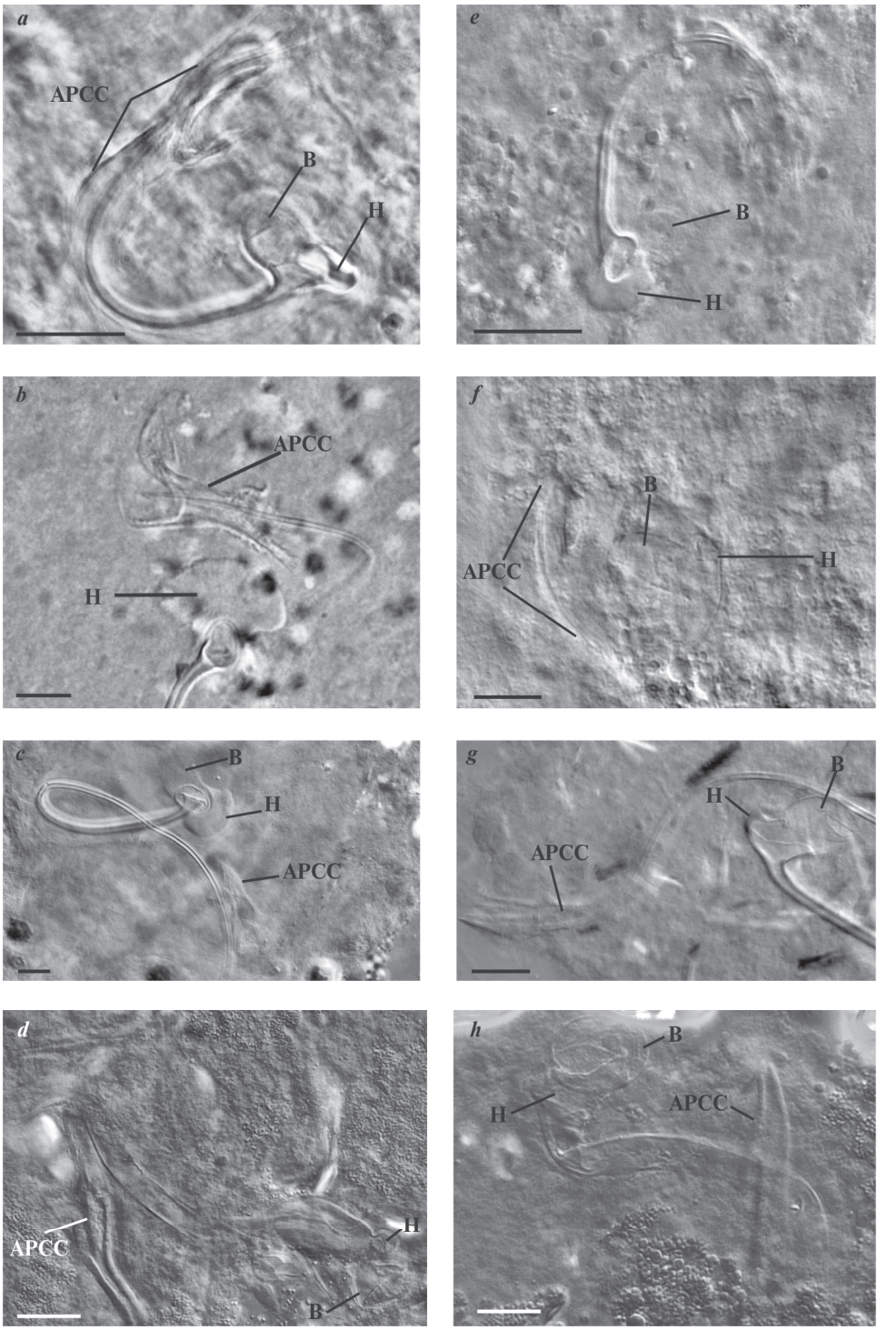

Fig. 2. Microphotographs of the copulatory complex of *L. confusus* (*a* and *e*), *L. kaohsianghsieni* (*b*, *c*, *g*), *L. parvicirrus* (*f*) and *L. bykhowskyi* (*d* and *h*, both examined type specimens are presented, which exhibit the base obtained from different views) with illustration of morphological variations in the base of the copulatory organ. Scale bars 10 μm.

Рис. 2. Микрофотографии копулятивного комплекса *L. confusus* (*a* и *e*), *L. kaohsianghsieni* (*b*, *c*, *g*), *L. parvicirrus* (*f*) и *L. bykhowskyi* (*d* и *h*, исследованы оба типовых экземпляра, показано основание в разных ракурсах) с иллюстрацией морфологических вариаций строения основания копулятивного органа. Масштабные линейки 10 мкм.

(2012)). However, the Red Sea is excluded from the present study and no further discussion will be conducted in this paper.

The third and seventh feature redefines the structure of the accessory piece and ventral bar (see the next section for detailed information). Remaining features, which specify morphology of haptor, hooks, anchors and dorsal bar, were known from previous descriptions of *Ligophorus* spp. but never used as characters for generic discrimination.

Description of taxonomically important characters and related terminology

Copulatory complex

We define three main types of accessory piece of the copulatory complex in *Ligophorus* spp.: claw- (fig. 1, *a*, *b*; 3, *a*, *b*, *f*), rod- (fig. 1, *d*; 3, *c*), and cross-shaped (fig. 1, *c*; 3, *d*, *e*). Among them, the claw-shaped (resembling a crustacean claw or chela) is the commonest one, whereas the rod-shaped piece is currently exhibited by two species (*L. acuminatus*, *L. rectus* sp. n.) and the cross-shaped by six (*L. mugilinus*, *L. kaohsianghsieni*, *L. macrocolpos*, *L. huitrempe*, *L. mediterraneus* and *L. saladensis*). Within the claw-shaped category we recognize three subtypes: pincer-like (fig. 1, *b*; 3, *a*, *f*), arrow-like (fig. 1, *a*; 3, *b*) and duck-billed claw (fig. 4, *d* of Abdallah et al. (2009)).

The accessory piece of the male copulatory complex of herein studied species is always bilobed. In all species of *Ligophorus* except in *L. rectus* sp. n. only one of the lobes supports the copulatory organ. This lobe will be referred to as the "main lobe", whereas the other will be designated as the "secondary lobe" (fig. 1, *a-c*; 3, *a-f*). The copulatory organ of *L. rectus* sp. n. passes through both lobes; they will be termed herein "proximal" and "distal", reflecting their position along the axis of the copulatory organ (fig. 1, *d*). The main lobe or proximal and distal lobes are tunnelled (fig. 1, *b*; 3, *a*, *e*, *f*) to accommodate the copulatory organ. The tunnel is clearly visible on specimens with the copulatory organ completely withdrawn into the body (fig. 3, *a*, *e, f*). In species with a funnel-shaped distal end of the accessory piece we may observe the tunnel opening at the dis-

Fig. 3. Microphotographs of the main types of the accessory piece (*a-f*) and systems of muscles associated with the male copulatory complex (*a*, *g*), and the distal end of the vagina (*h-l*): *a*, *f*, *g* — accessory piece with the distal position of the copulatory organ entrance (*f* — the distal portion of the accessory piece barely shown); *b-e*, accessory piece with the proximal position of the copulatory organ entrance; *a*, *b*, *f*, *g* — claw-shaped accessory piece: *a*, *f*, *g* — pincerlike (*L. pilengas*, *L. llewellyni* and *L. cheleus*, respectively, the tunnel (T) perforating a distal ring of the main lobe is shown) and *b* — arrow-like (*L. vanbenedenii*); *c* — rod-shaped accessory piece (*L. acuminatus*); *d* and *e*, cross-shaped accessory piece (*L. mediterraneus* and *L. kaohsianghsieni*). On *a-c* and *f* articulation of the secondary lobe with the main one by a simple joint is shown. On *d* and *e*, articulation of the secondary lobe with the main one lengthways along all its length (*e*) or only along its part (*d*) is illustrated; *h* and *i* — funnel-shaped distal end of the vagina: *h* — thin-walled (*L. angustus*) and *i* — thick-walled (*L. minimus*); *j* and *k* — scyphoid distal end of the vagina: *j* — broad (*L. kaohsianghsieni*) and *k* — narrow (*L. mugilinus*); *l* — vaginal external opening of *L. mugilinus*, fibre fastening the distal end of the vagina to the tegument is shown. Scale bar 10 μm. See Material and methods section for abbreviations of sclerotized structures.

Рис. 3. Микрофотографии основных типов вспомогательного аппарата (*a-f*) и мышечной системы, связанной с мужским копулятивным комплексом (*a*, *g*), и дистального конца вагины (*h-l*): *a*, *f*, *g* — вспомогательный аппарат с дистальным расположением входа копулятивного органа (*f*, показана только дистальная часть вспомогательного аппарата); *b-e* — вспомогательный аппарат с проксимальным расположением входа копулятивного органа. *a*, *b*, *f*, *g* — клешневидный вспомогательный аппарат: *a*, *f*, *g* — пинцетообразный (*L. pilengas*, *L. llewellyni* и *L. cheleus* соответственно показана полая трубка (T) прободающая дистальное кольцо основной доли); *b* — стреловидный (*L. vanbenedenii*). *c* — палочковидный вспомогательный аппарат (*L. acuminatus*). *d* и *e* — крестообразный вспомогательный аппарат (*L. mediterraneus* и *L. kaohsianghsieni*). На *a-c*, *f* показана артикуляция дополнительной доли вспомогательного аппарата с основной при помощью простого соединения. На *d* и *e* иллюстрируется артикуляция дополнительной доли с основной по всей ее длине (*e*) или ее части (*d*). *h* и *i* — воронкообразный дистальный конец вагины: *h* — тонкостенный (*L. angustus*) и *i* — толстостенный (*L. minimus*). *j* и *k* — чашеобразный дистальный конец вагины: *j* — широкий (*L. kaohsianghsieni*) и *k* — узкий (*L. mugilinus*); *l* — вагинальное внешнее отверстие *L. mugilinus*, показано крепление дистального конца вагины к тегументу. Масштабная линейка 10 мкм. Аббревиатуры названий склеротизированных структур см. в гл. Материал и методы.

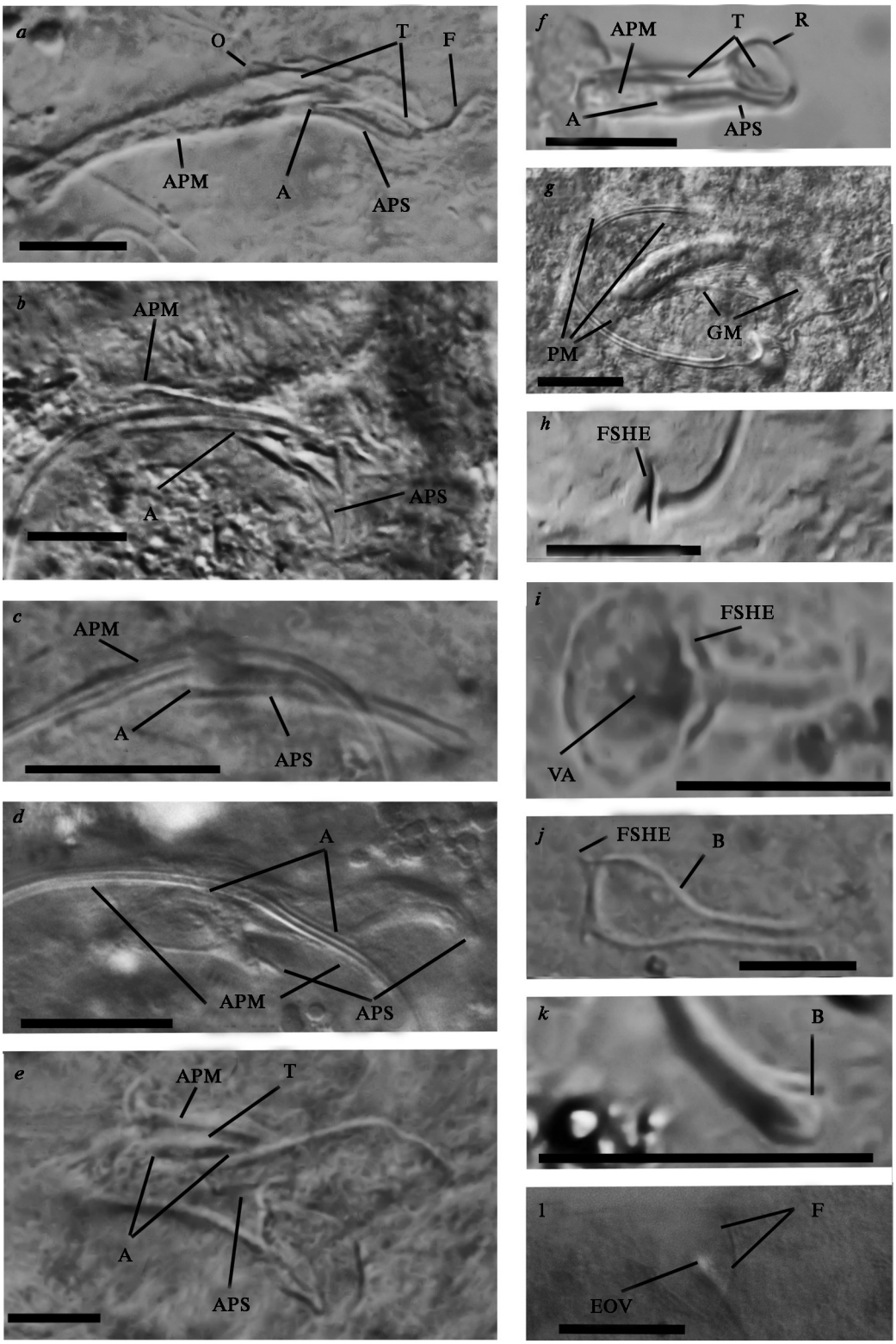

Fig. 3. Microphotographs of the main types of the accessory piece (*a-f*) and systems of muscles associated with the male copulatory complex (*a*, *g*), and the distal end of the vagina (*h-l*).

Рис. 3. Микрофотографии основных типов вспомогательного аппарата (*a-f*) и мышечной системы, связанной с мужским копулятивным комплексом (*a*, *g*), и дистального конца вагины (*h-l*).

tal round edge of the main lobe (fig. 3, *f*). The secondary lobe in all rod and claw-shaped accessory pieces (except *L. uruguayense*) articulates with the main lobe to form a simple joint (fig. 1, *a*, *b*, *d*; 3, *a-c*, *f*). In *L. uruguayense* the secondary lobe articulates with the main one along the proximal part of the latter. In the cross-shaped accessory piece, the secondary lobe articulates with the main one along all (fig. 1, *c*; 3, *e*) or part (fig. 3, *d*) of its length, and so is considered herein to connect by a suture. In all types of accessory piece, the two lobes are connected by a rigid joint.

Three main types of position of the male copulatory organ entrance into the accessory piece are observed in *Ligophorus*: distal (fig. 1, *a*, *c*, *d*; 3, *a, f*), proximal (fig. 1, *b*; 3, *b-e*) and medial. The latter feature is known only for three species (*L. minimus*, *L. brasiliensis* and *L. miroshnichenki* sp. n.), while the other two cases are common. Species with distal entrance are characterized by having a complex opening structure at the upper side of the distal portion of the accessory piece. Usually it represents an inconspicuous funnel-shaped membranous extinction perforated by tunnel, the latter runs throughout the distal portion of the main lobe and comes out the ventral surface of the worm body (fig. 1, *b*; 3, *a*, *f*).

Four variations in the shape of the male copulatory organ are observed for *Ligophorus* spp., namely, winding (fig. 1, *c*), C- (fig. 1, *a*, *b*) or J-shaped (fig. 1, *d*). The first shape is typical for *L. kaohsianghsieni* and *L. macrocolpos*; J-shaped for *L. rectus* sp. n.; while C-shaped is for all other species considered in the present study.

Dmitrieva et al. (2009 b) do not consider the degree of convolution of the copulatory organ; the tubular structure of the accessory piece (see Discussion of Dmitrieva et al. (2009 b) and page 8 of Gerasev et al. (2010)); and the position of the copulatory organ entrance in the accessory piece as useful feature for species discrimination, but our observations show consistent types by species. First, they argued that "the copulatory tube can move freely inside the accessory piece, which forms a U-shaped gutter only partly enclosing tube. The accessory piece is rigid and its position in the worm body is determined by crimped ligaments... which fasten it to the tegument surrounding the male genital pore and through which the tube can be extended to the exterior. The copulatory tube and the accessory piece are not directly connected, but a muscular sheath (''sleeve'' of Llewellyn and Anderson, 1984) surrounding the tube is attached to the accessory piece". Second, it was considered that "the point of attachment of the muscular sheath surrounding the tube to the accessory piece, and its shape, can be used as characters for differentiating species". Third, they observed that "...in living worms the copulatory tube does not coil either proximally (which would hinder the functioning of the MCO in the same way as a curved piston would in a syringe), or especially distally, where it protrudes from the body only during copulation".

But, both the rigid connection between the male copulatory organ and accessory piece and the coiled copulatory organ had never been presented in previous papers concerning *Ligophorus* spp. This conception was falsely ascribed to Rubtsova et al. (2006 a, b; 2007). Rubtsova et al. (2006 b, p. 252) characterized the shape of the copulatory organ as C-shaped or forming a single coil. The latter morphological feature concerned *L. ellochelon* and *L. leporinus*, which are transferred to another genus or considered incertae sedis in the present study, respectively.

Second, as it is shown in fig. 3, *f*, the distal end of the accessory piece is ring-shaped. The ring is pierced by the tunnel serving as guide for the copulatory organ. Further, the O-shaped cross-section of the accessory piece represents the hollow tube in specimens with the copulatory organ retracted from the accessory piece (fig. 3, *a, e*, *f*). The same interpretation of the morphology of the accessory piece was made by Llewellyn and Anderson (1984), who characterized the accessory piece as a "hollow cylindrical sheath".

Third, according to Llewellyn and Anderson (1984) and our own observations, the distal end of the accessory piece (not the complete structure) is connected with the tegument

of the neighbouring ventral surface of the body by muscular fibres. A protractor muscular sheath or a sleeve extending from the expanded proximal base of the copulatory organ is attached to either the proximal end of the accessory piece and its proximal extension or the distal (medial) portion through a funnel-shaped membranous extension. Therefore, most species with the proximal position of the copulatory organ entrance possess an expanded proximal end of the main lobe of the accessory piece (fig. 3, *b*, *e*), while species with the distal position of the copulatory organ entrance have an expansion in the distal part and usually tapered proximal end (fig. 3, *a*). The described functional morphology of the copulatory complex by Llewellyn and Anderson (1984) and supplemented in the present study (see also the last paragraph of the present section) characterizes *Ligophorus* spp. with a tubular accessory piece, while other species with a concave accessory piece have some morphological distinctions. For example, specimens examined herein of *L. bykhowskyi* possess an expanded distal end of the accessory piece of the copulatory complex (fig. 2, *d*) to which is attached a protractor muscular sheath extending from the expanded proximal base of the copulatory organ. Further studies are needed to reveal specific features of the functional morphology of the male copulatory complex of species with a simple concave accessory piece.

Fourth, Dmitrieva et al. (2009 b) proposed to use the point of attachment of the muscular sheath surrounding the copulatory organ to the accessory piece as characters for differentiating species. However, this feature is actually the position of copulatory organ entrance at the accessory piece, because the copulatory organ moves only inside the protractor muscular sheath.

Finally, it is quite possible that the problem lies in an incomplete understanding by Llewellyn and Anderson (1984) and Dmitrieva et al. (2009 a, b) of the functional morphology of the male copulatory complex. Llewellyn and Anderson (1984) correctly described three systems of muscle or fibres associated with the copulatory complex and their function. Namely, i) the copulatory organ protractor muscle (fig. 3, *g*); ii) the retractor muscle; and iii) the fibres tethering the accessory piece to tegument (fig. 3, *a*). However, the proposed functional morphology overlooks the role of the muscles that surround the main and secondary lobe of the accessory piece and serve to move the latter and to guide the distal end of the copulatory organ (fig. 3, *g*). It was observed in the present study that in living worms the proximal part of the accessory piece moves and is used by the worm as a shaft to guide the copulatory organ when it protrudes from the body.

Distal end of vagina

The distal end of the vagina is characterised by high intraspecific stability with some shape variation. We recognize two main types: funnel-shaped (fig. 1, *e*; 3, *h*, *i*) and scyphoid (fig. 1, *f*; 3, *j*, *k*). The funnel-shaped type represents the simple extinction of the vagina with a thinning wall (fig. 3, *h*, *i*), while the scyphoid end consists of a bulb that turns into typically inconspicuous extinction (fig. 3, *j*, *k*). The tapering wall of the distal end of the vagina turns into fibres, which fasten it to the tegument surrounding the external opening of the vagina (fig. 3, *l*). According to the texture of the funnel-shaped distal end of the vagina, two variations are observed, thin (fig. 3, *h*) and thick-walled (fig. 3, *i*). The scyphoid distal end of the vagina can be broad (fig. 3, *j*) or narrow (fig. 3, *k*).

Ventral bar morphology

Dmitrieva et al. (2009 a, b) pointed out that the ventral and dorsal sides of the transverse ventral bar differ in morphology, which according to our observations is correct. These authors also claimed that the median knoll[1] and wing-shaped laminae[2] are always

[1] Median knoll by Dmitrieva et al. (2009 a, b) = anteromedian process in the present study.
[2] Wing-shaped laminae by Dmitrieva et al. (2009 a, b) = flaps in the present study.

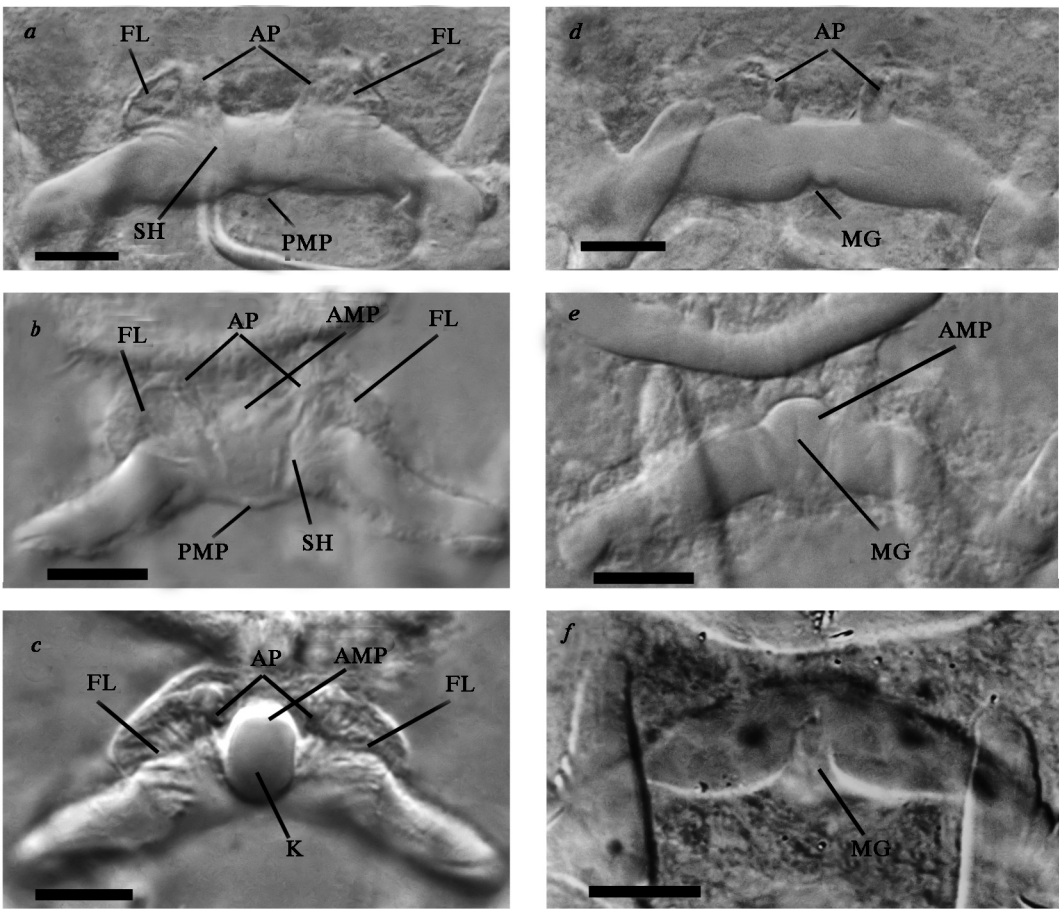

Fig. 4. Microphotographs of the morphological variations of the ventral side (*a-c*) and the dorsal one (*d-f*) of the ventral bar of *L. pilengas*. Each pair of pictures is taken from the same specimen with exception of *c* and *f*; *a*, *d* and *b*, *e* illustrate the variation of presence and absence of the anteromedian process on the ventral bar; *c* indicates the occurrence of the median knot on the ventral side in some specimens; *d-f* show a difference in the median groove; *a-d* demonstrate anterior protuberances of the bar. Scale bars 10 μm. See Material and me-thods section for abbreviations of sclerotized structures.

Рис. 4. Микрофотографии морфологической изменчивости вентральной (*a-c*) и дорсальной стороны (*d-f*) вентральной срединной пластинки *L. pilengas*. Каждая пара фотографий сделана с одного и того же экземпляра, за исключением *c* и *f*; позиции *a*, *d* и *b*, *e* иллюстрируют изменчивость наличия и отсутствия антеромедианного выроста вентральной пластинки; *c* изображено наличие медиального узла на вентральной стороне у некоторых экземпляров; *d-f* показаны различия в медиальной бороздке; *a-d* показаны передние протуберанцы срединной пластинки. Масштабные линейки 10 мкм. Аббревиатуры названий склеротизированных структур см. в гл. Материл и методы.

present on the dorsal side of the ventral bar. However, many characters such as the anteromedian process, median knot and groove are highly variable within some species. For example, the ventral bar of *L. pilengas* (fig. 4) shows several morphological variations: i) the anteromedian process may be absent (fig. 4, *a*, *d*) or present (fig. 4, *b*, *c* and *e*); ii) the knot may be absent (fig. 4, *a, b*) or present (fig. 4, *c*); iii) the median groove may be shallow (fig. 4, *d*), deep (fig. 4, *f*) or reaching to the fracture (fig. 4, *e*). In addition, the comparison of juvenile and adult specimens of *L. pilengas* revealed differences in the morphology of the ventral shield of the bar. Normally younger specimens possess a simple and thin shield (fig. 4, *a*), whereas in older specimens the shield is usually thicker with the knot present (fig. 4, *c* and 5, *d*, *e*).

Despite the high intraspecific variability of the ventral bar morphology, several types for the anteromedian process and finger-like anterior protuberances can be iden-

tified. With some exceptions, the anteromedian process of the ventral bar may be: i) absent; ii) present or absent; if present, it is small, knoll-shaped; iii) present, tall, Λ-shaped. The finger-like anterior protuberances are disposed on: i) ventral side of bar or ii) dorsal side of bar. The ventral or dorsal side of the ventral bar was defined in the present study by a relative position of the dorsal bar and the first ventral pair of hooks (numeration according to Mizelle, 1936).

If we consider different characteristics of the ventral bar as a complex structure, then at least four morphological variations can be recognized. The first type of ventral bar is the simplest one and represents the following structure: the finger-like anterior protuberances of the ventral shield not reaching the level of the dorsal side of the bar; the knot present or absent; the anteromedian process absent; the median groove on the dorsal side present; some species with the posteromedian prolongation of shield, extending to or beyond level of posterior end of the bar (fig. 1, *g*; 4, *a* and *d*). The second morphological type is distinguished from the first one by the presence of the anteromedian process that is formed by the "body" of the bar and lies more dorsally in relation to the shield and anterior protuberances; the knot of shield on the ventral side of the bar present or absent; if present, the ventral knot is attached to the dorsal anteromedian process (fig. 1, *h*; 4, *b, c*, *e* and 5, *a*, *f*). The third type is complicated by the structure of the finger-like anterior protuberances of the ventral shield (fig. 5, *b*), which are extended to the dorsal level of the bar, where they are reduced to a pair of small plates (fig. 1, *i*; 5, *c, g* and *h*); the anteromedian process on the dorsal side between the pair of small plates (fig. 1, *i*, 5, *h*); the ventral knot attached (fig. 1, *i*; 5, *c*) to the dorsal anteromedian process (for example, in *L. domnichi* a V or T-shaped knot of the ventral shield attached to a Λ-shaped dorsal anteromedian process fig. 5, *g* or in *L. szidati* ∩-shaped (fig. 5, *d*) and Λ-shaped (fig. 5, *i*), respectively). The pair of small plates in different species occupies an anterolateral (fig. 1, *i*, 5, *h*) or lateral (fig. 5, *i*) position in relation to the anteromedian process. The fourth type differs from all previous ones in position of the finger-like anterior protuberances that occupy the dorsal side of the ventral bar form a V-shaped structure; the anteromedian process on the dorsal side of the bar is absent; instead, median groove is present, formed by rising protuberances (fig. 1, *j*; 5, *e, j*). However, due to the high morphological variability of some structures of the ventral bar within species (see above), two or even three morphological types can be exhibited by different specimens of the same species. In the present study, drawings of *Ligophorus* species are supplied by one pattern of the ventral bar with an illustration of visible features of both sides.

Anchor morphology

The distinction among anchor types is based on the ratio between the point and shaft lengths of the blade. Other parts such as the anchor base and roots continue to grow after formation of the anchor blade (Bychowsky, 1957). Therefore the relative sizes or position of tips of these features cannot be as useful as that of the blade components. So, the ratio between the point to the root lengths, the relative position of the tip of the outer root to the tip of the inner root and the point to the inner root were used herein as secondary traits for anchor description. Three main types of anchors are identified herein: i) blade sharply bent, shaft about 1.5 times longer or more than the point (fig. 6, *a*, *b*, *d*); ii) blade sharply bent, shaft and point subequal in length (fig. 6, *c*); iii) blade rounded (fig. 6, *e*, *f*).

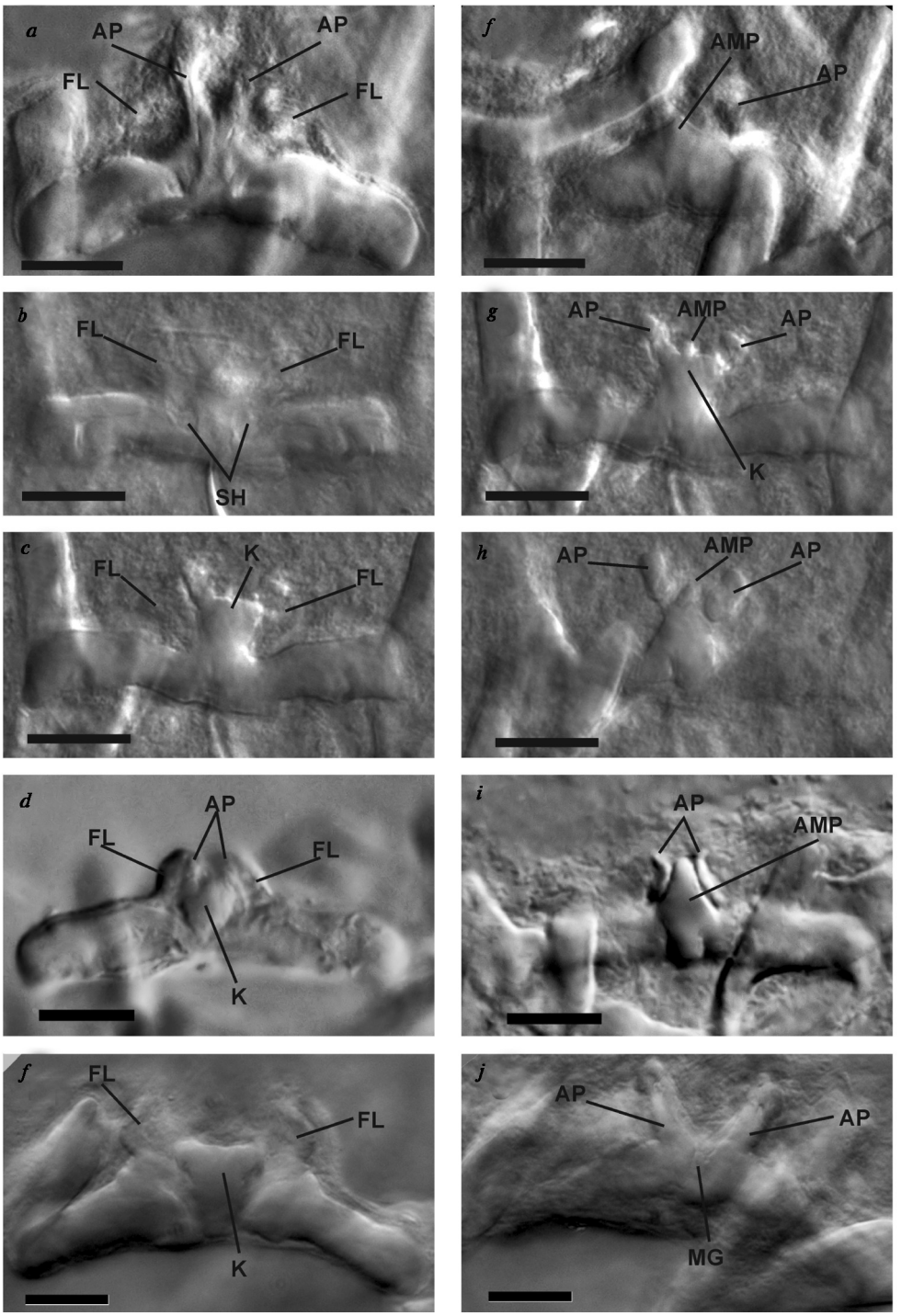

Fig. 5. Microphotographs of the ventral side (*a-e*) and the dorsal one (*f-j*) of the ventral bar with illustration of the main morphological types. Each pair of pictures is taken from the same specimen of *L. cephali* (*a* and *f*), *L. szidati* (*d* and *i*) and *L. chabaudi* (*e* and *j*); *b*, *c* and *g*, *h*, represent set of pictures from the most ventral (*b*) to the most dorsal view (*h*) of the ventral bar of *L domnichi.* Scale bars 10 μm.

Рис 5. Микрофотографии вентральной (*a-e*) и дорсальной стороны (*f-j*) вентральной пластинки с иллюстрацией основных морфологических типов. Каждая пара фотографий снята с одного и того же экземпляра *L. cephali* (*a* и *f*), *L. szidati* (*d* и *i*) и *L. chabaudi* (*e* и *j*); *b*, *c* и *g*, *h*, предоставляют серию фотографий от наиболее вентрального (*b*) до наиболее дорсального вида (*h*) вентральной пластинки. Масштабные линейки 10 мкм.

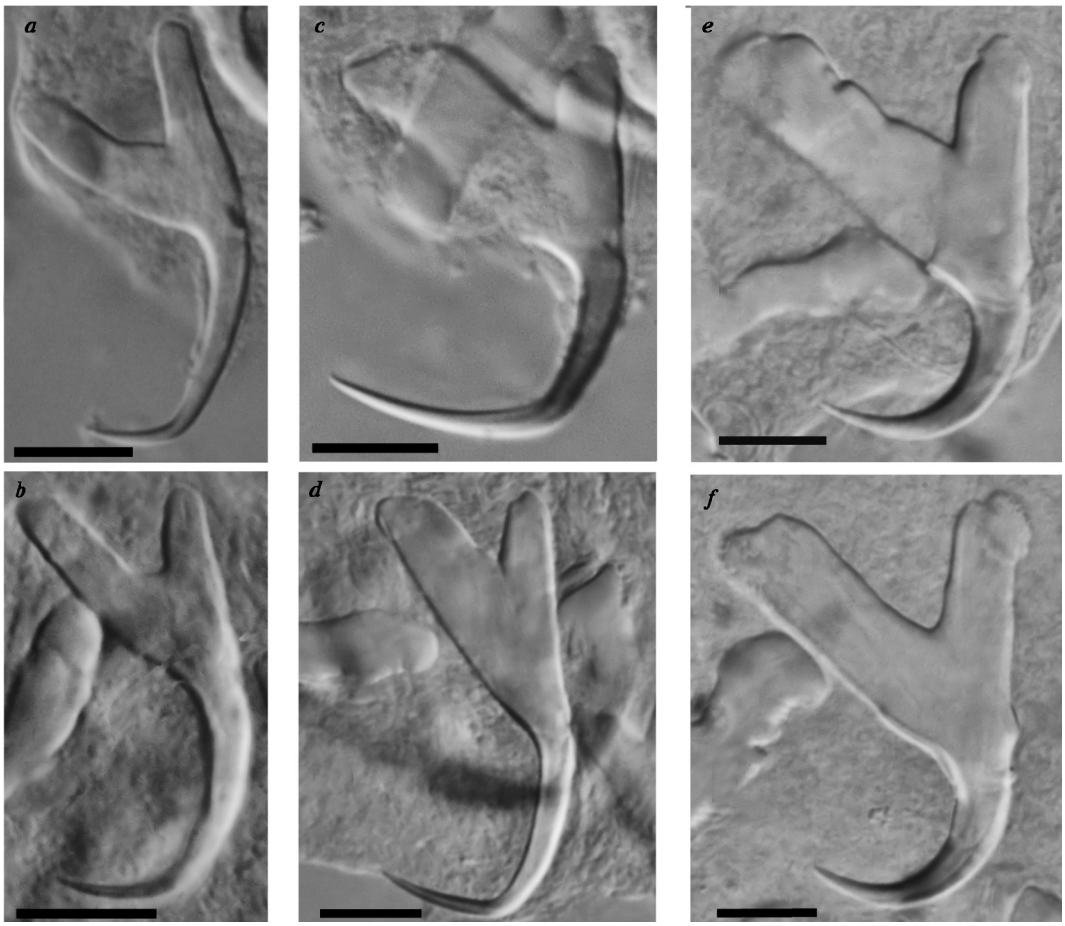

Fig. 6. Microphotographs of the shape diversity of ventral (*a*, *c*, *e*) and dorsal (*b*, *d*, *f*) anchors of *Ligophorus* species from patterns of *L. vanbenedenii* (*a*, *b*), *L. szidati* (*c*, *d*) and *L. kaohsianghsieni* (*e*, *f*); *a*, *b* and *d* — blade sharply bent, shaft about 1.5 times longer or more than the point; *c* — blade sharply bent, shaft and point subequal in length; *e* and *f* — blade rounded. Scale bars 10 μm.

Рис. 6. Микрофотографии разнообразия форм вентральных (*a, c, e*) и дорсальных (*b, d, f*) срединных крючьев видов *Ligophorus* на примере *L. vanbenedenii* (*a*, *b*), *L. szidati* (*c*, *d*) и *L. kaohsianghsieni* (*e*, *f*); *a, b* и *d* — лезвие резко изогнуто, рукоятка в 1,5 раза или более длиннее острия; с — лезвие резко изогнуто, рукоятка и острие почти одинаковой длины; е и *f* — лезвие плавно изогнуто, угол между рукояткой и лезвием слабо выражен. Масштабные линейки 10 мкм.

Valid species

Ligophorus vanbenedenii (Parona et Perugia, 1890) Euzet et Suriano, 1977
(fig. 3, *b*; 7, *a-g*; table 2)

Synonyms: *Tetraonchus vanbenedenii* Parona et Perugia, 1890; *Ancyrocephalus vanbenedenii* (Parona et Perugia, 1890) Johnston et Tiegs, 1922; *Haplocleidus vanbenedenii* (Parona et Perugia, 1890) Palombi, 1949; *Haliotrema vanbenedenii* (Parona et Perugia, 1890) Young, 1968.

Records: 1. Parona and Perugia (1890); 2. Euzet and Suriano (1977); 3. Gussev (1985); 4. Mikailov and Seidli (1989); 5. Radujković and Euzet (1989); 6. Dmitrieva and Gerasev (1996); 7. Miroshnichenko and Maltsev (1998); 8. Merella and Garippa (2001); 9. Gaevskaja et al. (2002); 10. Radujković (2002); 11. Dzikowski et al. (2003); 12. Mariniello et al. (2004); 13. Sarabeev and Balbuena (2004); 14. Dmitrieva et al. (2005); 15. Rubtsova et al. (2005); 16. Popjuk (2009); 17. Present study.

Type host: *Lz. aurata* (1–17).

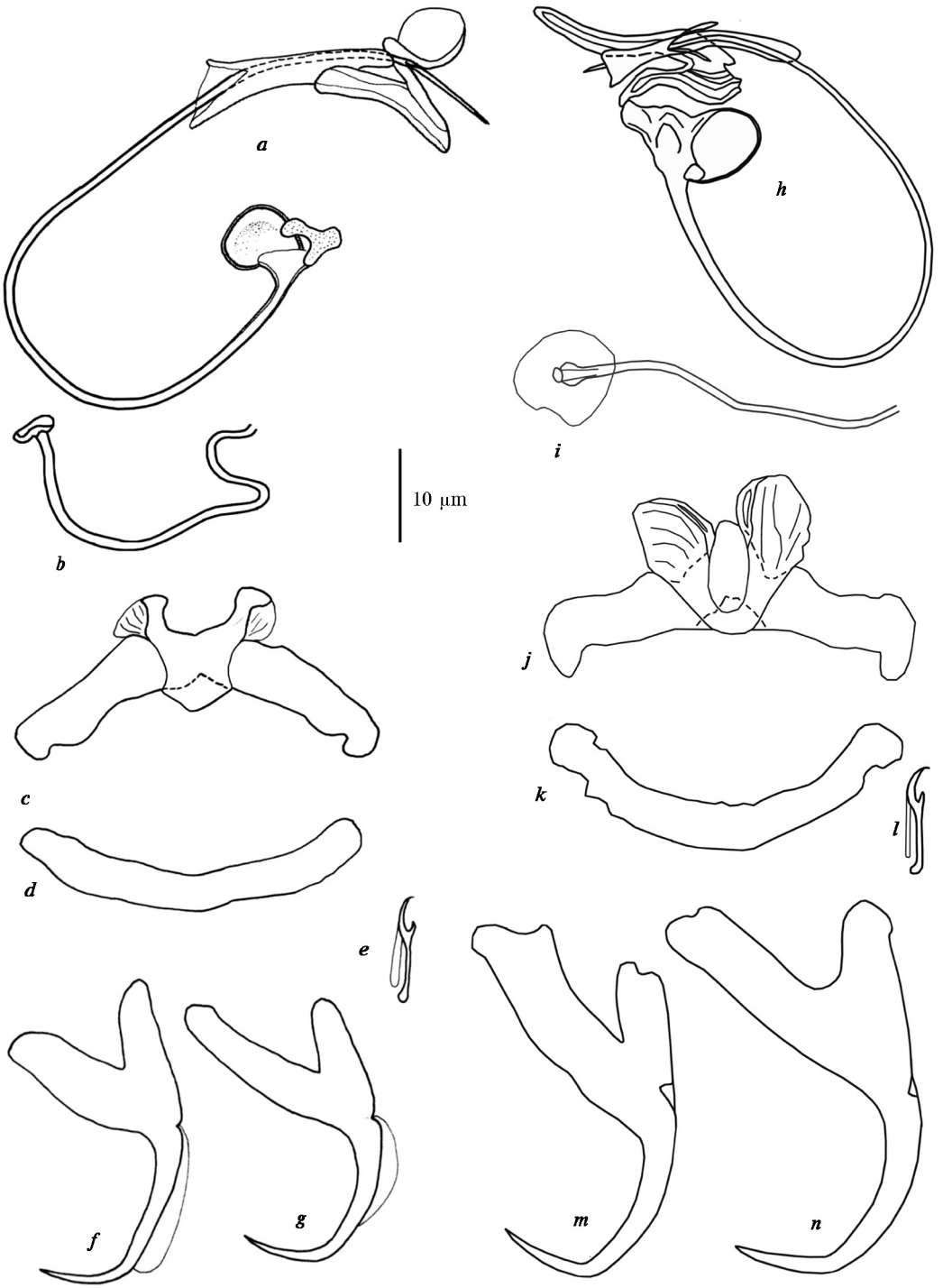

Fig. 7. Haptor and genital sclerotized structures of *Ligophorus vanbenedenii* (Parona et Perugia, 1890) (*a-g*) and *Ligophorus mugilinus* (Hargis, 1955) (*h-n*). *a*, *h* — male copulatory complex: copulatory organ and accessory piece; *b*, *i* — vagina; *c*, *j* — ventral bar; *d*, *k* — dorsal bar; *e*, *l* — hook; *f*, *m* — ventral anchor; *g*, *n* — dorsal anchor.

Рис. 7. Склеротизированные гаптоpальные и генитальные структуры *Ligophorus vanbenedenii* (Parona et Perugia, 1890) (*a-g*) и *Ligophorus mugilinus* (Hargis, 1955) (*h-n*). *a*, *h* — мужская копулятивная система: копулятивный орган и вспомогательный аппарат; *b*, *i* — вагина; *c*, *j* — вентральная пластинка; *d*, *k* — дорсальная пластинка; *e*, *l* — краевой крючок; *f*, *m* — вентральный срединный крючок; *g*, *n* — дорсальный срединный крючок.

Table 2. Metric characters of *L. vanbenedenii* and *L. mugilinus*
Таблица 2. Метрические характеристики *L. vanbenedenii* и *L. mugilinus*

Characters*	*Ligophorus vanbenedenii* ex *Liza aurata* from Mediterranean Sea: Júcar Estuary, Ebro Delta and Gulf of Valencia, Spain				*Ligophorus mugilinus* ex *Mugil cephalus* from Northwest Atlantic, Charleston coastal waters, USA			
	Mean	SD	Range	N	Mean	SD	Range	N
Body length	743	100.9	585–994	91	702	93.1	616–806	5
Body width	127	31.1	58–175	91	115	17.4	100–142	5
Pharynx length	32	5.6	22–40	15	40	10.0	30–50	3
Pharynx width	30	4.4	22–40	15	38	12.0	26–50	3
Testis length	49	10.8	30–63	16	43	4.0	38–45	3
Testis width	26	5.2	20–35	15	27	1.0	26–28	3
Ovary length	63	8.4	55–80	10	72	11.0	65–85	3
Ovary width	28	5.3	20–38	13	24	1.2	23–25	3
Haptor length	54	11.1	30–70	15	69	19.0	50–88	3
Haptor width	95	22.8	50–130	15	118	27.5	100–150	3
VAA	29	1.6	26–34	91	37	1.3	36–39	5
VAB	24	1.3	21–26	91	25	1.0	24–27	5
VAC	9	1	7–11	91	9	1.0	8–10	5
VAD	12	1.1	10–14	91	18	0.9	17–19	5
VAE	8	0.6	7–9	91	9	0.6	8–10	5
VAF	16	1.1	15–18	14	17	2.3	14–18	3
VAG	32	1.5	29–35	91	34	1.5	32–36	5
DAA	31	1.3	28–34	91	41	1.3	39–42	5
DAB	22	1.0	20–25	91	28	0.9	27–29	5
DAC	7	0.7	5–9	91	9	0.5	9–10	5
DAD	13	0.9	12–16	91	18	0.7	17–19	5
DAE	8	0.6	7–9	91	10	0.3	9–10	5
DAF	14	2.2	11–18	14	20	2.5	17–22	3
DAG	29	1.3	26–33	91	37	1.1	35–38	5
HTL	12	0.7	11–13	91	12	0.7	11–13	5
VBL	38	2.1	30–45	91	39	2.8	37–43	5
VBDP	11	1.8	8–15	15	8	2.4	5–11	5
DBL	35	1.9	32–41	91	35	2.9	32–39	5
APTL	27	1.7	22–32	91	30	2.6	27–33	5
APML	22	1.3	20–24	10	23	2.6	20–25	3
APMW	3	0.4	2–3	16	3	0.6	3–4	3
APSL	11	1.7	7–13	17	22	0.6	22–23	3
COL	89	9.9	72–112	8	79	4.7	73–85	5
COW	0.9	0.1	0.8–1	19	0.9	0.2	0.7–1	3
VL	47	6.9	35–60	14	44	5.9	35–51	5

* See Material and methods section for abbreviations of metric variables of sclerotized characters.

Other hosts: *M. cephalus* (6), *C. labrosus* (17) and *Lz. saliens* (17).

Type locality: Mediterranean Sea, Gulf of Genoa (1), Italy.

Additional localities: Mediterranean Sea: Gulf of Santa Pola (17), Júcar Estuary (17), Gulf of Valencia (13, 15, 17), Ebro Delta (17), Spain; Sète (2), France; Mistras Lagoon, Sardinia (8), Lesina Lagoon (12), Italy; Boka Kotorska Bay (5, 10), Montenegro; Mediterranean coast of northern Israel (11), Israel. Black Sea: Sozopol Bay (17), Bulgaria; Sevastopol coastal waters, Crimea (3, 6, 9, 14, 16), Kerch Channel (6, 7, 13, 17), Ukraine. Azov Sea: Sivash Lake (7, 17), Molochny Estuary (17), Berdyanskiy Bay (17), Ukraine. Caspian Sea, Kyzylagachskiy Bay (4), Azerbaijan.

Type specimens: not mentioned in original description.

Material deposited: two voucher specimens ex *Lz. aurata* from the Júcar Estuary at the BMNH 2008.8.19.3–4, three from the Ebro Delta at the IZAN M–19 and 59 from the Gulf of Valencia at the ZNUMZ 11900010–11900028.

Redescription

Based on 91 mature specimens from the Júcar Estuary, the Gulf of Valencia and the Ebro Delta, Spain. Body fusiform, maximum width at level of gonads. One terminal and two bilateral cephalic lobes well developed. Cephalic glands posterolateral to pharynx. Testis shape varies from ovate to elongate-ovate; copulatory organ C-shaped, long, thin, enters accessory piece proximally; base of copulatory organ with thick-walled heel; accessory piece claw-shaped, arrow-like; some individuals with slightly bent accessory piece. Secondary lobe joins main lobe twice by simple joint middistally and distally. Main lobe tubular, straight, elongated, clearly narrowing distally; secondary lobe beak-shaped with characteristic auricle, shorter than main lobe, extending beyond level of distal end of main lobe. Ovary U-shaped; oviduct and ootype short, Mehlis' glands conspicuous, comprising elongated glandular cells, occupying space between prostatic reservoir and seminal receptacle. Uterus elongated; genital pore ovate; vagina straight or winding; vaginal aperture midventral; distal end of vagina funnel-shaped, thin-walled. Peduncle broad, narrowing posteriorly, slightly longer than wide, or length and width subequal. Haptor subhexagonal, wider than long. Pairs of anchors subequal in shape and size, outer length of ventral anchor slightly longer than that of dorsal anchor. Both anchors with sharply bent blade, shaft 1.4–2.3 times longer than point, the latter not reaching level of tip of inner root; outer root and point subequal in length, inner root longer than point. Tip of outer root of ventral anchor extending beyond level of that of inner root; tip of outer root of dorsal anchor extending to or beyond level of tip of inner root. Transverse bars similar in length. Ventral bar represented by two morphological variations with first one prevailing: i) bar with knot on ventral shield, anterolateral flaps of the latter connected to pair of finger-like anterior protuberances, forming together V-shaped structure on dorsal side of bar; anteromedian process on dorsal side absent, instead median groove present, which is formed by rising protuberances; some specimens with massive shield, its posteromedian margin extending beyond posterior level of bar; ii) shield with knot and anterior finger-like protuberances; small anteromedian process present, lies more dorsally in relation to anterior protuberances. Transverse dorsal bar yoke-shaped with rounded extremities.

Remarks

L. vanbenedenii can be distinguished by its possession of a claw-shaped, arrow-like accessory piece of the copulatory complex with a beak-shaped secondary lobe, the latter is characterised by a distal auricle and double joining with the main lobe.

The original description of this species by Parona and Perugia (1890) was incomplete. Euzet and Suriano (1977) provided a redescription, which contained minor inaccuracies concerning the shapes of the ovary and ventral bar, and the accessory piece of the copulatory complex was not sufficiently described to meet current taxonomic needs. The present redescription provides finer details of the morphology of the accessory piece of the copulatory complex and the ventral bar and redefines the shape of the ovary. Measurements of this species presented by Euzet and Suriano (1977), Dmitrieva and Gerasev (1996) and Mariniello et al. (2004) fall within the range or overlap widely with those reported herein. The morphometric variability of *L. vanbenedenii* and its dependence on size, sex of host and infrapopulation size was studied by Rubtsova et al. (2005). It was established, that morphometric characteristics of *L. vanbenedenii* vary more widely than was known from previous works, and the size of the haptoral sclerotized structures was directly related to host size. However, there was no relation between metric characters and sex of fish from the size of sclerotized structures of genitalia and worm body size. The infrapopulation size of *L. vanbenedenii* had no detectable effect on their morphometry.

We have made no attempt to compile the numerous records of *A. vanbenedenii* from different mullet fish before the erection of *Ligophorus* because it has been shown that these designations apply to different species of *Ligophorus* (Euzet, Suriano, 1977). Therefore it is impossible to ascertain which of these early records actually corresponded to *L. vanbenedenii*. The records of Zhang and Ji (1981), Gussev (1985), Wu et al. (1991), Zhang (2001) and Wu et al. (2006, 2007) from atypical hosts, *M. cephalus*, *Lz. ramada*, *Lz. haematocheilus* and *Lz. affinis*, are probably erroneous. The specimens of *Ligophorus* from *M. cephalus* off Chongwu coastal waters, the East China Sea, presented by Zhang and Ji (1981) and forms redrawn as *L. vanbenedenii* from *Lz. ramada* in the Black Sea and from *Lz. haematocheilus* in the Liao-Ho River by Gussev (1985) differ from *L. vanbenedenii* by the distal position of copulatory organ entrance of the accessory piece, which is claw-shaped, pincer-like with a bowed secondary lobe (rather than the copulatory organ which enters the accessory piece proximally, the latter is claw-shaped, arrow-like with a beak-shaped secondary lobe in *L. vanbenedenii*) and unequal sizes of the ventral anchor roots (compare figures 1–4 of Zhang and Ji (1981), figures 328 A and B of Gussev (1985), figures 3–5 of Euzet and Suriano (1977) and figure 7, *a*, *c*, *f* and *g* of the present study). The form presented by Gussev (1985) from *Lz. haematocheilus* considered herein to be a new species and is described below. Further identification of the specimens of *Ligophorus* described by Zhang and Ji (1981) and Gussev (1985) from *M. cephalus* and *Lz. ramada*, respectively, is impossible. The illustrations of *A. vanbenedenii* by Zhang and Ji (1981) seem to represent several forms for which composite measurements are presented (see table of Zhang and Ji (1981)). Gussev's (1985) record of this species includes only figures of sclerotized parts, no measurements or description were supplied. Wu et al. (1991) provided drawings and measurements of *L. vanbenedenii* from *M. cephalus* and *Lz. haematocheilus* off Zhejiang, the East China Sea. All metric characters except DAD fall within the range or overlap widely with those obtained by Euzet and Suriano (1977) and in the present study. However figure 162 of Wu et al. (1991) combines original drawings of the haptoral sclerotized complex with redrawn illustrations of the genital structures depicted in Euzet and Suriano (1977). The lack of original figures for these structures precludes confirmation of the identity of these specimens, because their morphology is unique for each species of *Ligophorus*. Zhang's (2001) records of *L. vanbenedenii* from *M. cephalus* and *Lz. affinis* off Fujian and Guangdong Provinces, the East and South China Seas were illustrated by figures of *A. vanbenedenii* depicted in Zhang and Ji (1981). These specimens differ from the descriptions of *L. vanbenedenii*, supplied by Euzet and Suriano (1977) and in the present study, by having different measurement ranges for most sclerotized characters. VAA, VAB, DAA, DAB and VBL were larger and VAE, DAD and DAE were smal-ler than those of *L. vanbenedenii* (Euzet, Suriano, 1977; table 2 of the present study). Finally, phylogenetic analysis based on 28S rRNA gene sequence (Blasco-Costa et al., 2012) indicated that specimen identified as *L. vanbenedenii* by Wu et al. (2006, 2007) from atypical host, *M. cephalus*, in the Pacific does not represent *L. vanbenedenii* known from the Mediterranean *Lz. aurata* and its high genetic divergence from other *Ligophorus* spp. suggests that it may represent a different genus. Thus, all the forms mentioned above should be considered as *species inquirendae*. Although sometimes spelled *L. vanbenedeni* (e. g. Gaevskaya et al., 2002; Dmitrieva et al., 2007), by virtue of article 33.4 of the ICZN (Ride et al., 1999), the original ending – *ii* (Parona, Perugia, 1890) should be kept and thus *L. vanbenedenii* is the correct spelling.

Since the golden and thicklip grey mullets were introduced into the Caspian Sea from the Black Sea between 1931–1934 (Kuliev, Ragimov, 2006), several alien species of *Ligophorus*, including *L. vanbenedenii*, have been recorded on their typical host (Mikailov, Seidli, 1989).

Ligophorus mugilinus (Hargis, 1955) Euzet et Suriano, 1977
(fig. 3, *k*; 7, *h-n*; table 2)

Synonyms: *Pseudohaliotrema mugilinus* Hargis, 1955; *Haliotrema mugilinus* (Hargis, 1955) Yamaguti, 1963.

Records: 1. Hargis (1955); 2. Skinner (1975); 3. Sarabeev et al. (2005); 4. Dmitrieva et al. (2009 a).

Type host: *M. cephalus* (1–4).

Type locality: NW Atlantic, Gulf of Mexico, Alligator Harbor, Florida (1, 3, 4), USA.

Additional localities: NW Atlantic: Biscayne Bay, Florida (2), Charleston, South Carolina (3), USA.

Type specimens: holotype and two paratypes (USNPC 049342, 049342 and 049343, respectively) (1).

Material deposited: two specimens off Charleston, South Carolina, USA at the BMNH 2005.1.7.7 (3) and three at the ZNUMZ 11900029–11900030 (the present study).

Redescription

Based on five specimens from Charleston, South Carolina, USA. Body fusiform with maximum width at level of gonads. One terminal and two bilateral cephalic lobes well developed. Cephalic glands posterolateral to pharynx. Testis shape varies from ovate to elongate-ovate; copulatory organ C-shaped, long, thin, enters accessory piece proximally; base of copulatory organ with thick-walled heel; accessory piece cross-shaped. Main lobe of accessory piece slightly bowed, elongated, cylindrical, some specimens with dilated distal end. Secondary lobe of accessory piece massive, V-shaped with unequal branches, subequal in length with main lobe, extending beyond distal end of main lobe; upper branch of secondary lobe straight or backwardly curved, longer than lower one, articulated with main one lengthways distal part of the latter. Ovary U-shaped; oviduct, ootype and uterus not observed; Mehlis' glands occupying intervitellarial body space between prostatic reservoir and seminal receptacle. Vagina winding or coiled; vaginal aperture dextroventral; distal end of vagina scyphoid and narrow. Peduncle broad, short, subequal in width and length, tapering posteriorly. Haptor subhexagonal, wider than long. Pairs of anchors subequal in shape, inner length of ventral anchor slightly shorter than that of dorsal anchor. Both anchors with sharply bent blade, shaft 1.5 to 2.3 times longer than point, the latter not reaching level of tip of inner root, outer root shorter and more slender than inner root; outer root and point subequal in length. Tip of outer root of ventral anchor may extend to level of that of inner root; inner root longer than point. Tip of outer root of dorsal anchor extending to or past level of that of inner root; inner root longer than point. Bars equal in length. Ventral bar with ∩-shaped knot of ventral shield attached to Λ-shaped dorsal anteromedian process, lateral flaps of the latter contiguous to anterior protuberances, situated ventrally in relation to anteromedian process. Transverse dorsal bar yoke-shaped with enlarged and rounded extremities, posteromedian process poorly developed or absent.

Remarks

L. mugilinus is very similar to *L. mediterraneus* and *L. saladensis* in possessing a C-shaped, long and thin copulatory organ, which enters a cross-shaped accessory piece proximally; a massive secondary lobe of the accessory piece, subequal in length with the main lobe, extending beyond the distal end of the main one; a longer upper branch of the secondary lobe than the lower one; the secondary lobe articulates with the main one along the distal part of the latter; a scyphoid distal end of the vagina; and similar anchor shape. However, the secondary lobe of the accessory piece of the male copulatory organ of *L. mugilinus* is V-shaped with a straight or backwardly curved upper branch, whereas in *L. mediterraneus* it is V-shaped with a hook-shaped, inwardly curved upper branch and

in *L. saladensis* trident-shaped with a straight upper branch. In addition, the ventral bar of *L. mugilinus* has a ∩-shaped median knot on the ventral shield attached to a Λ-shaped anteromedian process, while in *L. mediterraneus* the median knot is V-shaped and the dorsal anteromedian process is absent, the anterior protuberances are finger-shaped, forming together a V-shaped structure on the dorsal side of the bar; and in *L. saladensis* the knot is absent. Further, *L. mugilinus* differs from both species in the relative position of the tips of the outer and inner root of the ventral anchor (the tip of the outer root does not reach that of the inner root vs. the tip of the outer root protruding further out than that of the inner root in *L. mediterraneus* and *L. saladensis*). The ratio of VAD to VAC in *L. mugilinus* (1.7–2.1) falls outside the variation range reported in *L. mediterraneus* (1.2–1.6) (Sarabeev et al., 2006) and *L. saladensis* (1.3).

The original description of *L. mugilinus* by Hargis (1955) is generally correct with two inaccuracies about the shape of the ovary and the number of head organs. The redescription by Sarabeev et al. (2005) provided new information on measurements of sclerotized structures and the morphology of the accessory piece of the copulatory complex. However, detailed information on the morphology of the ventral bar was not supplied, and the general shape of the accessory piece and its lobes was misinterpreted. The shape of the accessory piece was described as claw-shaped with a small secondary lobe.

Dmitrieva et al. (2009 a), based on a single specimen collected from formalin-fixed gills of *M. cephalus*, redrew this species and provided some metric measurements, which were considered to be useful for discrimination of *L. mugilinus* and *L. mediterraneus*. However, the measurements of the five specimens of *L. mugilinus* used in the present study indicate wide overlap in the proposed metric characters between *L. mugilinus* and *L. mediterraneus* (VBS 8.4 ± 1.1 [7–10] (5) vs. 8.2 ± 1.1 [7–11] (17); VOP 19 ± 2.2 [17–22] (4) vs. 21.6 ± 1.8 [19–27] (17); VSR 17 ± 2 [14–18] (4) vs. 18 ± 1.9 [16–22] (17); DIP 28.2 ± 1 [27–30] (6) vs. 25.5 ± 3.1 [22–35] (17), respectively)[1]. So, the proposed four new measurements (BVS, VOP, VSR and DIP) cannot be used for distinguishing *L. mugilinus* from *L. mediterraneus*. The present redescription redefines the shape of the ovary and the accessory piece of the copulatory complex and its lobes, as well as supplements previous studies about the relative position of the roots and point of anchors.

Numerous records of this species from Mediterranean localities (e. g. Euzet, Suriano, 1977; Mariniello et al., 2004; Sarabeev, Balbuena, 2004) actually correspond to *L. mediterraneus* (Sarabeev et al., 2005). The two reports of *L. mugilinus* from *Mugil curema* in the Caribbean Sea (Fuentes, Nasir, 1990; García, Williams, 1985) are uncertain (Sarabeev et al., 2005). Wu et al. (1991) provided a brief description of specimens identified as *L. mugilinus* from *M. cephalus* and *Lz. haematocheilus* off Zhejiang, the East China Sea (China). However, there are substantial morphological differences between these worms and the material of *L. mugilinus* from Charleston (USA). Namely, the accessory piece of the copulatory complex is claw-shaped (figure 163 (2) of Wu et al., 1991), rather than cross-shaped as in *L. mugilinus*; the anteromedian process on the ventral bar is absent (fig. 163 (1) of Wu et al., 1991), whereas it is present in *L. mugilinus*; and the shape of the anchors does not correspond to that of *L. mugilinus* (compare illustration of Wu et al. (1991) and fig. 7, *h*, *j*, *m* and *n* of the present study). The specific identity of these specimens cannot be resolved at present due to their insufficient description.

Ligophorus kaohsianghsieni (Gussev, 1962) Gussev, 1985
(fig. 2, *b*, *c*, *g*; 3, *e*, *j*; 8, *a-g*; table 3)

Synonym: *Ancyrocephalus kaohsianghsieni* Gussev, 1962

Records: 1. Gussev (1962); 2. Ji et al. (1982); 3. Gussev (1985); 4. Wu et al. (1991); 5. Ermolenko (1992); 6. Dmitrieva (1996); 7. Maltsev and Zhdamirov (1996); 8. Maltsev

[1] For the definition of measurements and abbreviations (VOP, VSR and DIP) see fig. 2, table 1 of Dmitrieva et al. (2009).

and Miroshnichenko (1998); 9. Miroshnichenko and Maltsev (1998); 10. Domnich and Sarabeev (1999); 11. Domnich and Sarabeev (2000); 12. Sarabeev (2000); 13. Sarabeev and Domnich (2000); 14. Gaevskaja et al. (2002); 15. Sarabeev and Balbuena (2004); 16. Dmitrieva et al. (2005); 17. Present study.

Type host: *Lz. haematocheilus* (1–8, 10–15, 17).

Other hosts: *Lz. aurata*, (6, 9, 16); *M. cephalus* (4).

Type locality: Yellow Sea, Liao-Ho River (1, 3, 6), China.

Additional localities: Sea of Japan: Tumen-Ula River (3, 6), Posiet Bay (17), Razdol'naya Delta (5, 17), Russia. East China Sea: Zhejiang (4), Northeast of China (2), China. Black Sea: Crimean coastal waters, Crimea (6, 14, 16), Kerch Channel (7–9, 15, 17), Ukraine. Azov Sea: Sivash Lake (7–12, 17), Utlyutsky Estuary (17), Molochny Estuary (7–13, 15, 17), Ukraine.

Type specimens: deposited at the ZIN (3, 6), accession number not available.

Material deposited: voucher material ex *Lz. haematocheilus* from the Kerch Channel at the BMNH 2008.8.19.5 (1 specimen), IZAN M–10 (3 specimens) and ZNUMZ 11900031–11900039 (13 specimens).

Redescription

Based on 18 mature worms from the Kerch Channel, Ukraine. Body fusiform with maximum width at level of testis. One terminal and two bilateral cephalic lobes well developed. Cephalic glands posterolateral to pharynx. Testis shape varies from ovate to elongate-ovate; copulatory organ winding, long, thin, enters accessory piece proximally; base of copulatory organ with thick-walled heel; accessory piece cross-shaped, secondary lobe articulates with main lobe lengthwise along full length of the latter. Main lobe of accessory piece proximally extended and tapered distally, cylindrical, straight; secondary lobe Y-shaped with membranous plates of irregular shape at distal ends, longer than main lobe, extending beyond both proximal and distal ends of main lobe. Ovary U-shaped; oviduct, ootype and uterus not observed, Mehlis' glands conspicuous, elongated glandular cells, extending between prostatic reservoir and seminal receptacle. Vagina coiled; vaginal aperture midventral; distal end of vagina scyphoid and broad 8 ± 0.8 (7–9) (7) in diameter. Peduncle broad, tapered posteriorly, longer than wide or subequal in width and length. Haptor subtetragonal or subhexagonal, wider than long. Pairs of anchors subequal in shape and size; both anchors with round blade, shaft about 1 to 1.9 times longer than point, the latter not reaching level of tip of inner root, outer root shorter than inner root, outer root and point subequal in length, inner root longer than point. Tip of outer root of ventral anchor may extend to level of that of inner root, tip of outer root of dorsal anchor extending to or beyond level of that of inner root. Ventral bar shorter than dorsal one. Ventral bar with knot on ventral shield, anterolateral flaps of the latter connect with pair of finger-like anterior protuberances, forming together V-shaped structure on dorsal side of bar; anteromedian process on dorsal side absent, instead median groove present, which is formed by rising protuberances; some specimens with massive shield, their posteromedian margin extending beyond posterior level of bar. Transverse dorsal bar yoke-shaped with posteromedian knob-like process, anteromedian shield present or absent.

Remarks

L. kaohsianghsieni can be easily distinguished from all other species of *Ligophorus* by the unique morphology of: i) the accessory piece of the copulatory complex with characteristic membranous plates at distal ends of the secondary lobe; ii) the scyphoid and broad distal end of the vagina; iii) the round blade of both anchors. In the morphology of the copulatory complex, *L. kaohsianghsieni* closely resembles *L. macrocolpos*. The two species share the following features: a winding and long copulatory organ, a cross-

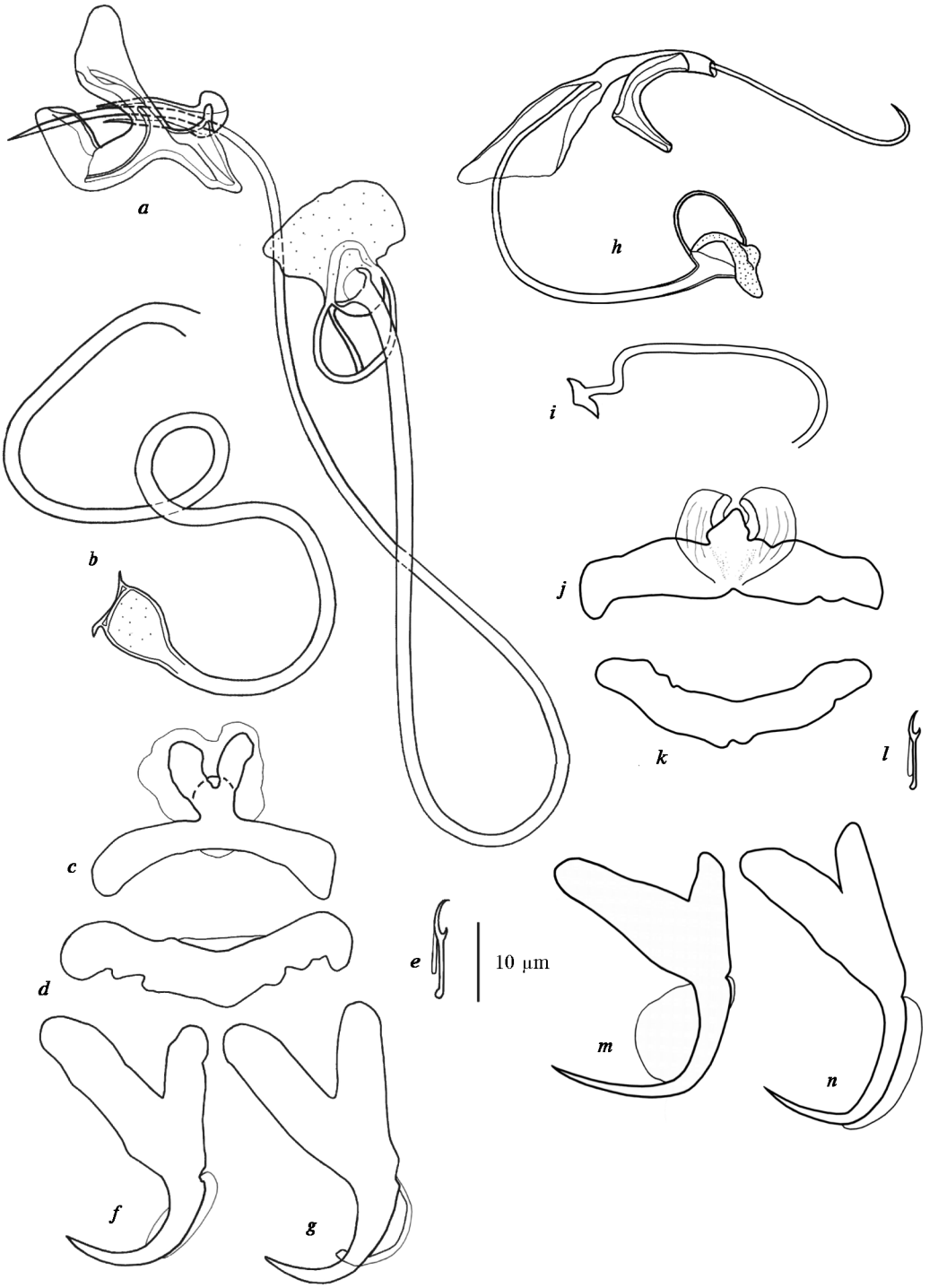

Fig. 8. Haptor and genital sclerotized structures of *Ligophorus kaohsianghsieni* (Gussev, 1962) (*a-g*) and *Ligophorus szidati* Euzet et Suriano, 1977 (*h-n*): *a*, *h* — male copulatory complex: copulatory organ and accessory piece; *b*, *i* — vagina; *c*, *j* — ventral bar; *d*, *k* — dorsal bar; *e*, *l* — hook; *f*, *m* — ventral anchor; *g*, *n* — dorsal anchor.

Рис. 8. Склеротизированные гаптоpальные и генитальные структуры *Ligophorus kaohsianghsieni* (Gussev, 1962) (*a-g*) и *Ligophorus szidati* Euzet et Suriano, 1977 (*h-n*): *a*, *h* — мужская копулятивная система: копулятивный орган и вспомогательный аппарат; *b*, *i* — вагина; *c*, *j* — вентральная пластинка; *d*, *k* — дорсальная пластинка; *e*, *l* — краевой крючок; *f*, *m* — вентральный срединный крючок; *g*, *n* — дорсальный срединный крючок.

Table 3. Metric characters of *L. kaohsianghsieni* and *L. szidati*
Таблица 3. Метрические характеристики *L. kaohsianghsieni* и *L. szidati*

Characters*	*Ligophorus kaohsianghsieni* ex *Liza haematocheilus* from Black Sea, Kerch Channel; Azov Sea, Sivash Lake, Ukraine				*Ligophorus szidati* ex *Liza aurata* from Mediterranean Sea: Júcar Estuary, Gulf of Santa Pola, Spain			
	Mean	SD	Range	N	Mean	SD	Range	N
Body length	1,249	152		18	864	126	702–1,053	19
Body width	256	45.9	200–350	16	153	26.5	105–199	19
Pharynx length	74	14.3	55–100	18	36	6.1	30–50	19
Pharynx width	68	18.4	35–100	18	34	5.6	22–40	19
Testis length	80	10.9	63–95	12	53	11.1	30–70	18
Testis width	45	10.2	30–63	15	28	5.6	20–43	18
Ovary length	173	24.4	137–213	11	67	12.2	55–90	14
Ovary width	64	9.3	50–75	16	28	7	13–35	16
Haptor length	91	13.2	70–113	18	57	17.1	38–113	19
Haptor width	153	53	95–250	18	90	22.3	48–125	19
VAA	38	2	34–40	12	32	1.6	30–35	14
VAB	24	1.1	22–25	12	23	1.0	22–25	14
VAC	9	0.9	7–10	13	6	0.7	5–7	15
VAD	20	1.4	17–22	11	16	1.5	14–18	15
VAE	10	1.3	8–12	14	18	1.1	16–20	15
VAF	14	1.8	12–17	11	15	1.2	13–16	10
VAG	33	1.4	29–34	12	29	1.3	28–32	14
DAA	39	2.3	35–42	12	39	1.6	37–41	15
DAB	25	2.2	22–29	12	30	1.9	28–35	15
DAC	11	1.5	8–13	12	7	1.0	5–9	15
DAD	18	2.3	15–22	12	13	1.1	12–15	15
DAE	11	1.2	10–13	12	12	0.9	11–13	15
DAF	16	2	13–19	12	18	1.3	17–22	11
DAG	36	3.1	30–41	12	37	2	34–43	15
HTL	13	0.9	11–14	12	13	0.6	12–13	15
VBL	37	1.8	34–40	12	40	1.2	37–41	15
VBDP	9	1.4	8–12	13	2	0.7	2–4	10
DBL	42	2.4	38–45	12	36	1.9	34–41	15
APTL	37	4.6	33–50	15	28	2.1	25–33	14
APML	20	2.7	15–23	12	“	“	“	“
APMW	5	0.8	4–6	14	2	0.4	2–3	11
APSL	36	4.2	30–42	15	9	1.2	8–12	12
COL	209	24.6	180–250	16	81	12.1	66–105	15
COW	1.2	0.2	1–1.5	15	0.8	0.1	0.5–1	11
VL	122	18.7	95–150	15	38	6.6	33–50	10

* See Material and methods section for abbreviations of metric variables of sclerotized characters.

shaped accessory piece, the secondary lobe of the accessory piece articulates with the main lobe lengthwise along full length of the latter, a cylindrical, proximally extended and distally tapered main lobe; a Y-shaped secondary lobe longer than the main lobe and extending beyond both proximal and distal ends of the main lobe; the ventral bar with the knot on the ventral shield; anterolateral flaps of the shield connect with anterodorsal finger-like protuberances, the latter forming together a V-shaped structure on the dorsal side of the bar; the dorsal anteromedian process absent. In addition to the unique characteristics described above, *L. kaohsianghsieni* differs from *L. macrocolpos* by having smaller ratio of the shaft to the point of both pair of anchors, smaller sizes of VAB, VAF, VAG, VBL and larger measurements of the body, pharynx, ovary, VAD, DAE, APTL and APSL.

Gussev's (1962) original description of *L. kaohsianghsieni* from the Pacific included only drawings of the sclerotized structures. A later redescription (Gussev, 1985)

added some metric data. Dmitrieva (1996) provided drawings and measurements of sclerotized characters of *L. kaohsianghsieni* from the Black Sea and rivers of the Russian Pacific region from *Lz. haematocheilus* and *Lz. aurata* based on the type-specimens from Gussev's (1962) collection at the ZIN. The present study supplements these previous descriptions by clarifying the morphology of the accessory piece of the copulatory complex and supplying new data on the shape and measurements of the ovary, testis, peduncle and haptor of this species. The variable ranges of most of the metric characters of our specimens of *L. kaohsianghsieni* either fall within the range or overlap widely with those of Gussev (1985) and Dmitrieva (1996); only four characters were smaller, namely the lengths of the dorsal anchor point, the transverse ventral bar, the copulatory organ and the accessory piece of the male copulatory complex. Apart from such metric differences, no other morphological differences between our specimens and those described previously were observed.

The type-host of this species, *Lz. haematocheilus*, was introduced in the late 1970s into the Black Sea and the Sea of Azov. Given the previous records of *L. kaohsianghsieni* in the Western Pacific (Gussev, 1962, 1985), this species was most probably brought to the Black Sea together with its host (Dmitrieva, 1996).

Ligophorus szidati Euzet et Suriano, 1977
(fig. 5, *d*, *i*; 8, *h-n*; table 3)

Records*:* 1. Euzet and Suriano (1977); 2. Gussev (1985); 3. Radujković and Petrović (1986); 4. Mikailov and Seidli (1989); 5. Radujković and Euzet (1989); 6. Dmitrieva and Gerasev (1996); 7. Miroshnichenko and Maltsev (1998); 8. Merella and Garippa (2001); 9. Gaevskaja et al. (2002); 10. Radujković (2002); 11. Dzikowski et al. (2003); 12. Mariniello et al. (2004); 13. Sarabeev and Balbuena (2004); 14. Popjuk (2009); 15. Present study.

Type host: *Lz. aurata* (1–15).

Other hosts: *Lz. saliens* (15) and *Lz. haematocheilus* (15).

Type locality: Mediterranean Sea, Sète (1), France.

Additional localities: Mediterranean Sea: Gulf of Santa Pola (15), Júcar Estuary (15), Gulf of Valencia (15), Ebro Delta (15), Spain; Mistras Lagoon, Sardinia (8), Lesina Lagoon (12), Italy; Boka Kotorska Bay (3, 5, 10), Montenegro; Mediterranean coast of northern Israel (11), Israel. Black Sea: Sozopol Bay (15), Bulgaria; Sevastopol coastal waters, Crimea (2, 6, 9, 14), Kerch Channel (6, 7, 13, 15), Ukraine. Azov Sea: Sivash Lake (7, 15), Molochny Estuary (15), Berdyanskiy Bay (15), Ukraine. Caspian Sea, Kyzylagachskiy Bay (4), Azerbajdzhan.

Type specimens: not designated in original description.

Material deposited: voucher material ex *Lz. aurata* from the Júcar Estuary at the BMNH 2008.8.19.6–10 (5 specimens) and ZNUMZ 11900040, 11900042–11900044, 11900046 (9 specimens) and from the Gulf of Santa Pola at the IZAN M–18 (2 specimens) and ZNUMZ 11900041, 11900045 (3 specimens).

Redescription

Based on the 19 mature worms from the Júcar Estuary and Gulf of Santa Pola, Spain. Body fusiform, with maximum width at level of gonads. One terminal and two bilateral cephalic lobes well developed. Cephalic glands posterolateral to pharynx. Testis shape varies from ovate to elongate-ovate; copulatory organ C-shaped, long, thin, enters accessory piece proximally; base of copulatory organ with thick-walled heel; accessory piece claw-shaped, pincerlike, secondary lobe joins main lobe middistally by simple joint. Main lobe of accessory piece proximally extended and tapered distally, cylindrical, bowed; secondary lobe C-shaped, shorter than main lobe, not reaching level of distal end of main lobe. Ovary

U-shaped; oviduct and ootype short, Mehlis' glands conspicuous, comprising large glandular cells, extending between prostatic reservoir and seminal receptacle, uterus elongated, runs dorsomedially to common ovate genital pore. Vagina straight or winding; vaginal aperture midventral, distal end of vagina funnel-shaped, thin-walled. Peduncle broad, elongated, longer than wide, tapering posteriorly. Haptor subhexagonal, wider than long. Pairs of anchors dissimilar in shape and size; inner, main outer and shaft length of ventral anchor shorter than those of dorsal anchor; point length of ventral anchor longer than that of dorsal one. Ventral anchor with sharply bent blade at midpoint, elongated point subequal in length with shaft, point extending to level of tip of inner root, the latter at least two times longer than outer root, tip of outer root extending to or beyond level of that of inner root, outer root shorter than point, inner root and point subequal in length. Dorsal anchor with sharply bent blade, shaft 1.3–1.9 times longer than point, the latter not reaching level of tip of inner root, outer root shorter than inner root, tip of outer root extending to or beyond level of that of inner root, outer root shorter than point, inner root and point subequal in length. Bars equal in length. Ventral bar with knot on ventral shield, lateral flaps of shield contiguous to anterior protuberances, the latter extending to dorsal side of bar, where they reduced to pair of small plates; anteromedian process on dorsal side between pair of small plates; ∩-shaped knot of ventral shield attached to Λ-shaped dorsal anteromedian process; pair of small plates occupies lateral position. Transverse dorsal bar yoke-shaped, with rounded extremities, posteromedian process present or absent.

Remarks

L. szidati closely resembles *L. angustus* and *L. confusus* in the morphology of the anchor/bar and the male copulatory complex. Namely, these three species share the following characteristics: a C-shaped long and thin copulatory organ, which enters the accessory piece proximally; the base of the copulatory organ with a thick-walled heel; a claw-shaped, pincerlike accessory piece with a proximally extended main lobe; dissimilarity in shape and size between the dorsal and ventral pair of anchors; a sharply bent blade of the ventral anchor; the shaft and the point of the ventral anchor about equal in length; the ventral bar with median knot on the ventral shield and anteromedian process on the dorsal side, anterior protuberances reduced dorsally to two small plates; the latter occupy a lateral position in relation to the anteromedian process. *L. szidati* differs from both species by having a distally tapering main lobe (vs. expanded in both compared species), a C-shaped secondary lobe of the accessory piece of copulatory complex (vs. spatulate or J-shaped in *L. angustus* and *L. confusus*, respectively) and the point of the ventral anchor extending to the level of the tip of the inner root (vs. the point not reaching the level of the tip of the inner root). In addition, in *L. szidati* the distal portion of the main lobe width of the accessory piece of the male copulatory complex is smaller than in the other two species; this species also differs from *L. angustus* in the larger point of the ventral anchor and the main part length of the dorsal anchor; and from *L. confusus* in the smaller length of the secondary lobe of the accessory piece.

The sclerotized structures of this species were adequately described by Euzet and Suriano (1977) but their description lacked data on the shape and measurements of the ovary, testis, peduncle, and haptor. The present, amended redescription supplies these data and further clarifies the morphology of the accessory piece and the ventral bar. The metric measurements of our specimens from the Azov Sea were quite close to those provided by Euzet and Suriano (1977) and Mariniello et al. (2004) from the Mediterranean Sea and, thus, appear to fall within the range of intraspecific variation.

This species, as well as *L. vanbenedenii*, was introduced from the Black Sea to the Caspian Sea together with its type-host (Mikailov, Seidli, 1989).

Ligophorus chabaudi Euzet et Suriano, 1977
(fig. 5, *e*, *j*; 9, *a-g*; table 4)

Records: 1. Euzet and Suriano (1977); 2. Radujković and Euzet (1989); 3. Caillot et al. (1999); 4. Merella and Garippa (2001); 5. Radujković (2002); 6. Mariniello et al. (2004); 7. Rubtsova et al. (2006 a); 8. Dmitrieva et al. (2009 b); 9. Dmitrieva et al. 2013; 10. Present study.

Type host: *M. cephalus* (1–10).

Type locality: Mediterranean Sea, Sète (1), France.

Additional localities: Mediterranean Sea: Júcar Estuary (7, 10), Ebro Delta (7, 10), Gulf of Valencia (10), Spain; Rhone River Delta (7), Biguglia Pond, Corsica (3), France; Mistras Lagoon, Sardinia (4, 8), Oristano Lagoon, Sardinia (6), Tarquinia Lagoon (6), Italy; Boka Kotorska Bay (2, 5), Montenegro. Sea of Japan: Posiet Bay (8, 9), Kiyevka Bay (10), Razdol'naya Delta (10), Russia. Yellow Sea, Off Zhifu, Yantai (9), China. Sunda Sea (9).

Type specimens: four neotypes from the Thau Lagoon, Sète at the NMNH (293 HG Tg 210).

Material deposited: voucher specimens from the Júcar Estuary at the NMNH 294 HG Tg 211, from the Ebro Delta at the BMNH 2005.11.4.8–10 (6 specimens) (Rubtsova et al., 2007), from the Kiyevka Bay at the BMNH 2008.8.19.11–15 (5 specimens), IZAN M–4 (3 specimens) and from Razdol'naya Delta at the ZNUMZ 11900047 (1 specimen) (10).

Redescription

Based on the eight voucher specimens from the Kiyevka Bay, Russia and eight specimens from the Razdol'naya Delta, Russia. Body fusiform with maximum width at level of gonads. One terminal and two bilateral cephalic lobes well developed. Cephalic glands posterolateral to pharynx. Testis shape varies from ovate to elongate-ovate; copulatory organ C-shaped, long, thin, enters accessory piece through membranous opening on top of distal part of main lobe; base of copulatory organ with thick-walled heel; accessory piece claw-shaped, pincerlike, secondary lobe joins main lobe middistally by simple joint. Main lobe of accessory piece cylindrical, straight, elongated with membranous bulb-shaped expansion in distal part, sharply tapering to distal tip; secondary lobe short, straight or slightly bowed, shorter than main lobe, not reaching level of distal tip of main lobe. Ovary U-shaped; oviduct and ootype not observed, Mehlis' glands occupying intervitellarial body space between prostatic reservoir and seminal receptacle. Uterus elongated, runs to ovate genital pore. Vagina winding; vaginal aperture midventral; distal end of vagina funnel-shaped, thin-walled. Peduncle broad, short, subequal in width and length, tapering posteriorly. Haptor subhexagonal, wider than long. Pairs of anchors subequal in shape and size; both anchors with sharply bent blade, shaft 1.5–2.6 times longer than point, the latter not reaching level of tip of inner root, outer root smaller than inner root; tip of outer root extending to or beyond level of that of inner root. Point of ventral anchor shorter than roots, point and outer root of dorsal anchor subequal in length, inner root longer than point. Bars similar in length. Ventral bar with V-shaped knot on ventral shield, anterolateral flaps of the latter connect with pair of finger-like anterior protuberances, forming together V-shaped structure on dorsal side of bar; anteromedian process on dorsal side absent, instead median groove present, which is formed by rising protuberances; some specimens with massive shield, its posteromedian margin extending beyond posterior level of bar. Transverse dorsal bar yoke-shaped with rounded extremities, posteromedian process poorly developed or inconspicuous.

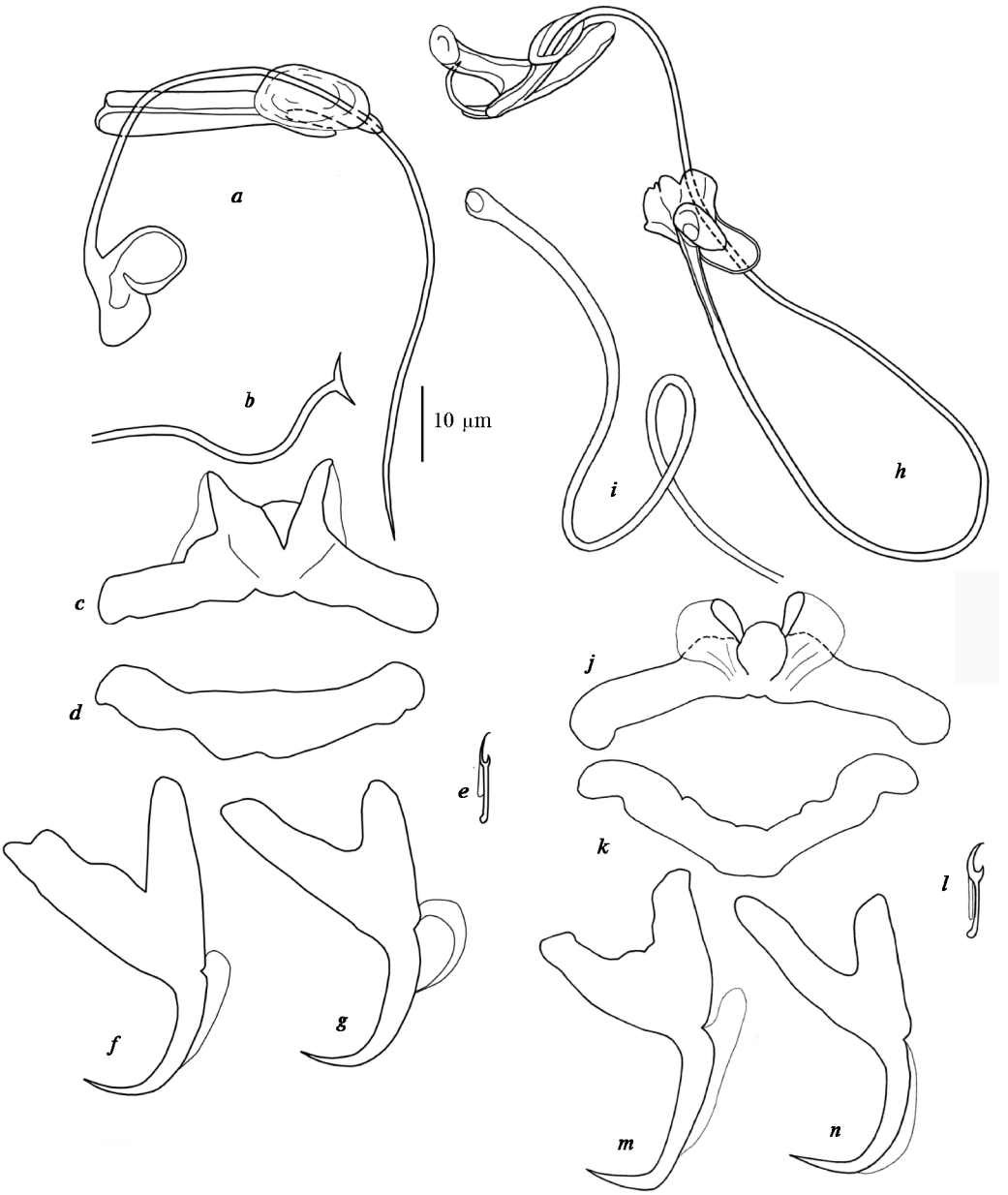

Fig. 9. Haptor and genital sclerotized structures of *Ligophorus chabaudi* Euzet et Suriano, 1977 (*a-g*) and *Ligophorus macrocolpos* Euzet et Suriano, 1977 (*h-n*): *a*, *h* — male copulatory complex: copulatory organ and accessory piece; *b*, *i* — vagina; *c*, *j* — ventral bar; *d*, *k* — dorsal bar; *e*, *l* — hook; *f*, *m* — ventral anchor; *g*, *n* — dorsal anchor.

Рис. 9. Склеротизированные гаптоpальные и генитальные структуры *Ligophorus chabaudi* Euzet et Suriano, 1977 (*a-g*) и *Ligophorus macrocolpos* Euzet et Suriano, 1977 (*h-n*): *a*, *h* — мужская копулятивная система: копулятивный орган и вспомогательный аппарат; *b, i* — вагина; *c*, *j* — вентральная пластинка; *d*, *k* — дорсальная пластинка; *e*, *l* — краевой крючок; *f*, *m* — вентральный срединный крючок; *g*, *n* — дорсальный срединный крючок.

Remarks

This species closely resembles *L. domnichi*, *L. pacificus*, *L. triangularis* sp. n. and *L. abditus* in possessing a C-shaped, long and thin copulatory organ, the latter enters the accessory piece distally; a claw-shaped, pincerlike accessory piece with a distally expand-

Table 4. Metric characters of *L. chabaudi* from different regions
Таблица 4. Метрические характеристики *L. chabaudi* из разных регионов

Characters*	*Ligophorus chabaudi* ex *Mugil cephalus* from Sea of Japan: Razdol'naya Delta, Kiyevka Bay, Russia				*Ligophorus chabaudi* ex *Mugil cephalus* from Mediterranean Sea: Júcar Estuary, Ebro Delta, Spain			
	Mean	SD	Range	N	Mean	SD	Range	N
Body length	826	97	670–1,110	12	879	89	760–1,170	11
Body width	114	22.3	80–150	12	128	15	100–150	11
Pharynx length	40	5.3	32–50	15	42	5.8	30–50	23
Pharynx width	37	4.0	30–43	16	40	9.2	25–70	20
Testis length	58	15.4	40–85	15	54	8.6	40–70	21
Testis width	27	7.4	20–45	13	29	5.8	20–38	19
Ovary length	87	16.2	60–110	14	80	11.7	60–100	16
Ovary width	31	7.4	20–50	16	31	6.2	20–40	21
Haptor length	59	8.4	45–80	16	60	11.4	40–80	22
Haptor width	116	20.7	75–150	16	124	23.0	80–150	21
VAA	39	3.1	32–42	12	40	2.0	36–42	19
VAB	26	2.8	22–29	12	25	2.8	22–30	19
VAC	14	1.9	12–17	12	14	1.3	12–16	19
VAD	19	2.0	17–22	11	20	1.8	17–22	19
VAE	9	1.2	7–11	13	9	0.9	7–10	20
VAF	18	1.6	14–20	15	18	1.5	16–21	23
VAG	40	2.8	34–44	12	39	3.0	34–45	19
DAA	39	3.6	32–43	12	39	3.1	32–43	17
DAB	28	1.6	25–30	12	28	1.5	26–30	17
DAC	10	1.8	7–13	12	10	1.6	7–13	17
DAD	19	2.2	16–23	13	19	2.2	15–23	17
DAE	9	0.9	8–11	12	10	0.9	8–11	18
DAF	18	1.7	15–20	13	20	1.4	17–22	21
DAG	37	1.4	36–40	12	38	1.9	36–43	17
HTL	13	1.1	12–16	13	13	0.7	12–14	18
VBL	47	2.6	41–50	13	48	2.0	43–51	18
VBDP	13	1.2	12–16	13	12	1.7	8–16	17
DBL	47	2.1	41–49	11	47	2.6	41–52	16
APTL	35	3.5	30–42	15	36	2.7	32–42	11
APML	“	“	“	“	“	“	“	“
APMW	7	1.6	5–10	14	7	1.3	5–10	11
APSL	10	2	7–12	15	9	1.8	7–12	18
COL	98	10.3	85–120	16	96	11.7	75–110	13
COW	1	0.1	0.7–1	13	1	0.1	0.8–1	13
VL	51	9.8	35–65	10	46	5.3	35–50	7

* See Material and methods section for abbreviations of metric variables of sclerotized characters.

ed main lobe and a relatively small, straight or bowed secondary lobe; subequal dorsal and ventral pairs of anchors; anchors with a sharply bent blade, the shaft about 1.5–2.5 times longer than the point, the latter not reaching level of tip of inner root. *L. chabaudi* differs from these species in a membranous and bulb-shaped expansion in the distal part of the accessory piece, which is heavily-sclerotized and bulb-shaped in *L. domnichi* and membranous subtriangular in *L. pacificus*. In addition, in relation to *L. domnichi* and *L. pacificus*, this species can be distinguished by the morphology of the ventral bar (the dorsal anteromedian process absent and the finger-like anterior protuberances, forming together a V-shaped structure on the dorsal side of the bar in *L. chabaudi* vs. the dorsal anteromedian process present and anterior protuberances reduced dorsally to pair of small plates in *L. domnichi* and *L. pacificus*). The ventral anchor outer root, ventral and dorsal bar of *L. chabaudi* is longer (12–17, 41–51, 41–52 vs. 5–11, 32–42, 32–39 in *L. domnichi*, respectively) and the secondary lobe of the accessory piece

in this species is shorter (7–13 vs. 16–21 in *L. domnichi* (Rubtsova et al., 2007)). For more detailed information on the differentiation of *L. chabaudi* from *L. triangularis* sp. n. and *L. abditus*, see the Remarks for these species.

It is also convenient to briefly distinguish between *L. chabaudi* and *L. cephali*, because both occur on *M. cephalus* sympatrically in the Mediterranean and share the following suite of characters: a C-shaped, long and thin copulatory organ; the distal end of the latter enters the accessory piece distally; a claw-shaped, pincerlike accessory piece; subequal in the shape and size of anchor pairs; both anchors with a sharply bent blade, the shaft about 1.5–3 times longer than the point, the latter not reaching level of the tip of the inner root. *L. chabaudi* can be distinguished from *L. cephali* as follows: i) the shape of the distal part of main lobe of the accessory piece, which expands in *L. chabaudi*, whereas it narrows in *L. cephali*; ii) the shape and size of the secondary lobe of the accessory piece, which in *L. chabaudi* is straight or slightly bowed and short (7–13), while in *L. cephali* is winding and long (11–21); iii) the larger ventral and dorsal bar (41–51 and 41–52 vs. 34–51 and 32–52 in *L. cephali*); iv) the dorsal anteromedian process absent, the finger-like anterior protuberances, forming together a V-shaped structure on the dorsal side of the ventral bar, the knot on the ventral shield always present in *L. chabaudi*, whereas in *L. cephali* the anteromedian process present on the dorsal side, the anterior protuberances are situated ventrally in relation to the anteromedian process, the knot is usually absent.

The current redescription redefines the morphology of the copulatory complex and the ventral bar of *L. chabaudi*. The previous descriptions of this species by Euzet and Suriano (1977) and Rubtsova et al. (2006 a), while adequate, lacked morphometric information of the ovary, testis, peduncle and haptor. These are provided herein for comparative purposes, as well as measurements and drawings of the haptoral armament and the copulatory complex of *L. chabaudi* from the Sea of Japan. No substantial morphometric differences were found between specimens sampled from the Western Mediterranean Sea and the Sea of Japan (table 4). The present study confirms the report of *L. chabaudi* from the Sea of Japan by Dmitrieva et al. (2009 b).

Previous records of this species from the type-host in the Black and the Azov Seas (Dmitrieva, Gerasev, 1996; Sarabeev, Balbuena, 2004; Miroshnichenko, Maltsev, 2004) probably correspond to *L. cephali* (Rubtsova et al., 2006 a). The present study reinforces the assumption that *L. chabaudi* does not occur in the Black and the Azov Seas. Wu et al. (1991) registered this species from two mullet hosts, *M. cephalus* and *Lz. haematocheilus*, off Zhejiang, the East China Sea (China) and provided a brief description of their specimens. Figures of sclerotized structures of this species (164 of Wu et al. (1991)), as well as *L. vanbenedenii*, seem to combine original drawings of the haptoral sclerotized complex with redrawn illustrations of the genital structures depicted in Euzet and Suriano (1977). These distinctions and lack of original pictures of the genital structures precludes confirmation of the identity of these specimens and suggests that the records of *L. chabaudi* by Wu et al. (1991) are probably invalid.

Ligophorus macrocolpos Euzet et Suriano, 1977
(fig. 9, *h-n*; table 5)

Records: 1. Euzet and Suriano (1977); 2. Radujković and Petrović (1986); 3. Radujković and Euzet (1989); 4. Merella and Garippa (2001); 5. Radujković (2002); 6. Mariniello et al. (2004); 7. Present study.

Type host: *Lz. saliens* (1–7).

Type locality: Mediterranean Sea, Sète (1), France.

Additional localities: Mediterranean Sea: Sète (1), France; Júcar Estuary (7), Gulf of Valencia (7), Spain; Mistras Lagoon, Sardinia (4), Lesina Lagoon (6), Italy; Boka Kotorska Bay (2, 3, 5), Montenegro. Black Sea: Sozopol Bay (7), Bulgaria.

Table 5. Metric characters of *L. macrocolpos* and *L. acuminatus*
Таблица 5. Метрические характеристики *L. macrocolpos* и *L. acuminatus*

Characters*	*Ligophorus macrocolpos* ex *Liza saliens* Mediterranean Sea: Ebro Delta Spain				*Ligophorus acuminatus* ex *Liza saliens* Mediterranean Sea: Ebro Delta, Spain			
	Mean	SD	Range	N	Mean	SD	Range	N
Body length	698	116	553–936	17	674	62	585–810	15
Body width	131	28	82–175	17	101	13.8	82–129	15
Pharynx length	33	5.7	25–45	12	27	6.3	17–37	11
Pharynx width	31	6.8	20–45	12	26	7.0	15–36	11
Testis length	54	8.4	38–75	17	42	7.3	30–60	19
Testis width	27	4.7	20–38	16	25	5.6	15–35	19
Ovary length	103	14.9	75–125	12	94	16.5	63–115	19
Ovary width	31	7.8	18–40	15	23	10.1	10–58	19
Haptor length	57	12.0	35–75	13	53	7.0	40–63	10
Haptor width	138	30.0	100–183	13	101	17.8	80–130	10
VAA	37	1.4	35–39	16	38	1.8	35–41	15
VAB	32	2.0	29–34	16	29	1.7	28–33	15
VAC	9	0.6	8–9	16	9	1.0	7–10	15
VAD	13	1.5	11–16	16	12	1.0	11–13	15
VAE	9	1.0	8–11	16	7	0.7	7–9	15
VAF	22	1.6	19–24	11	22	1.1	20–23	10
VAG	41	2.1	37–43	16	38	2.0	35–42	15
DAA	37	2.8	32–42	16	35	1.4	33–37	15
DAB	25	1.4	23–29	16	25	1.5	22–28	15
DAC	9	0.8	8–11	16	7	0.4	5–7	15
DAD	16	1.5	13–18	16	14	0.9	13–16	15
DAE	8	1.0	7–9	16	7	0.9	5–8	15
DAF	20	2.0	17–23	11	21	1.9	19–25	9
DAG	35	1.6	32–38	16	32	1.6	29–34	15
HTL	14	0.7	13–14	16	13	0.7	11–14	15
VBL	45	3.3	40–51	16	38	1.3	35–39	15
VBDP	9	1.2	7–11	8	8	0.7	7–9	11
DBL	46	4.3	39–54	16	37	3.4	34–47	15
APTL	25	2.8	21–30	14	23	2.6	18–26	14
APML	15	2.3	12–20	11	9	1.7	6–12	13
APMW	3	0.3	3–4	10	3	0.7	2–4	9
APSL	25	2.0	22–29	10	12	1.8	9–15	12
COL	167	15.9	131–190	16	74	6.8	66–85	15
COW	1	0.1	1–1.2	10	0.8	0.2	0.5–1	13
VL	106	22.4	86–158	14	24	4.8	17–31	15

* See Material and methods section for abbreviations of metric variables of sclerotized characters.

Type specimens: not mentioned in original description.

Material deposited: voucher material from the Ebro Delta at the BMNH 2008.8.16–19 (4 specimens), IZAN M–12 (2 specimens) and ZNUMZ 11900056 (1 specimen).

Redescription

Based on 17 adult worms from the Ebro Delta, Spain. Body fusiform with maximum width at level of gonads. One or two terminal, and two bilateral cephalic lobes well developed. Cephalic glands posterolateral to pharynx. Testis elongate to ovate; copulatory organ winding, long, thin, enters accessory piece proximally; base of copulatory organ with thick-walled heel; accessory piece cross-shaped, secondary lobe articulates with main lobe lengthwise of all length of the latter. Main lobe of accessory piece proximally extended and tapered distally, cylindrical, straight; secondary lobe Y-shaped, longer than main lobe, its distal end extending beyond level of distal end of main lobe, proximal end of secondary lobe

extending to or slightly beyond level of that of main lobe. Ovary U-shaped; oviduct, ootype and uterus not observed; Mehlis' glands conspicuous, comprising elongated glandular cells, occupying body space between prostatic reservoir and seminal receptacle. Vagina coiled or winding; vaginal aperture midventral; distal end of vagina scyphoid and narrow. Peduncle broad, short, wider than long or subequal in width and length, tapering posteriorly. Haptor subhexagonal, wider than long. Pairs of anchors unequal; outer and main part length of ventral anchor longer than those of dorsal anchor. Ventral anchor with sharply bent blade, shaft 1.9 to 2.9 times longer than point, the latter not reaching level of tip of inner root; inner root enormously expanded basally, slightly longer than outer root; tip of outer root extending beyond level of that of inner root; outer root and point subequal in length, inner root longer than point; massive base. Dorsal anchor with sharply bent blade, shaft 1.9 to 3.2 times longer than point, the latter not reaching level of tip of inner root; outer root shorter than inner root; tip of outer root extending to or beyond level of that of inner root; outer root and point subequal in length, inner root longer than point. Bars subequal in length. Ventral bar with knot on ventral shield, anterolateral flaps of the latter connect with pair of finger-like anterior protuberances, forming together V-shaped structure on dorsal side of bar; anteromedian process on dorsal side absent, instead median groove present, which is formed by rising protuberances; some specimens with massive shield, its posteromedian margin extending beyond posterior level of bar. Transverse dorsal bar yoke-shaped with small posteromedian knob-like process.

Remarks

L. macrocolpos can be easily distinguished from other species of *Ligophorus* by: i) a cross-shaped accessory piece of the copulatory complex with a Y-shaped secondary lobe, longer than the main lobe; ii) winding and significantly longer copulatory organ and vagina; iii) a scyphoid distal end of the vagina. These features are shared with *L. kaohsianghsieni*. For a differential diagnosis between these species, see Remarks for *L. kaohsianghsieni*.

Euzet and Suriano (1977) described *L. macrocolpos* based on 25 live and two stained whole mount individuals. None of these worms were deposited in any collection. Dmitrieva and Gerasev (1996) described a specimen as *L. macrocolpos* from a non type-host, *Lz. aurata*. However, the specimen depicted by these authors can be distinguished from *L. macrocolpos* by the different shape of both the ventral and dorsal anchors, and the accessory piece of the copulatory complex (fig. 4 in Dmitrieva, Gerasev (1996), fig. 17 and 18 in Euzet and Suriano (1977), and fig. 9, *h*, *m* and *n* of the present study). In addition the metric characters reported fall outside the variation ranges reported in *L. macrocolpos*. Therefore its ascription to *L. macrocolpos* is questionable. The present redescription provides new information on the shape of the ovary, peduncle, and haptor and detailed data on the structure of the accessory piece of the copulatory complex and the ventral bar. All metric characters of the specimens of the present study conform to those reported by Euzet and Suriano (1977) and Mariniello et al. (2004).

Ligophorus acuminatus Euzet et Suriano, 1977
(fig. 3, *c*; 10, *a-g*; table 5)

Records: 1. Euzet and Suriano (1977); 2. Radujković and Petrović (1986); 3. Radujković and Euzet (1989); 4. Dmitrieva and Gerasev (1996); 5. Merella and Garippa (2001); 6. Radujković (2002); 7. Mariniello et al. (2004); 8. Present study.

Type host: *Lz. saliens* (1–8).

Type locality: Mediterranean Sea, Sète (1), France.

Additional localities: Mediterranean Sea: Júcar Estuary (8), Ebro Delta (8), Gulf of Valencia (8), Spain; Mistras Lagoon, Sardinia (5), Lesina Lagoon (7), Italy; Boka

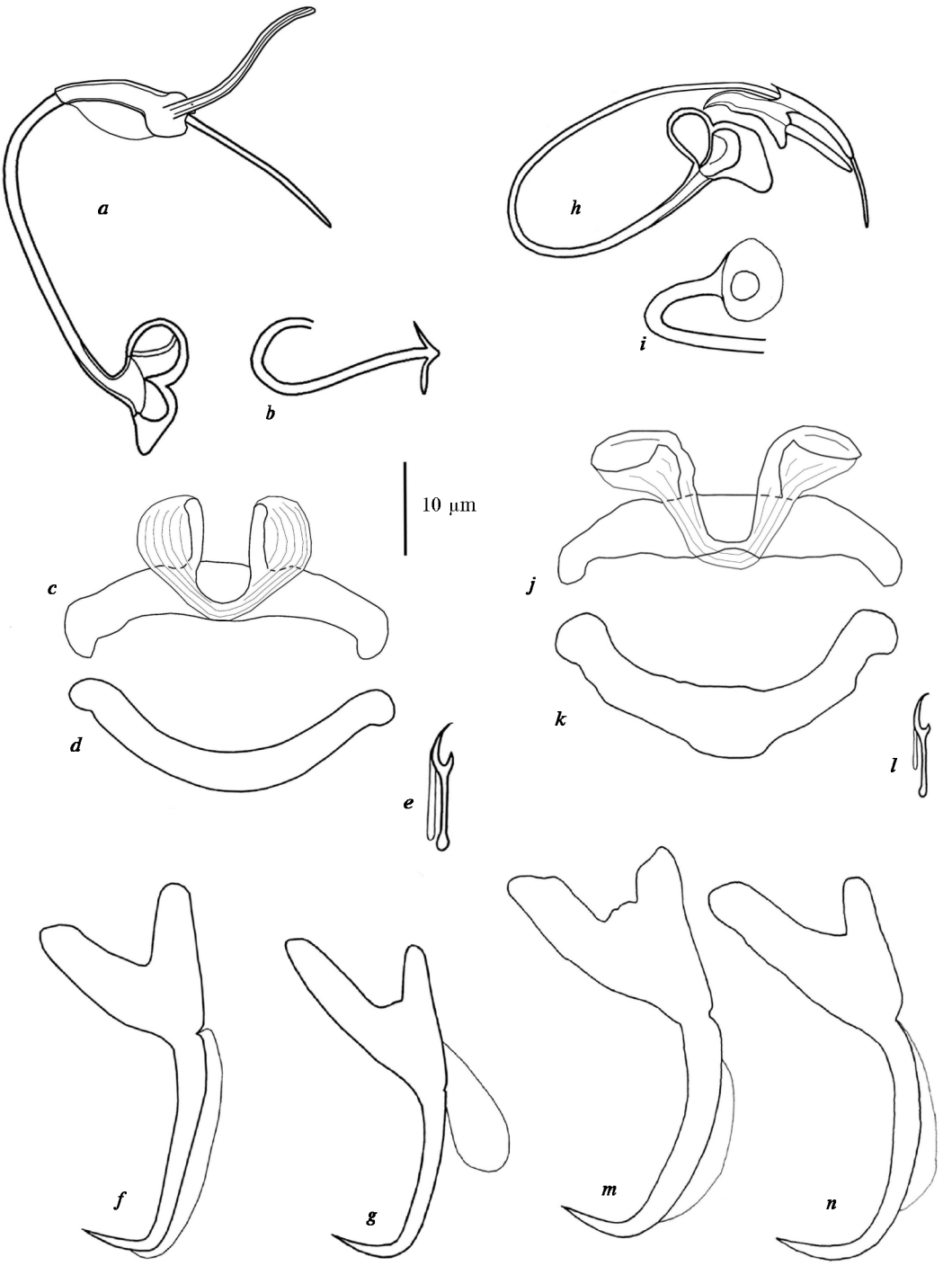

Fig. 10. Haptor and genital sclerotized structures of *Ligophorus acuminatus* Euzet et Suriano, 1977 (*a-g*) and *Ligophorus minimus* Euzet et Suriano, 1977 (*h-n*): *a*, *h* — male copulatory complex: copulatory organ and accessory piece; *b*, *i* — vagina; *c*, *j* — ventral bar; *d*, *k* — dorsal bar; *e*, *l* — hook; *f*, *m* — ventral anchor; *g*, *n* — dorsal anchor.

Рис. 10. Склеротизированные гапторальные и генитальные структуры *Ligophorus acuminatus* Euzet et Suriano, 1977 (*a-g*) и *Ligophorus minimus* Euzet et Suriano, 1977 (*h-n*): *a*, *h* — мужская копулятивная система: копулятивный орган и вспомогательный аппарат; *b*, *i* — вагина; *c*, *j* — вентральная пластинка; *d*, *k* — дорсальная пластинка; *e*, *l* — краевой крючок; *f*, *m* — вентральный срединный крючок; *g*, *n* — дорсальный срединный крючок.

Kotorska Bay (2, 3, 6), Montenegro. Black Sea: Sozopol Bay (8), Bulgaria; Sevastopol coastal waters, Crimea (4), Ukraine.

Type specimens: not mentioned in original description.

Material deposited: voucher material from the Ebro Delta at the BMNH 2008.8.16.20–21 (2 specimens), IZAN M–1 (2 specimens) and ZNUMZ 11900051, 11900052, 11900054 (6).

Redescription

Based on 19 mature worms from the Ebro Delta, Spain. Body fusiform with maximum width at level of gonads. One terminal and two bilateral cephalic lobes well developed. Cephalic glands posterolateral to pharynx. Testis varies from ovate to elongate-ovate; copulatory organ C-shaped, long, thin, enters accessory piece proximally; base of copulatory organ with thick-walled heel. Accessory piece rod-shaped, comprising ovate main lobe with heavily sclerotized bulb-shaped distal end and tubular, winding, narrowing distally secondary lobe; the latter articulates with main lobe by simple joint, turning up from distal end of main lobe. Ovary U-shaped; oviduct, ootype and uterus not observed; Mehlis' glands conspicuous, extending between prostatic reservoir and seminal receptacle. Vagina winding; vaginal aperture midventral; distal end of vagina funnel-shaped, thin-walled. Seminal receptacle ovate. Peduncle broad, short, wider than long, or subequal in width and length, tapering posteriorly. Haptor subhexagonal, wider than long. Pairs of anchors subequal in shape with distinction in larger size of outer and main part length of ventral anchor than those of dorsal anchor. Both anchors with sharply bent blade, shaft 2.7 to 3.5 times longer than point in ventral anchor and 2.9 to 4.2 in dorsal one; point not reaching level of tip of inner root; outer root shorter than inner root; size differences of roots more apparent in dorsal anchor; outer root and point subequal in length, inner root longer than point. Tip of outer root of ventral anchor extending to or beyond level of that of inner root; tip of outer root of dorsal anchor may extend to level of that of inner root. Bars subequal in length. Ventral bar with finger-like anterior protuberances situated ventrally, not reaching level of dorsal side of bar; dorsal anteromedian process and ventral knot present or absent; some specimens with posteromedian prolongation of shield extending beyond level of posterior end of bar. Transverse dorsal bar yoke-shaped with rounded extremities.

Remarks

L. acuminatus differs from all species of *Ligophorus* in the unique morphology of the accessory piece of the copulatory complex, which is rod-shaped and consists of an ovate main lobe and a tubular, winding, secondary lobe, which turns upwards from the distal end of the main lobe.

The species is similar to *L. minimus*, *L. heteronchus*, in the morphology of both the ventral and dorsal anchor/bar complexes. Indeed, the pairs of anchors are subequal in shape; both anchors with a sharply bent blade, the shaft about 2.6 times longer or more than the point; the latter does not reach the level of the tip of the inner root, the outer root is shorter than the inner root; the tip of the outer root of the ventral anchor extends to or beyond the level of that of the inner root; bars are subequal in length; the ventral bar with the knot on the ventral shield; the finger-like anterior protuberances of the ventral bar situated ventrally, usually not reaching level of the dorsal side of the ventral bar; the anteromedian process of the ventral bar usually absent. In addition to the unique characteristics described above, *L. acuminatus* differs from *L. minimus* in: i) the texture of the distal end of the vagina (thin-walled vs. thick-walled in the latter species); ii) smaller measurements for DAA, DAB, DAG, VBDP and APML; and from *L. heteronchus* in the smaller length of APML.

L. acuminatus resembles *L. imitans* and *L. parvicirrus* in the shape of the ventral and dorsal anchor, but differs from *L. imitans* by having: i) the finger-like anterior protuberances of the ventral bar situated ventrally, usually not reaching level of the dorsal side of the ventral bar, rather than reaching the dorsal side of the bar in the latter species; ii) smaller length of APML; and from *L. parvicirrus* by: i) a sclerotized vagina *vs.* non sclerotized in the latter species; ii) the absence in the latter species of a lobular, massive posteromedian process; and iii) the smaller length for APML, PW and larger PL.

This species is redescribed herein in order to better characterize the shapes of the body, testis, ovary, peduncle and haptor, and to clarify the morphology of the accessory piece of the copulatory complex and the ventral bar. The ranges of variation of all metric characters of the specimens examined (except the length of the copulatory organ) fall within the range, or overlap widely, with those reported by Euzet and Suriano (1977) and Mariniello et al. (2004). The copulatory organ of the present specimens was slightly shorter than reported by Euzet and Suriano (1977).

Ligophorus minimus Euzet et Suriano, 1977
(fig. 3, *i*; 10, *h-n*; table 6)

Records: 1. Euzet and Suriano (1977); 2. Radujković and Petrović (1986); 3. Radujković and Euzet (1989); 4. Merella and Garippa (2001); 5. Radujković (2002); 6. Mariniello et al. (2004); 7. Present study.

Type host: *Lz. saliens* (1–7).

Type locality: Mediterranean Sea, Sète (1), France.

Additional localities: Mediterranean Sea: Júcar Estuary (7), Ebro Delta (7), Gulf of Valencia (7), Spain; Mistras Lagoon, Sardinia (4), Lesina Lagoon (6), Italy; Boka Kotorska Bay (2, 3, 5), Montenegro. Black Sea: Sozopol Bay (7), Bulgaria.

Type specimens: not mentioned in original description.

Material deposited: voucher material from the Ebro Delta at the BMNH 2008.8.16.22–24 (3 specimens), IZAN M–14 (2 specimens), 11900050, 11900051, 11900053–11900061 (16 specimens).

Redescription

Based on 39 specimens from the Ebro Delta, Spain. Body fusiform with maximum width at level of gonads. One terminal and two bilateral cephalic lobes well developed. Cephalic glands posterolateral to pharynx. Testis shape varies from ovate to elongate-ovate; copulatory organ C-shaped, long, thin, enters accessory piece medially on top of main lobe; base of copulatory organ with thick-walled heel; accessory piece claw-shaped, pincerlike, secondary lobe joins main lobe medially by simple joint. Main lobe of accessory piece triangle-shaped, slightly bowed with tapered proximal part and frequently inconspicuous tubular prolongation in distal part; secondary lobe cylindrical straight, shorter than main lobe, extending slightly beyond level of distal end of main lobe. Ovary U-shaped; oviduct, ootype and uterus not observed, Mehlis' glands inconspicuous, extending across intervitellarial body space between prostatic reservoir and seminal receptacle. Vagina short, bowed; vaginal aperture midventral; distal end of vagina funnel-shaped, thick-walled. Peduncle broad, short, wider than long, tapering posteriorly. Haptor subhexagonal, wider than long. Pairs of anchors subequal in shape and size, except shorter inner length in ventral anchor than in dorsal; both anchors with sharply bent blade, shaft 2.6 to 4 times longer than point, the latter not reaching level of tip of inner root, outer root and point shorter than inner root, outer root and point subequal in length. Tip of outer root of ventral anchor extending to or beyond level of that of inner root; tip of outer root of dorsal anchor may extend to level of that of inner root. Bars subequal in length. Ventral bar widest in middle and laterally tapered; ventral knot and dorsal anteromedian process pre-

Table 6. Metric characters of *L. minimus* and *L. angustus*
Таблица 6. Метрические характеристики *L. minimus* и *L. angustus*

Characters*	*Ligophorus minimus* ex *Liza salienss* from Mediterranean Sea, Ebro Delta, Spain				*Ligophorus angustus* ex *Chelon labrosus* from Mediterranean Sea, Júcar Delta, Spain			
	Mean	SD	Range	N	Mean	SD	Range	N
Body length	554	67	450–687	37	889	142	646–1,228	28
Body width	91	19	60–131	34	188	25.5	121–234	28
Pharynx length	25	5.0	18–35	17	32	6.6	23–42	12
Pharynx width	24	5.5	17–35	17	28	4.4	23–35	12
Testis length	37	4.6	27–45	19	70	15.1	50–100	14
Testis width	25	5.4	15–35	21	32	7.9	20–47	13
Ovary length	50	8.8	38–70	12	81	13.0	63–103	21
Ovary width	25	7.0	15–42	21	33	8.4	20–55	21
Haptor length	59	13.6	40–90	16	55	12.0	38–76	13
Haptor width	104	22.3	70–150	16	72	19.4	30–90	13
VAA	42	2.4	38–48	38	31	1.6	28–35	28
VAB	33	2.2	29–37	38	23	1.3	21–25	28
VAC	8	1.0	6–10	38	4	0.9	3–6	28
VAD	16	1.8	12–19	37	15	1.7	12–18	28
VAE	8	0.7	7–9	37	13	0.9	12–15	28
VAF	25	1.5	22–28	37	15	0.9	12–16	27
VAG	41	2.4	35–45	37	27	1.6	25–30	28
DAA	46	2.6	41–51	37	36	1.9	33–40	28
DAB	36	2.0	32–40	37	26	2.3	22–30	28
DAC	7	0.8	5–9	38	6	1.1	5–8	28
DAD	16	1.4	13–18	37	15	1.4	12–18	28
DAE	9	0.8	7–10	37	12	1.1	11–14	28
DAF	27	1.5	24–30	37	15	1.3	13–18	23
DAG	43	2.0	39–48	37	32	1.9	29–37	28
HTL	14	0.7	13–15	38	13	0.9	12–15	28
VBL	39	3.2	33–50	38	37	3.5	33–48	28
VBDP	13	1.6	9–15	38	4	1.1	2–5	25
DBL	39	3.7	32–50	38	35	2.5	32–41	28
APTL	19	2.1	16–24	38	30	3.9	25–38	27
APML	“	“	“	“	“	“	“	“
APMW	3	0.5	3–4	12	7	0.8	6–9	11
APSL	10	1.4	7–12	17	13	1.6	10–17	23
COL	79	5.0	65–86	38	85	5.1	76–98	28
COW	0.9	0.1	0.7–1	11	0.9	0.1	0.8–1	9
VL	24	3.9	16-30	36	34	4.3	28–43	23

* See Material and methods section for abbreviations of metric variables of sclerotized characters.

sent or absent; finger-like anterior protuberances situated ventrally, usually not reaching level of dorsal side of bar; some specimens with posteromedian prolongation of shield extending beyond level of posterior end of bar. Transverse dorsal bar yoke-shaped with small posteromedian process and rounded extremities.

Remarks

L. minimus can be easily distinguished from all other species of *Ligophorus* by the following unique set of features: i) the medial position of the copulatory organ entrance on top of the main lobe of the accessory piece; ii) the morphology of the main lobe of the accessory piece, which represents a slightly bowed, triangle-shaped structure with a tapered proximal part and a thin tubular prolongation in the distal part; iii) the texture of the distal end of the vagina, which is thick-walled.

The morphology of both the ventral and dorsal anchor/bar complexes of *L. minimus* closely resembles that of *L. acuminatus* and *L. heteronchus*. The three species share the following features: the pairs of anchors are subequal in shape; both anchors with a sharply bent blade, the shaft about 2.6 times longer or more than the point; the latter does not reach the level of the tip of the inner root and the outer root is shorter than the inner root; the tip of the outer root of the ventral anchor extends to or beyond the level of that of the inner root; the bars are subequal in length; the ventral bar with the knot on the ventral shield; the finger-like anterior protuberances of the ventral bar situated ventrally, usually not reaching the level of the dorsal side of the ventral bar; the anteromedian process of the ventral bar usually absent. Further to the unique characteristics described above, *L. minimus* differs from *L. heteronchus* in larger VAD, DAA, DAB and DAG. See also Remarks for *L. acuminatus* for discrimination of these species.

L. minimus resembles *L. imitans* and *L. parvicirrus* in the shape of the ventral and dorsal anchor, but differs from *L. imitans* by having: i) the finger-like anterior protuberances of the ventral bar situated ventrally, usually not reaching level of the dorsal side of the ventral bar, rather than reaching the dorsal side of the bar in the latter species; ii) larger DAA, DAB, DAF, DAG, VBDP and smaller VL; and from *L. parvicirrus* by: i) the sclerotized vagina vs. non sclerotized in the latter species; ii) the absence of characteristic for *L. parvicirrus* a lobular, massive posteromedian process of the ventral bar; iii) smaller size for APTL, COW and larger COL.

The original description of *L. minimus* by Euzet and Suriano (1977) included one inaccuracy regarding the shape of the accessory piece of the copulatory complex: it represented a tiny, cone-shaped piece, 8 μm in length. Our examination of this species revealed that the main lobe of the accessory piece represents a complicated structure, which is substantially longer (table 6). Additionally, the present redescription provides new information on the shape and size of the testis, ovary, haptor and ventral bar.

Ligophorus heteronchus Euzet et Suriano, 1977
(fig. 11, *a-g*; table 7)

Synonym: *Ligophorus euzeti* Dmitrieva and Gerasev, 1996 (junior synonym).

Records: 1. Euzet and Suriano (1977); 2. Mikailov and Seidli (1989); 3. Dmitrieva and Gerasev (1996); 4. Merella and Garippa (2001); 5. Mariniello et al. (2004); 6. Present study.

Type host: *Lz. saliens* (1–6).

Type locality: Mediterranean Sea, Sète (1), France.

Additional localities: Mediterranean Sea: Júcar Estuary (6), Ebro Delta (6), Gulf of Valencia (6), Spain; Mistras Lagoon, Sardinia (4), Lesina Lagoon (5), Italy. Black Sea: Sozopol Bay (6), Bulgaria; Sevastopol coastal waters, Crimea (3), Ukraine. Caspian Sea, Kyzylagachskij Gulf (2), Azerbaidzhan.

Type specimens: not mentioned in original description.

Material deposited: voucher material from the Ebro Delta at the BMNH 2008.8.16.25–26 (2 specimens), IZAN M–8 (2 specimens) and ZNUMZ 11900049, 11900051, 11900052, 11900062–11900064 (6 specimens).

Redescription

Based on 42 mature specimens: 30 specimens from the Ebro Delta, Spain, and 12 specimens from the Sozopol Bay, Bulgaria. Body fusiform with maximum width at level of gonads. One terminal and two bilateral cephalic lobes well developed. Cephalic glands posterolateral to pharynx. Testis shape varies from ovate to elongate-ovate; copulatory organ C-shaped, long, thin, enters accessory piece proximally; base of copulatory organ with thick-walled heel; accessory piece claw-shaped, pincerlike. Main lobe of accessory

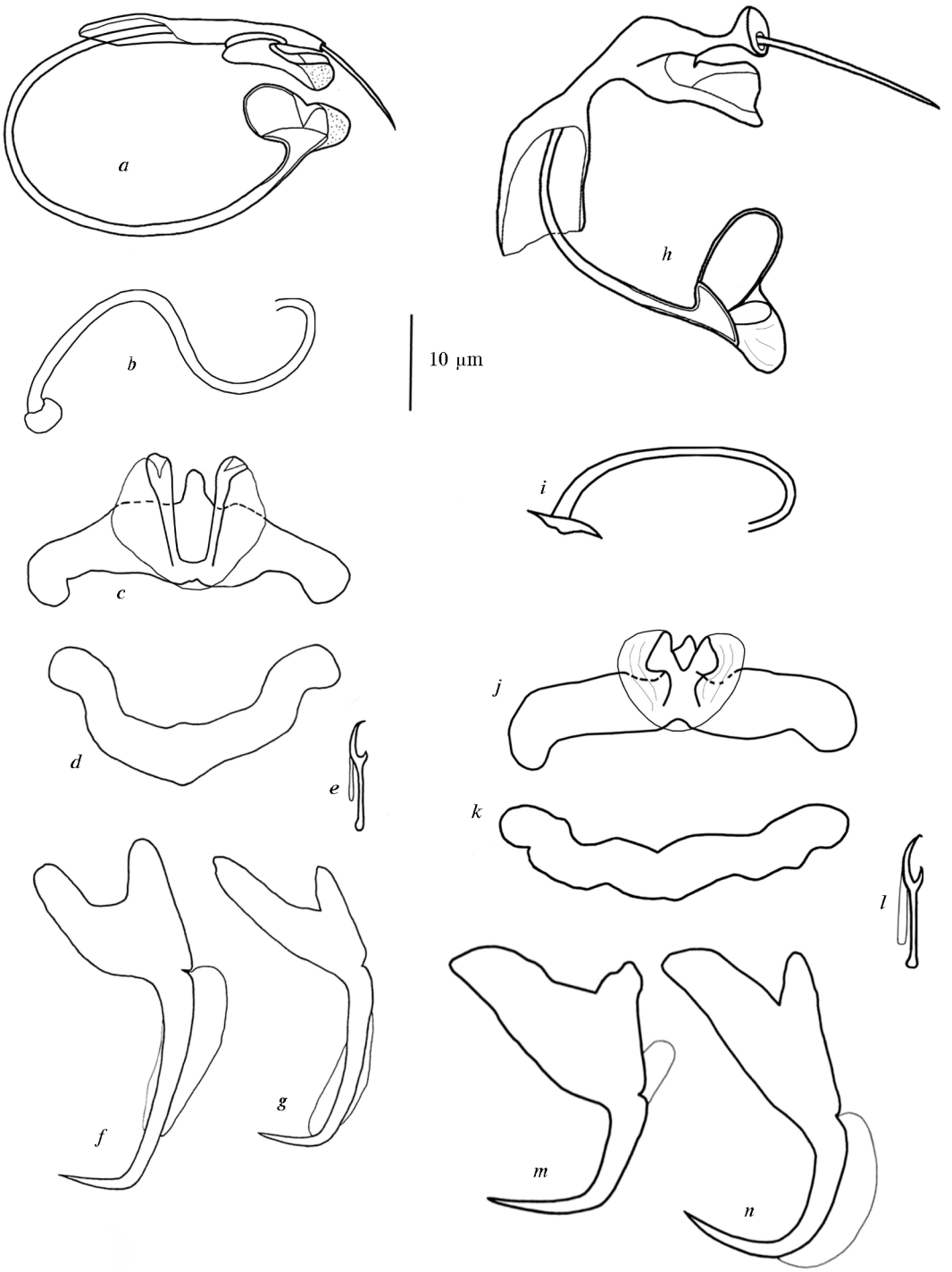

Fig. 11. Haptor and genital sclerotized structures of *Ligophorus heteronchus* Euzet et Suriano, 1977 (*a-g*) and *Ligophorus angustus* Euzet et Suriano, 1977 (*h-n*): *a*, *h* — male copulatory complex: copulatory organ and accessory piece; *b*, *i* — vagina; *c*, *j* — ventral bar; *d*, *k* — dorsal bar; *e*, *l* — hook; *f*, *m* — ventral anchor; *g*, *n* — dorsal anchor.

Рис. 11. Склеротизированные гапторальные и генитальные структуры of *Ligophorus heteronchus* Euzet et Suriano, 1977 (*a-g*) и *Ligophorus angustus* Euzet et Suriano, 1977 (*h-n*): *a, h* — мужская копулятивная система: копулятивный орган и вспомогательный аппарат; *b, i* — вагина; *c*, *j* — вентральная пластинка; *d*, *k* — дорсальная пластинка; *e*, *l* — краевой крючок; *f*, *m* — вентральный срединный крючок; *g*, *n* — дорсальный срединный крючок.

Table 7. Metric characters of *L. heteronchus* from different regions
Таблица 7. Метрические характеристики *L. heteronchus* из разных регионов

Characters*	*Ligophorus heteronchus* ex *Liza saliens*							
	from Mediterranean Sea, Ebro Delta, Spain				from Black Sea, Sozopol, Bulgaria			
	Mean	SD	Range	N	Mean	SD	Range	N
Body length	545	96.5	379–702	27	513	84.1	400–650	9
Body width	100	21.6	58–140	28	111	23.2	70–140	9
Pharynx length	24	4.2	18–30	13	34	2.9	28–38	12
Pharynx width	22	4.3	15–30	13	32	3.1	28–35	9
Testis length	43	14.2	22–65	14	41	6.8	30–50	9
Testis width	23	3.5	17–30	14	24	4.9	15–30	8
Ovary length	63	12.7	50–80	13	64	12.7	50–80	9
Ovary width	25	3.9	17–33	16	26	2.4	21–30	10
Haptor length	57	12.9	30–75	12	65	10.4	50–80	7
Haptor width	93	18.1	70–118	12	93	17.5	70–120	8
VAA	38	2.7	33–44	30	41	5.9	31–48	9
VAB	32	2.6	27–39	30	37	5.1	30–42	10
VAC	8	0.8	7–9	30	6	1.0	4–7	10
VAD	11	1.4	8–13	30	9	2.3	7–12	10
VAE	8	0.9	5–9	30	8	0.8	7–9	10
VAF	28	4.4	23–33	11	28	4.2	23–32	10
VAG	39	2.8	35–47	30	43	5.6	35–48	10
DAA	35	2.0	30–38	30	35	2.3	32–40	10
DAB	27	2.4	23–34	29	30	2.5	26–32	10
DAC	5	1.0	4–8	30	4	0.9	3–6	10
DAD	13	1.3	10–16	30	11	1.7	8–12	10
DAE	7	0.7	5–8	30	6	0.9	5–7	10
DAF	22	2.8	18–25	11	23	2.4	19–26	10
DAG	33	2.5	28–39	27	33	3.1	29–36	10
HTL	12	0.9	11–14	30	12	1.5	10–14	9
VBL	35	2.5	30–39	30	45	4.9	35–50	9
VBDP	6	0.7	5–7	13	9	2.8	6–13	9
DBL	32	3.6	26–37	30	42	4.8	33–46	9
APTL	24	3.6	21–35	30	31	3.2	25–35	10
APML	21	3.7	18–30	10	29	3.0	24–33	10
APMW	2.5	0.3	2–3	12	3	0.5	1.5–3	10
APSL	12	2.1	8–15	10	15	2.4	10–17	10
COL	82	9.3	66–114	30	98	9.6	85–115	10
COW	0.8	0.1	0.5–0.9	12	0.9	0.1	0.8–1	8
VL	37	4.2	32–45	20	43	7.2	35–55	8

* See Material and methods section for abbreviations of metric variables of sclerotized characters.

piece cylindrical, slightly bowed, elongated, slightly extended proximally and narrowing distally; secondary lobe massive, bilobed forms gutter, V-shaped in cross section, extended distally, from J-shaped to wedge-like in profile, joins main lobe middistally by simple joint; shorter than main lobe, extending beyond level of distal tip of main lobe. Ovary U-shaped; oviduct, ootype and uterus not observed; Mehlis' glands conspicuous, occupying intervitellarial body space between prostatic reservoir and seminal receptacle. Vagina winding; vaginal aperture midventral; distal end of vagina funnel-shaped, thin-walled. Peduncle broad, short, wider than long, tapering posteriorly. Haptor subhexagonal, wider than long. Pairs of anchors subequal in shape and unequal in size; inner, main part, shaft and outer length of ventral anchor longer than those of dorsal anchor. Both anchors with sharply bent blade, shaft about 2.6 to 5 times longer than point, the latter not reaching level of tip of inner root, outer root shorter than inner one; size differences between roots more apparent in dorsal anchor. Tip of outer root of ventral anchor extend-

ing to or beyond level of that of inner root; point, outer and inner root subequal in length; inner root of ventral anchor enormously expanded basally. Tip of outer root of dorsal anchor extending to level of tip of inner root; outer root and point subequal in length, inner root longer than point. Bars subequal in length or ventral bar larger than dorsal one. Ventral bar widest at middle and laterally tapered; knot on ventral shield usually absent; dorsal anteromedian process usually present; finger-like anterior protuberances situated ventrally, reaching or not level of dorsal side of bar; some specimens with posteromedian prolongation of shield extending beyond level of posterior end of bar. Transverse dorsal bar yoke-shaped with small, knob-like posteromedian process.

Remarks

This species differs from all other members of *Ligophorus* (except *L. imitans* and *L. rectus* sp. n.) by possessing larger inner, main part and outer lengths of the ventral anchor than those of the dorsal anchor. *L. heteronchus* most closely resembles *L. imitans* and *L. angustus* in the morphology of the male copulatory complex and further with *L. imitans* in the shape of the anchors. However, *L. heteronchus* exhibits the ventral position of the finger-like anterior protuberances in relation to the anteromedian process, or the finger-like anterior protuberances not reaching the level of the dorsal side of the bar if the anteromedian process absent; a massive, J-shaped to wedge-like secondary lobe of the accessory piece of the copulatory complex, extending beyond the level of the distal tip of the main lobe, whereas in *L. imitans* finger-like anterior protuberances extending beyond the dorsal level of the bar and the dorsal anteromedian process is absent; the secondary lobe is slender, J-shaped, extending to the level of the distal tip of the main lobe. *L. heteronchus* can be easily distinguished from *L. angustus* by its thin, distally narrowing main lobe of the accessory piece of the copulatory organ and the shape of both pairs of anchors, which is characterised by a short point, a slender base and a high range of ratio between shaft and point (2.6–5), whereas in the latter species the main lobe of the accessory piece of the copulatory organ is thick with a dome-shaped hemispherical expansion; anchors with a long point, a massive base and the ratio between the shaft and the point in range from 1 to 1.5. The morphology of both the ventral and dorsal anchor/bar complexes of *L. heteronchus* closely resembles that of *L. acuminatus* and *L. minimus*. Differential diagnoses for these species are provided in Remarks for *L. acuminatus* and *L. minimus*.

The present redescription provides new information on the shape of the testis, ovary, peduncle and haptor, the structure of the accessory piece of the copulatory complex and the ventral bar. The two previous descriptions of *L. heteronchus* by Euzet and Suriano (1977) and Dmitrieva and Gerasev (1996) (described as *L. euzeti* in the latter case) were based on six specimens in both cases. Therefore, it is not surprising that the ranges of most metric characters of the 42 specimens studied herein (table 7) are substantially larger. The smaller measurements of some characters of the ventral and dorsal anchors reported by Dmitrieva and Gerasev (1996) than those in the original description can be interpreted as resulting from intraspecific variation among different allopatric populations.

Dmitrieva and Gerasev (1996) described *L. euzeti* as a new species from the Black Sea *Lz. saliens*. No specimens were deposited in a recognized helminthological collection and our attempt to borrow specimens from the author's institutions, IBSS and ZIN, respectively, failed. The description of *L. euzeti* lacked information on the shape of the accessory piece and the distal end of the vagina, only the vagina length was given and it was noted that "...the accessory piece has a distinct form...". The differential diagnosis included the following statements: "...the described species is most similar to *L. heteronchus* Euzet et Suriano, 1977, parasitizing on Mediterranean leaping mullet (*Lz. saliens*), but

differs from it in the shape and smaller size of the anchors, the different shape of the accessory piece of the copulatory complex and a shorter vaginal armament...". However, the shape differences of the anchors and accessory piece of the copulatory complex between these two forms seem small (compare figure 26 of Euzet and Suriano (1977) with figure 1 of Dmitrieva and Gerasev (1996); see also the redescription of *L. heteronchus* in the present study). In addition, the shape variation of the accessory piece depicted in the description of Dmitrieva and Gerasev (1996) might result from a different spatial orientation of the structure than that presented in the original description. In addition, the comparison of metric characters of *L. heteronchus* obtained in the present study from the Mediterranean and the Black Sea with those of *L. euzeti* provided in the original description showed that the variation ranges of all characters either fall within the range or overlap widely (see table 7 of the present study and table in Dmitrieva and Gerasev, 1996). Therefore, we propose that *L. heteronchus* is a senior synonym of *L. euzeti*. Thus, the record of the latter off Sevastopol is ascribed to the former species. *L. heteronchus* was recorded by Mikailov and Seidli (1989) on *Lz. saliens* introduced into the Caspian Sea and it should be considered as an alien species in this sea.

Ligophorus angustus Euzet et Suriano, 1977
(fig. 11, *h-n*; table 6)

Records: 1. Euzet and Suriano (1977); 2. Anderson (1981); 3. Llewellyn and Anderson (1984); 4. Radujković and Petrović (1986); 5. Radujković and Euzet (1989); 6. Merella and Garippa (2001); 7. Radujcović (2002); 8. Mariniello et al. (2004); 9. Present study.

Type host: *C. labrosus* (1–9).

Type locality: Mediterranean Sea, Sète (1), France.

Additional localities: English Channel, Tamar estuary (2, 3), UK. Mediterranean Sea: Gulf of Santa Pola (9), Júcar Estuary (9), Ebro Delta (9), Spain; Mistras Lagoon, Sardinia (6), Oristano Lagoon, Sardinia (8), Ansedonia Lagoon (8), Italy; Boka Kotorska Bay (4, 5, 7), Montenegro.

Type specimens: not mentioned in original description.

Material deposited: voucher material from the Júcar Estuary at the BMNH 2008.8.16.27–30 (4 specimens), IZAN M–2 (6 specimens) and ZNUMZ 1190065–1190067 (3 specimens).

Redescription

Based on 28 adult worms from the Júcar Estuary, Spain. Body fusiform with maximum width at level of gonads. One terminal and two bilateral cephalic lobes well developed. Cephalic glands posterolateral to pharynx. Testis elongate-ovate; copulatory organ C-shaped, long, thin, enters accessory piece proximally; base of copulatory organ with thick-walled heel; accessory piece claw-shaped, pincerlike; secondary lobe joins main lobe middistally by simple joint. Main lobe of accessory piece cylindrical, bowed, elongated, expanded proximally and distally; its distal portion dome-shaped hemispherical and proximal portion spatulate; secondary lobe massive, gutter-shaped, spatulate, shorter than main lobe, extending to level of tip of distal end of main lobe. Ovary U-shaped; oviduct, ootype and uterus not observed, Mehlis' glands conspicuous, occupying intervitellarial body space between prostatic reservoir and seminal receptacle. Vagina winding; vaginal aperture midventral; distal end of vagina funnel-shaped, thin-walled. Peduncle broad, short, subequal in length and width, tapered posteriorly. Haptor subhexagonal, wider than long. Pairs of anchors unequal in shape and size; outer and inner length of ventral anchor shorter than those of dorsal anchor; base of ventral anchor thicker than that of dorsal anchor. Both anchors with sharply bent blade, shaft about 1–1.5 times longer than point; the lat-

ter not reaching level of tip of inner root; inner root at least twice longer than outer root, the latter shorter than point, inner root and point subequal in length. Tip of outer root of ventral anchor not reaching level of that of inner root; tip of outer root of dorsal anchor may extend to level of that of inner root. Bars subequal in length. Ventral bar with knot on ventral shield, lateral flaps of shield contiguous to anterior protuberances, the latter extending to dorsal side of bar, where they are reduced to pair of small plates, anteromedian process on dorsal side between pair of small plates; V-shaped knot of ventral shield attached to Λ-shaped dorsal anteromedian process; pair of small plates occupies lateral position. Transverse dorsal bar yoke-shaped with rounded extremities and small posteromedian process.

Remarks

L. angustus resembles *L. szidati* and *L. confusus* in having the following suite of characters: a C-shaped long and thin copulatory organ, which enters the accessory piece proximally; the base of the copulatory organ with a thick-walled heel; a claw-shaped, pincerlike accessory piece with a proximally extended main lobe; dorsal and ventral pair of anchors dissimilar in a shape and size; ventral anchor with a sharply bent blade; shaft and point of the ventral anchor subequal in length; the ventral bar with median knot on the ventral shield and anteromedian process on the dorsal side; anterior protuberances reduced dorsally to two small plates, the latter occupying a lateral position in relation to the anteromedian process. *L. angustus* differs from both species by having: i) a massive gutter-shaped and spatulate secondary lobe of the accessory piece of the copulatory complex (vs. C-shaped in *L. szidati* and J-shaped in *L. confusus*); ii) a dome-shaped hemispherical expansion at the distal portion of the main lobe of the accessory piece (vs. tapered in *L. szidati* and cordate hemispherical in *L. confusus*); iii) smaller measurements for VAE and DAF. Moreover, *L. angustus* can also be distinguished from *L. szidati* by the relative position of the point and the inner root in the ventral anchor (the point not reaching level of tip of inner root vs. point extending to the level of the tip of the inner root in *L. szidati*), as well as by the smaller measurements for VAC and larger APMW; from *L. confusus* by shorter VBL and APSL.

The original description of *L. angustus* was based on 40 alive and 10 stained and mounted specimens, and included data of the genital and haptoral sclerotized structures and body measurements (Euzet, Suriano, 1977). Further studies gave additional information of the functional morphology of the male and female copulatory structures (Llewellyn, Anderson, 1984). The present redescription provides new information on the morphometry of the pharynx, testis, ovary haptor and ventral bar. Haptoral and genital sclerotized structures have been redrawn and measured for comparative purposes. The ranges of variation of the metric characters of the specimens examined herein broadly fall within those previously reported (Euzet, Suriano, 1977; Llewellyn, Anderson, 1984; Mariniello et al., 2004). As an exception, the length of the outer root of the ventral and dorsal anchors reported by Mariniello et al. (2004) is substantially longer than both those presented herein and those of the original description (Euzet Suriano, 1977).

Ligophorus imitans Euzet et Suriano, 1977
(fig. 12, *a-g*; table 8)

Records: 1. Euzet and Suriano (1977); 2. Euzet and Sanfilippo (1983); 3. Hassan et al. (1990); 4. Caltran et al. (1995 a); 5. Caltran et al. (1995 b); 6. D'Amelio et al. (1996); 7. Abu Samak (1997); 8. Abu Samak and Hassan (1998); 9. Abu Samak and Hassan (1999); 10. Merella and Garippa (2001); 11. Mariniello et al. (2004); 12. Present study.

Type host: *Lz. ramada* (1–12).

Type locality: Mediterranean Sea, Sète (1), France.

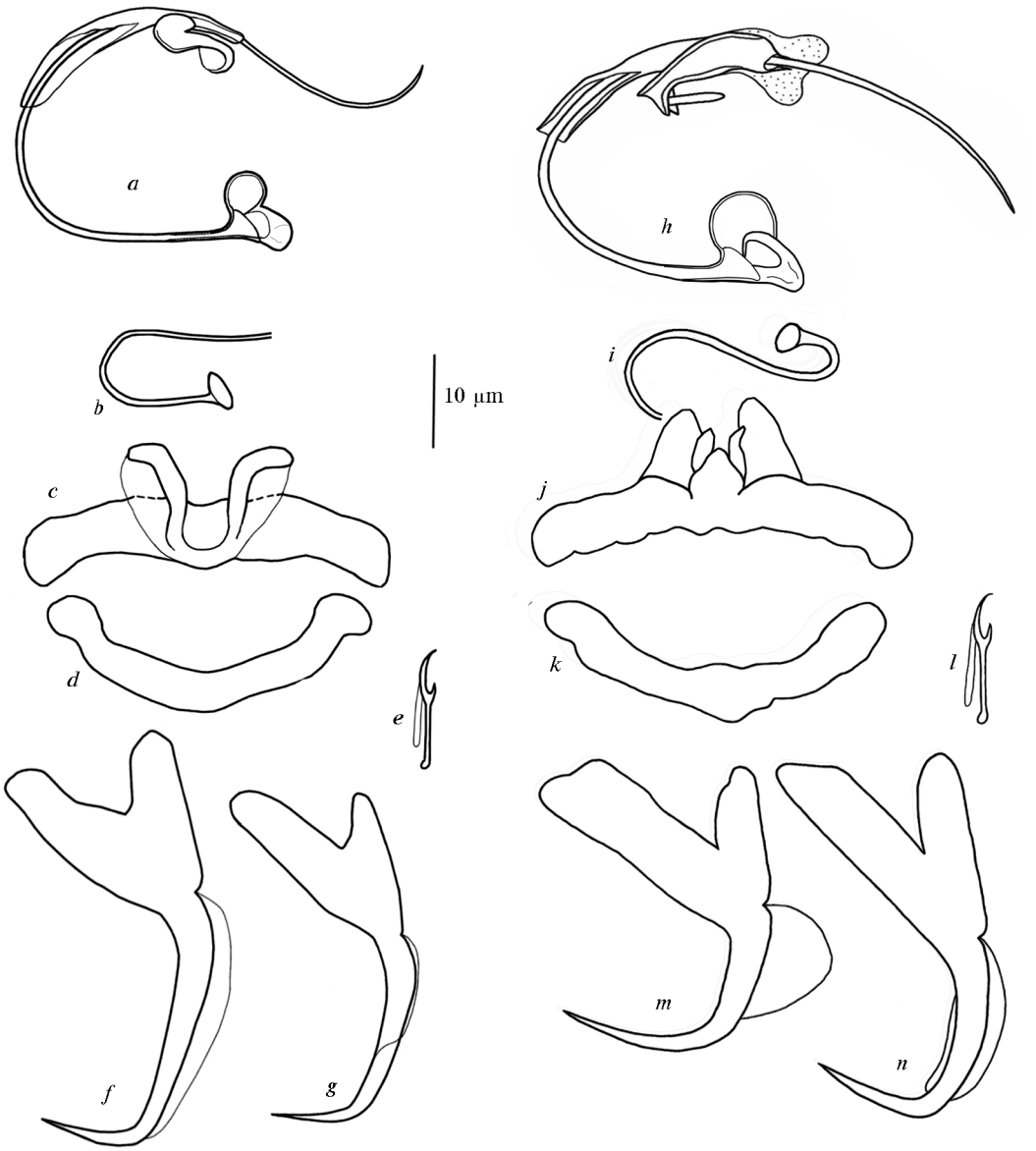

Fig. 12. Haptor and genital sclerotized structures of *Ligophorus imitans* Euzet et Suriano, 1977 (*a-g*) and *Ligophorus confusus* Euzet et Suriano, 1977 (*h-n*): *a*, *h* — male copulatory complex: copulatory organ and accessory piece; *b*, *i* — vagina; *c*, *j* — ventral bar; *d*, *k* — dorsal bar; *e*, *l* — hook; *f*, *m* — ventral anchor; *g*, *n* — dorsal anchor.

Рис. 12. Склеротизированные гапторальные и генитальные структуры *Ligophorus imitans* Euzet et Suriano, 1977 (*a-g*) и *Ligophorus confusus* Euzet et Suriano, 1977 (*h-n*): *a*, *h* — мужская копулятивная система: копулятивный орган и вспомогательный аппарат; *b*, *i* — вагина; *c*, *j* — вентральная пластинка; *d*, *k* — дорсальная пластинка; *e*, *l* — краевой крючок; *f*, *m* — вентральный срединный крючок; *g*, *n* — дорсальный срединный крючок.

Additional localities: Mediterranean Sea: Gulf of Santa Pola (12), Santa Pola Salt Marshes (12) Júcar Estuary (12), Gulf of Valencia (12), Ebro Delta (12), Spain; Thau Lagoon (2), Gulf of Lion (2), Vaccarès Lagoon (4, 5), France; Mistras Lagoon, Sardinia (10), Sabaudia Lagoon (6), Fusaro Lagoon, Naples (6), Lesina (15), Italy; Ras El Bar, Damietta (4, 7–9), Egypt.

Type specimens: not mentioned in original description.

Table 8. Metric characters of *L. imitans* and *L. confusus*
Таблица 8. Метрические характеристики *L. imitans* и *L. confusus*

Characters*	*Ligophorus imitans* ex *Liza ramada* from Mediterranean Sea, Gulf of Santa Pola, Spain				*Ligophorus confusus* ex *Liza ramada* from Mediterranean Sea, Ebro Delta, Spain			
	Mean	SD	Range	N	Mean	SD	Range	N
Body length	678	73.3	585–877	15	792	74.6	678–936	14
Body width	132	37.9	82–211	15	123	26.3	82–175	14
Pharynx length	26	2.8	22–30	10	28	4.4	20–33	11
Pharynx width	25	5.5	20–40	10	25	3.4	20–33	11
Testis length	46	7.4	33–65	25	59	10.7	35–75	13
Testis width	27	5.8	18–40	24	29	6.2	20–38	14
Ovary length	58	11.4	45–82	12	109	26.8	70–153	15
Ovary width	29	10.5	15–54	21	35	4.9	28–45	15
Haptor length	50	7.4	40–63	10	53	6.2	38–60	10
Haptor width	100	28.2	50–140	10	80	21.6	50–110	10
VAA	37	2.4	33–41	15	33	0.7	33–35	14
VAB	31	1.8	29–34	15	23	1.4	22–26	14
VAC	8	0.8	7–9	15	5	1.1	3–7	22
VAD	12	1.4	10–14	15	16	2.2	12–22	22
VAE	8	0.8	7–9	15	17	0.8	16–19	22
VAF	26	0.9	25–27	11	16	1.3	13–18	18
VAG	39	2.2	35–43	15	29	1.8	27–33	14
DAA	35	1.8	33–37	15	39	1.9	35–42	14
DAB	26	1.4	24–29	15	29	2.2	25–33	14
DAC	7	1.1	5–9	15	9	1.0	7–11	14
DAD	14	1.3	12–16	15	15	1.4	13–17	14
DAE	7	0.5	7–8	15	12	1.1	11–13	14
DAF	21	1.5	18–23	12	18	1.1	16–20	13
DAG	33	1.8	30–35	15	38	2.2	34–41	14
HTL	13	1.0	12–16	15	13	0.6	13–15	14
VBL	37	1.7	34–39	15	41	2.0	39–46	14
VBDP	5	0.8	6–12	10	5	0.5	4–5	10
DBL	32	1.5	29–35	15	38	1.8	35–42	14
APTL	24	2.3	21–28	14	31	2.8	26–35	14
APML	“	“	“	“	“	“	“	“
APMW	3	0.6	2–4	11	9	1.3	7–10	10
APSL	14	1.7	12–17	13	15	1.2	13–17	12
COL	90	11.7	66–105	14	86	5.2	79–98	14
COW	0.9	0.1	0.7–1	10	1	0.1	0.8–1	12
VL	46	5.3	35–53	10	35	3.7	29–39	12

* See Material and methods section for abbreviations of metric variables of sclerotized characters.

Material deposited: voucher material from the Gulf of Santa Pola at the BMNH 2008.8.16.31 (1 specimen), IZAN M–9 (2 specimens) and ZNUMZ 1190068–1190071 (8 specimens).

Redescription

Based on 25 adult worms from the Gulf of Santa Pola, Spain. Body fusiform with maximum width at level of gonads. One terminal and two bilateral cephalic lobes well developed. Cephalic glands posterolateral to pharynx. Testis shape varies from ovate to elongate-ovate; copulatory organ C-shaped, long, thin, enters accessory piece proximally; base of copulatory organ with thick-walled heel; accessory piece claw-shaped, pincerlike; secondary lobe joins main lobe middistally by simple joint. Main lobe of accessory piece cylindrical, bowed, elongate, extended proximally and narrowing distally; sec-

ondary lobe, bilobed forms gutter, V-shaped in cross section, extended distally, J-shaped in profile, shorter than main lobe, extending to level of distal tip of main lobe. Ovary U-shaped; oviduct, ootype and uterus not observed; Mehlis' glands conspicuous, formed by large round or square cells, occupying intervitellarial body space between prostatic reservoir and seminal receptacle. Vagina winding; vaginal aperture midventral; distal end of vagina funnel-shaped, thin-walled. Peduncle broad, short, subequal in length and width. Haptor subhexagonal, wider than long. Pairs of anchors subequal in shape and unequal in size; inner, main part, shaft and outer length of ventral anchor larger than those of dorsal anchor. Both anchors with sharply bent blade, shaft about 2.7 to 4 times longer than point, the latter not reaching level of tip of inner root, outer root and point shorter than inner root, outer root and point subequal in length. Tip of outer root of ventral anchor extending to or beyond level of that of inner root, tip of outer root of dorsal anchor may extend to level of that of inner root. Transverse ventral bar slightly longer than dorsal one. Ventral bar usually with thin, membranous knot on ventral shield, anterolateral flaps of the latter connect with pair of finger-like anterior protuberances, together forming V-shaped structure on dorsal side of bar; anteromedian process on dorsal side absent, instead median groove present, which is formed by rising protuberances; some specimens with posteromedian prolongation of shield extending beyond level of posterior end of bar. Dorsal bar yoke-shaped, small posteromedian process present or absent.

Remarks

This species differs from all other congeners in possessing a longer ventral than dorsal bar. All other species of *Ligophorus* have transverse bars subequal in length, except *L. hamulosus* and *L. rectus* sp. n., whose dorsal bar is longer than the ventral bar. *L. imitans* closely resembles *L. heteronchus* and *L. angustus* in the morphology of genital structures and further with *L. heteronchus* in the shape and size of both anchors. The differential diagnosis for these species is provided in Remarks for *L. heteronchus*. This species can easily be distinguished from *L. angustus* by its thin, distally narrowing main lobe of the accessory piece of the copulatory organ, absence of anteromedian process and the shape of both pairs of anchors, which is characterised by a short point, a slender base and a high range of ratio between shaft and point (2.7–4), whereas in the latter species the main lobe of the accessory piece of the copulatory organ is thick with a dome-shaped hemispherical expansion, anteromedian process absent, anchors with a long point, a massive base and the ratio between the shaft and the point in range of 1 to 1.5.

L. imitans resembles *L. acuminatus*, *L. minimus* and *L. parvicirrus* in the shape of the ventral and dorsal anchor, but differs from all these species in having finger-like anterior protuberances of the ventral bar reaching the dorsal side, rather than finger-like anterior protuberances situated ventrally, not reaching the level of the dorsal side of the ventral bar. Further, it differs from *L. acuminatus* in the larger APML; from *L. minimus* in the smaller DAA, DAB, DAF, DAG and larger VL; from *L. parvicirrus* in: i) a sclerotized vagina vs. a non sclerotized in the latter species; ii) smaller sizes for VAD, DAA, DAB, DAF, DAG, COW, and larger for VAF, APSL and COL.

Many taxonomic and ecological studies have focused on *L. imitans*, this probably being the most investigated species of *Ligophorus*. Euzet and Suriano (1977) provided an adequate description of the sclerotized structures of this species. Hassan et al. (1990) gave new information on the morphology of this species but the shape of the ovary was inaccurately reported. Abu Samak (1997) studied the morphology, development and hatching mechanism of the egg, and the anatomy of the oncomiracidium. She compared the morphology of the egg and its appendage between *L. imitans* and *L. parvicirrus*, and proposed that the interspecific variation for these traits could be used for species discrimination. The egg morphology was not studied herein because most of our worms lacked

eggs. Thus it seemed difficult to use egg characters for diagnostic purposes. Caltran et al. (1995 a, b) studied the morphological variability of the species in relation to natural populations and environment constraints. They showed that populations of *L. imitans* displayed large phenotypic plasticity along a continuum. The size of the haptoral sclerotized structures, according to their data, increases with host size, whereas the size of the genital sclerotized structures is independent of environmental variables. The present redescription provides new details of the structure of the accessory piece of the copulatory complex and the ventral bar, as well as new data on the shape and measurements of the ovary, pharynx, testis and haptor.

The metric characters of the specimens studied herein are closer to those reported by Euzet and Suriano (1977) than those by Hassan et al. (1990), Caltran et al. (1995 a) and Mariniello et al. (2004).

Ligophorus confusus Euzet et Suriano, 1977
(fig. 2, *a*, *d*; 12, *h-n*; table 8)

Records: 1. Euzet and Suriano (1977); 2. Euzet and Sanfilippo (1983); 3. Radujković and Euzet (1989); 4. D'Amelio et al. (1996); 5. Merella and Garippa (2001); 6. Radujković (2002); 7. Mariniello et al. (2004); 8. Oguz and Bray (2008) 9. Present study.

Type host: *Lz. ramada* (1–9).

Other hosts: *Lz. saliens* and *M. cephalus* (9).

Type locality: Mediterranean Sea, Sète (1), France.

Additional localities: Mediterranean Sea: Gulf of Santa Pola (9), Santa Pola Salt Marshes (9) Júcar Estuary (9), Gulf of Valencia (9), Ebro Delta (9), Spain; Thau Lagoon (2), France; Mistras Lagoon, Sardinia (5), Sabaudia Lagoon (4), Lesina (7), Italy; Boka Kotorska Bay (3, 6), Montenegro; Sea of Marmara, NW Anatolia (8), Turkey.

Type specimens: not mentioned in original description.

Material deposited: voucher material from the Ebro Delta at the BMNH 2008.8.16.32–38 (7 specimens), IZAN M–6 (2 specimens) and ZNUMZ 11900072–11900074 (5 specimens).

Redescription

Based on 14 adult worms from the Ebro Delta, Spain. Body fusiform with maximum width at level of gonads. One terminal and two bilateral cephalic lobes well developed. Cephalic glands posterolateral to pharynx. Testis elongated; copulatory organ C-shaped, long, thin, enters accessory piece proximally; base of copulatory organ with thick-walled heel; accessory piece claw-shaped, pincerlike, secondary lobe joins main lobe middistally by simple joint. Main lobe of accessory piece cylindrical, bowed, extended proximally, with complex structure in distal part; ventral side of the latter with cordate, hemispherical expansion, well stained by carmine or haematoxylin, dorsal side of distal part covered by secondary lobe; the latter J-shaped, shorter than main lobe, not reaching level of tip of distal end of main lobe. Ovary U-shaped; oviduct and ootype short, uterus elongated, Mehlis' glands conspicuous, comprising big square glandular cells, occupying intervitellarial body space between prostatic reservoir and seminal receptacle. Vagina winding; vaginal aperture midventral or dextroventral; distal end of vagina funnel-shaped, thin-walled. Peduncle broad, short, wider than long or length and width subequal. Haptor subhexagonal, wider than long. Pairs of anchors dissimilar in shape and size; inner, main part and outer length of ventral anchor shorter than those of dorsal anchor and opposite, point of ventral anchor longer. Ventral anchor with sharply bent blade at midpoint, elongated point subequal in length with shaft; point not reaching level of tip of inner root, outer root one half or less the length of inner root, tip of outer root may extend to level of that of inner root; point and inner root subequal in length, outer root one half or less

the length of point. Dorsal anchor with sharply bent blade, shaft 1.3–1.6 times longer than point, the latter not reaching level of tip of inner root, outer root shorter than point and one half or more the length of inner root, tip of outer root extending to or past level of that of inner root, the latter longer than point. Bars subequal in length. Ventral bar with knot on ventral shield, lateral flaps of shield contiguous to anterior protuberances, the latter extending to dorsal side of bar, where they are reduced to pair of small plates; anteromedian process on dorsal side between pair of small plates; ∩-shaped knot of ventral shield attached to Λ-shaped dorsal anteromedian process; pair of small plates occupies lateral position. Transverse dorsal bar yoke-shaped with slightly extending rounded extremities and small posteromedian process.

Remarks

L. confusus can be easily distinguished from all other species of *Ligophorus* by the unique morphology of the main lobe of the accessory piece of the male copulatory complex that exhibits a complex structure in the distal part, namely the ventral side of the distal part has a cordate, hemispherical expansion, which is well stained with carmine or haematoxylin, while the dorsal side is covered by the secondary lobe.

L. confusus is close to *L. angustus* and *L. szidati* in both the ventral and dorsal anchor/bar complexes and the proximal position of entrance of the copulatory organ into the accessory piece that is claw-shaped, pincerlike (see Remarks for *L. angustus* and *L. szidati* for differentiation between these three species).

The present redescription clarifies the structure of the accessory piece of the copulatory complex and the ventral bar, as well as providing new information on the shape of the body, ovary, testis, peduncle and haptor. All metric characters of the measured specimens (except that of the copulatory organ length) fall within the range of those shown in Euzet and Suriano (1977) and Mariniello et al. (2004). The length of the copulatory organ was slightly shorter in our specimens than that reported by Euzet and Suriano (1977).

Ligophorus parvicirrus Euzet et Sanfilippo, 1983
(fig. 2, *e*; 13, *a-f*; table 9)

Records: 1. Euzet and Sanfilippo (1983); 2. Hassan et al. (1990); 3. D'Amelio et al. (1996); 4. Abu Samak (1997); 5. Di Cave et al. (1997); 6. Abu Samak and Hassan (1998); 7. Abu Samak and Hassan (1999); 8. Mariniello et al. (2004); 9. Present study.

Type host: *Lz. ramada* (1–9).

Type locality: Mediterranean Sea, Gulf of Lion (1), France.

Additional localities: Mediterranean Sea: Gulf of Santa Pola (9), Júcar Estuary (9), Gulf of Valencia (9), Ebro Delta (9), Spain; Thau Lagoon (1), Vaccarès Lagoon, Camargue (1), France; Sabaudia Lagoon (3), Fusaro Lagoon, Naples (3), Lesina (8), Burano Lagoon (5), Italy; Ras El Bar, Damietta (2, 4, 6, 7), Egypt.

Type specimens: syntypes at NMNH (TJ 119 (129 TC MNHN), TJ 120 (130 TC MNHM) (1).

Material deposited: voucher material from the Gulf of Santa Pola at the BMNH 2008.8.16.39 (1 specimen), from the Ebro Delta at the IZAN M–16 (2 specimens) and ZNUMZ 11900079 (1 specimen).

Redescription

Based on 13 adult worms from the Gulf of Santa Pola and the Ebro Delta, Spain. Body fusiform with maximum width at level of gonads, some specimens with constriction at level of ovary. Two terminal and two bilateral cephalic lobes well developed. Cephalic glands lateral and posterolateral to pharynx. Testis shape varies from ovate to elongate-

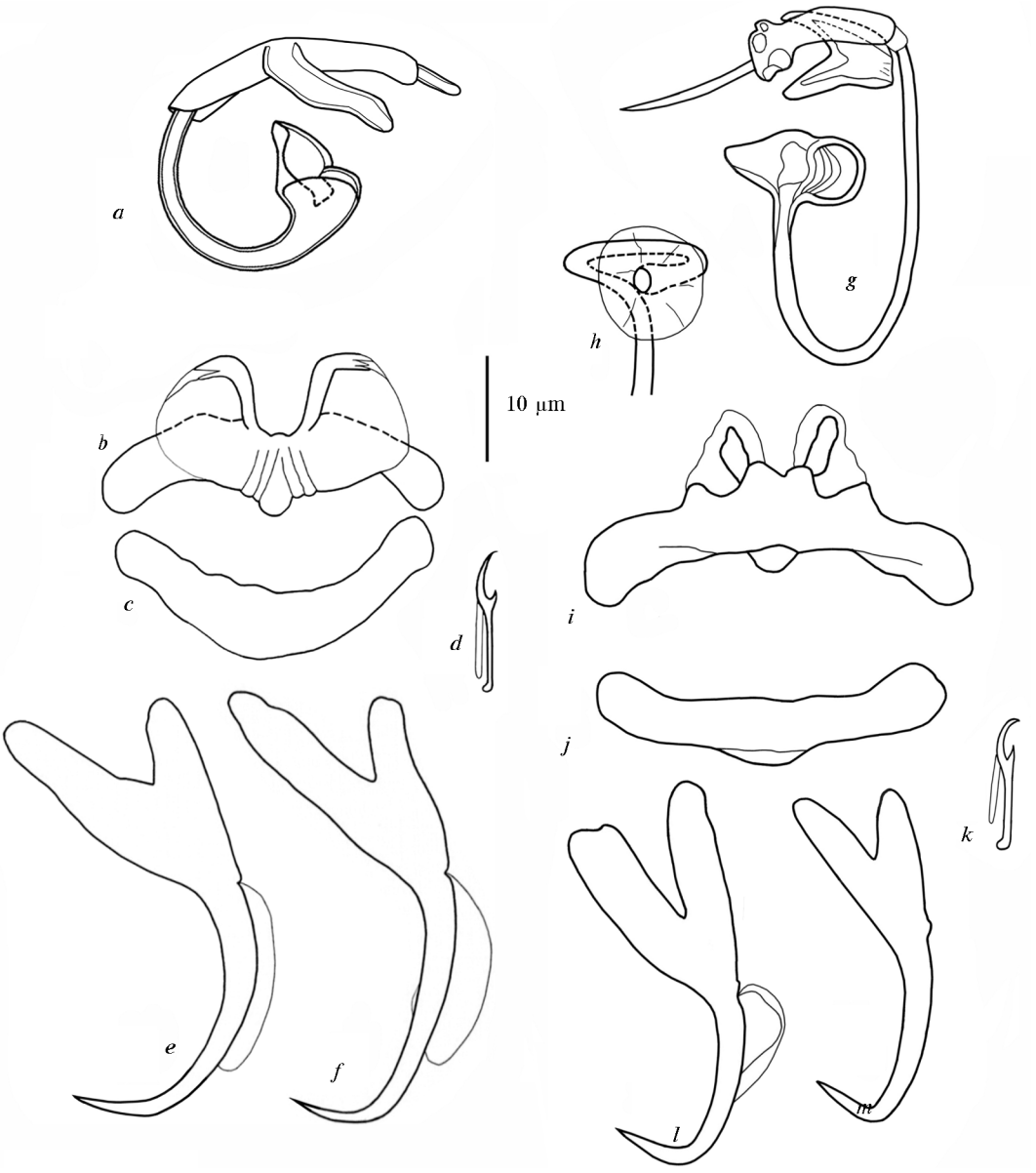

Fig. 13. Haptor and genital sclerotized structures of *Ligophorus parvicirrus* Euzet et Sanfilippo, 1983 (*a-f*) and *Ligophorus huitrempe* Fernández, 1987 (*g-m*): *a*, *g* — male copulatory complex: copulatory organ and accessory piece; *h* — vagina; *b*, *i* — ventral bar; *c, j* — dorsal bar; *d*, *k* — hook; *e*, *l* — ventral anchor; *f*, *m* — dorsal anchor.

Рис. 13. Склеротизированные гапторальные и генитальные структуры *Ligophorus parvicirrus* Euzet et Sanfilippo, 1983 (*a-f*) и *Ligophorus huitrempe* Fernández, 1987 (*g-m*): *a*, *g* — мужская копулятивная система: копулятивный орган и вспомогательный аппарат; *h* — вагина; *b*, *i* — вентральная пластинка; *c, j* — дорсальная пластинка; *d*, *k* — краевой крючок; *e*, *l* — вентральный срединный крючок; *f*, *m* — дорсальный срединный крючок.

ovate; copulatory organ C-shaped, thick, and relatively short, enters accessory piece proximally; base of copulatory organ with thin-walled heel; accessory piece claw-shaped, secondary lobe joins main lobe medially by simple joint. Main lobe of accessory piece cylindrical, slightly bowed, elongated; secondary lobe straight or slightly bowed, massive bare, shorter than main lobe, its distal end extending to or beyond level of tip of distal end of main lobe. Ovary U-shaped; oviduct, ootype and uterus not observed, Mehlis' glands con-

Table 9. Metric characters of *L. parvicirrus* and *L. huitrempe*
Таблица 9. Метрические характеристики *L. parvicirrus* и *L. huitrempe*

Characters*	*Ligophorus parvicirrus* ex *Liza ramada* from Mediterranean Sea, Gulf of Santa Pola and Ebro Delta, Spain				*Ligophorus huitrempe* ex *Mugil cephalus* from Southwest Pacific, Biobio River, Concepción, Chile			
	Mean	SD	Range	N	Mean	SD	Range	N
Body length	587	71.2	500–680	10	678	75.9	600–780	4
Body width	115	17.2	100–150	10	126	5.1	120–130	4
Pharynx length	24	4.3	20–30	12	30	3.6	25–33	4
Pharynx width	25	5.7	20–35	12	29	3.6	26–34	4
Testis length	58	11.6	40–75	10	57	4.9	51–62	4
Testis width	39	12.4	20–60	13	31	7.9	20–38	4
Ovary length	58	14.9	35–85	13	66	4.8	60–70	4
Ovary width	30	4.8	25–38	13	39	3.0	36–42	4
Haptor length	53	8.8	40–70	11	59	4.3	55–65	4
Haptor width	87	9.5	70–100	11	97	5.2	90–102	4
VAA	38	2.1	36–42	10	34	0.8	33–35	5
VAB	30	1.6	28–32	11	23	1	22–24	5
VAC	9	1.0	7–10	11	12	1.2	11–14	5
VAD	14	1.3	13–17	10	15	1.3	13–16	5
VAE	8	0.5	7–8	10	9	0.5	9–10	5
VAF	22	1.4	20–25	10	17	0.8	16–18	5
VAG	38	2.5	35–42	11	36	1.3	34–37	5
DAA	40	2.3	36–44	11	32	1.7	30–35	6
DAB	32	1.6	30–35	10	25	0.8	24–26	6
DAC	8	1.1	6–9	10	8	0.9	8–9	6
DAD	14	1.1	12–16	10	12	1.8	10–15	6
DAE	8	0.9	7–9	10	7	0.5	7–8	5
DAF	25	1.3	24–28	10	18	1.6	15–20	6
DAG	40	1.7	38–43	10	33	0.9	32–34	6
HTL	14	0.7	13–15	10	13	0.5	13–14	6
VBL	33	1.2	32–36	10	36	3.4	31–38	4
VBDP	7	1.3	5–10	10	6	0.5	6–7	4
DBL	33	1.2	31–34	10	35	1.0	34–36	4
APTL	28	3.2	25–33	10	18	2.0	16–20	3
APML	“	“	“	“	“	“	“	“
APMW	3	0.5	3–4	10	6	0.5	5–6	4
APSL	10	1.7	8–12	9	11	1.7	9–12	3
COL	36	3.1	32–42	10	76	4.6	71–80	3
COW	1.6	0.2	1.5–2	10	1	0	1	4
VL	–	–	–	–	39	6.2	35–48	4

* See Material and methods section for abbreviations of metric variables of sclerotized characters.

spicuous, comprising large round or square cells, occupying intervitellarial body space between prostatic reservoir and seminal receptacle; vagina non sclerotized; vaginal aperture midventral. Peduncle broad, short, subequal in length and width. Haptor subhexagonal, wider than long. Pairs of anchors subequal in shape and size; both anchors with sharply bent blade, shaft about 2.6–3.6 times longer than point, the latter not reaching level of tip of inner root, outer root shorter than inner root, tip of outer root extending to or past level of that of inner root; outer root and point subequal in length, inner root longer than point. Bars subequal in size; Ventral bar widest at middle and laterally tapered with knot on ventral shield, anterolateral flaps of the latter connect with pair of finger-like anterior protuberances, forming together V-shaped structure on dorsal side of bar; anteromedian process on dorsal side absent, instead median groove present, which is formed by rising protuberances; massive and lobular posteromedian process present on both sides. Transverse dorsal bar yoke-shaped, small posteromedian process present or absent.

Remarks

L. parvicirrus is easily distinguished from all other members of the genus through possessing the following suite of features: i) a thick and relatively short copulatory organ; ii) a thin-walled heel at the base of the copulatory organ; iii) a non sclerotized vagina; and iv) a massive and lobular posteromedian process on the ventral bar. *L. parvicirrus* shares the first feature with *L. hamulosus* and *L. simpliciformis*, and the first and third with *L. bykhowskyi, L. zhangi L. bipartitus* and *L. rectus* sp. n., but it clearly differs from these species by the claw-shaped accessory piece (rather than bowed with an expanded proximal end in *L. hamulosus*, *L. bykhowskyi* and *L. zhangi*; straight simple tube in *L. simpliciformis*; boomerang-shaped gutter in *L. bipartitus*; and rod-shaped in *L. rectus* sp. n.). Further, *L. parvicirrus* differs from *L. hamulosus*, *L. bipartitus* and *L. rectus* sp. n. in the subequal length of the ventral and dorsal bar (rather than the ventral bar being smaller than the dorsal one in these three species). Moreover, *L. parvicirrus* is distinguished from *L. hamulosus, L. simpliciformis*, *L. bykhowskyi, L. zhangi L. bipartitus* and *L. rectus* sp. n. by having larger measurements of VAF, DAF and smaller of VBL (except *L. hamulosus* and *L. rectus* sp. n.) and DBL (comparative data for *L. hamulosus* from Pan, 1999 and for *L. zhangi*, *L. simpliciformis* and *L. bipartitus* from Dmitrieva et al., 2012).

Previous descriptions of this species by Euzet and Sanfilippo (1983) and Hassan et al. (1990), while basically adequate, misdescribe the shape of the ovary and lack information on measurements of internal organs. The present redescription provides new information on the shape of the ovary and of the measurements of the testis, ovary, haptor and hooks, as well as clarifying the structure of the accessory piece of the copulatory complex and the ventral bar. The body and pharyngeal sizes of present specimens were smaller than those reported by Euzet and Sanfilippo (1983), whereas all other metric characters fall within the range or broadly overlap those in the original description.

Ligophorus huitrempe Fernández, 1987
(fig. 13, *g-m*; table 9)

Record: Fernández (1987).

Type host: *M. cephalus*.

Type locality: Southeast Pacific, Biobio River, Concepcion, Chile.

Type specimens: holotype and nine paratypes (MZUC 12676 and 12677–12685, respectively).

Redescription

Based on four paratypes (MZUC 12682–12685) from the Biobio River, Concepcion, Chile. Body fusiform, with maximum width at level of gonads. One terminal and two bilateral cephalic lobes well developed. Cephalic glands posterolateral to pharynx. Testis shape varies from ovate to elongate-ovate; copulatory organ C-shaped, long, thin, enters accessory piece proximally; base of copulatory organ with thick-walled heel; accessory piece cross-shaped. Main lobe of accessory piece cylindrical, bowed, elongated with heavily sclerotized bulb-shaped expansion at distal end. Secondary lobe V-shaped with equal branches, shorter than main lobe, not reaching level of distal tip of main lobe; upper branch of secondary lobe articulated with main one lengthways proximal part of the latter. Ovary U-shaped; oviduct ootype and uterus not observed, Mehlis' glands comprising several elongated glandular cells. Vagina winding or coiled; vaginal aperture dextroventral; distal end of vagina scyphoid and narrow. Peduncle elongated, longer than wide, tapering posteriorly. Haptor subhexagonal, wider than long. Pairs of anchors unequal in shape and size; inner and outer length, roots and point of ventral anchor longer than those of dorsal anchor. Ventral anchor with sharply bent blade, shaft about 1.7 to 1.9 times longer than point, the latter not reaching level of tip of inner root, outer root slightly shorter than inner root,

tip of outer root extending past level of that of inner root; both outer and inner root longer than point. Dorsal anchor with sharply bent blade, shaft about 2.3 to 2.6 times longer than point, the latter not reaching level of tip of inner root, outer root slightly shorter than inner one, tip of outer root extending to or past level of that of inner root; outer root and point subequal in length, inner root longer than point. Bars subequal in length. Ventral bar with V-shaped knot on ventral shield, anterolateral flaps of the latter connect with pair of finger-like anterior protuberances, forming together V-shaped structure on dorsal side of bar; anteromedian process on dorsal side absent, instead median groove present, which is formed by rising protuberance. Transverse dorsal bar yoke-shaped with enlarged, rounded extremities and posteromedian process.

Remarks

L. huitrempe is distinguished from all other species of the genus by the following combination of unique characters: i) the copulatory organ enters the accessory piece proximally, the latter with a heavily sclerotized bulb-shaped expansion at the distal end; ii) the cross-shaped accessory piece with a main lobe larger than the secondary one.

This species closely resembles *L. mugilinus L. mediterraneus* and *L. saladensis* based on the proximal position of the copulatory organ entrance at the cross-shaped accessory piece, which possesses a V-shaped secondary lobe articulated with the main lobe by a suture joint; a scyphoid and narrow distal end of the vagina; and the general shape of both the ventral and dorsal anchors. In addition to the unique suite of characters *L. huitrempe* clearly differs from *L. mugilinus* and *L. saladensis* by the absence of the anteromedian process of the ventral bar, as well as from all three species by smaller measurements for VAD, APL and APSL. *L. huitrempe* can be further distinguished from *L. mugilinus* by larger VAC and smaller DAA and DAD, and from *L. mediterraneus* by smaller DAE and VBDP.

Fernández's (1987) description of this species is basically adequate. However it has several inaccuracies: she reported four pairs of head organs, a subovate ovary and a claw-shaped accessory piece of the copulatory organ. Our re-examination of the paratypes revealed that *L. huitrempe* possesses three pairs of head organs, an elongated U-shaped ovary and a cross-shaped accessory piece. Further, the present redescription clarifies the shape of the ventral and dorsal bar.

Ligophorus chenzhenensis Hu et Li, 1992

Record: Hu and Li (1992).
Type host: *M. cephalus.*
Type locality: Yellow Sea, Chongming Island, Shanghai, China.
Type specimens: holotype at the DBSTU, accession number not available.

Remarks

Specimens of this species were not available for the present study. Hu and Li (1992) remarked that *L. chenzhenensis* "is similar to *L. imitans* Euzet et Suriano, 1977 and *L. vanbenedenii* (Parona, Perugia, 1890, Johnston, Tiegs, 1922) in the shape of opisthohaptor and supporting apparatus, but they are different in the size of middle anchors and ventral connective plate". But in light of the current evidence (Sarabeev, Balbuena, 2004 and the present study) this species closely resembles *L. pilengas* in the morphology of the accessory piece and haptoral sclerotized structures. Both species share the distal position of the copulatory organ entrances in the claw-shaped, pincerlike accessory piece, which is middistally bifurcated with the cylindrical, bowed, elongated main lobe and an elongated, bowed secondary lobe extending beyond the level of the distal tip of the main lobe; similar in shape and size pairs of anchors with sharply bent blade, shaft about 1.5 to

2.6 times longer than the point, the latter not reaching the level of the tip of the inner root, the outer root shorter than the inner root, the ventral bar with the widely separated protuberances and a poorly developed or inconspicuous anteromedian process. *L. chenzhenensis* differs from *L. pilengas* by possessing a straight main lobe with a sharply curved distal end of the accessory piece of the copulatory complex (bowed and slightly tapered distally in *L. pilengas*), and shorter copulatory organ length (Hu, Li, 1992). Details of the external and internal organ systems in this species are lacking, particularly on the ovary shape, the detailed morphology of the accessory piece and the ventral bar.

Ligophorus hamulosus Pan et Zhang, 1999

Record: 1. Pan (1999); 2. Zhang (2001).

Type host: *Liza macrolepis* (Smith) (1).

Type locality: South China Sea, Haikou (20°06' N, 110°38' E), Hainan Island (1, 2), China.

Type specimens: holotype at the DBHNU (HHK9605) (1).

Remarks

Unfortunately no types of *L. hamulosus* could be obtained to verify the original description of the sclerotized parts and define external and internal organ systems. The original description does not clearly show whether the accessory piece is bilobed. Nevertheless, the morphology of other sclerotized parts conforms to the generic diagnosis. Whereas Pan (1999) found this species to be similar to *L. imitans*, we have noted remarkable differences between them. *L. hamulosus* differs from *L. imitans* in the tubular, triangular accessory piece of the copulatory complex (rather than the claw-shaped in *L. imitans*), unequal sizes of anchor pairs and a presence of the anteromedian process on the ventral bar (Pan, 1999; Euzet, Suriano, 1977; present study). *L. hamulosus* is similar to *L. rectus* sp. n. in the morphology of genital and haptoral sclerotized structures. For the discrimination of these species see Remarks for *L. rectus* sp. n.

Ligophorus pilengas Sarabeev et Balbuena, 2004
(fig. 3, *a*; 4; 14, *a-g*; table 10)

Synonyms: *Ligophorus chabaudi* Euzet and Suriano, 1977, sensu Dmitrieva (1996), Maltsev and Miroshnichenko (1998), Domnich and Sarabeev (1999), Domnich and Sarabeev (2000 a), Domnich and Sarabeev (2000 b), Sarabeev (2000), Sarabeev and Domnich (2000), Gaevskaja et al. (2002); *Ligophorus gussevi* Miroshnichenko and Maltsev, 2004 (junior synonym synonymized by Balbuena et al., 2006).

Records: 1. Dmitrieva (1996); 2. Maltsev and Miroshnichenko (1998); 3. Domnich and Sarabeev (1999); 4. Domnich and Sarabeev (2000); 5. Sarabeev (2000); 6. Sarabeev and Domnich (2000); 7. Gaevskaja et al. (2002); 8. Sarabeev and Balbuena (2004); 9. Miroshnichenko and Maltsev (2004); 10. Dmitrieva et al. (2005); 11. Balbuena et al. (2006); 12. Dmitrieva et al. (2007); 13. Present study.

Type host: *Lz. haematocheilus* (1–9, 11–13).

Other hosts: *Lz. aurata* (10) and *Lz. saliens* (13).

Type locality: Azov Sea, Utlyukskiy Estuary (8), Ukraine.

Additional localities: Black Sea: Sozopol Bay (13), Bulgaria; Crimean coastal waters, Crimea (1, 7, 10, 12), Kerch Channel (2, 8, 9, 11, 13), Ukraine. Azov Sea: Sivash Lake (2, 9, 13), Utlyutsky Estuary (13), Molochny Estuary (2–6, 8–9, 11, 13), Obitochna Bay (13), Ukraine. Sea of Japan: Posiet Bay (13), Razdol'naya Delta (13), Artemovka Delta (13), Russia.

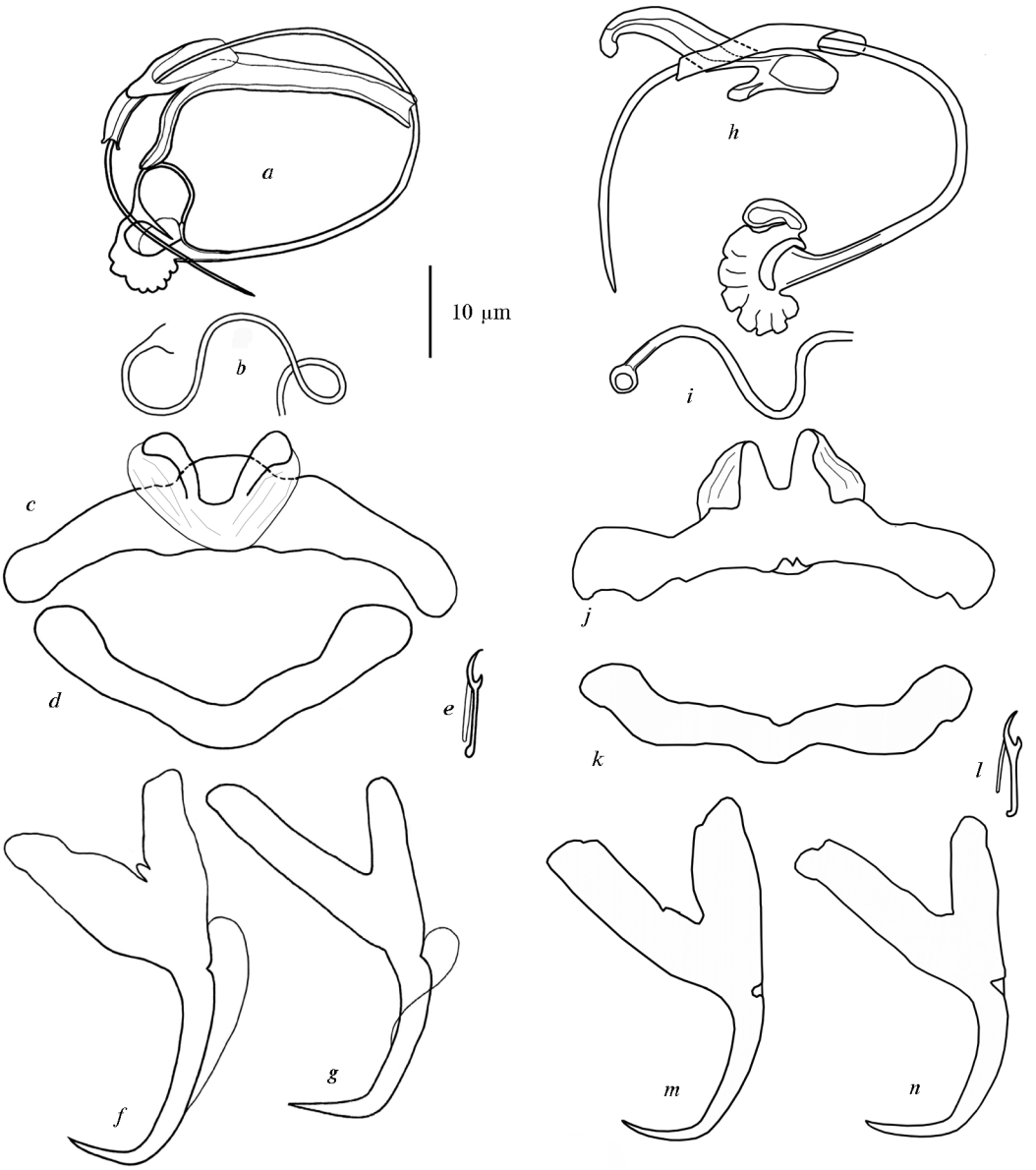

Fig. 14. Haptor and genital sclerotized structures of *Ligophorus pilengas* Sarabeev et Balbuena, 2004 (*a-g*) and *Ligophorus mediterraneus* Sarabeev, Balbuena et Euzet, 2005 (*h-n*): *a*, *h* — male copulatory complex: copulatory organ and accessory piece; *b*, *i* — vagina; *c*, *j* — ventral bar; *d*, *k* — dorsal bar; *e*, *l* — hook; *f*, *m* — ventral anchor; *g*, *n* — dorsal anchor.

Рис. 14. Склеротизированные гапторальные и генитальные структуры *Ligophorus pilengas* Sarabeev et Balbuena, 2004 (*a-g*) и *Ligophorus mediterraneus* Sarabeev, Balbuena et Euzet, 2005 (*h-n*): *a*, *h* — мужская копулятивная система: копулятивный орган и вспомогательный аппарат; *b*, *i* — вагина; *c*, *j* — вентральная пластинка; *d*, *k* — дорсальная пластинка; *e*, *l* — краевой крючок; *f*, *m* — вентральный срединный крючок; *g*, *n* — дорсальный срединный крючок.

Type specimens: holotype and 13 paratypes (BMNH 2003.8.4.1 and 2003.8.4.13–14 respectively) (9).

Material deposited: voucher material from the Posiet Bay at the BMNH 2008.8.16.40 (1 specimen), IZAN M–17 (1 specimen) and ZNUMZ 1190081 (1 specimen).

Table 10. Metric characters of *L. pilengas* and *L. mediterraneus*
Таблица 10. Метрические характеристики *L. pilengas* и *L. mediterraneus*

Characters*	*Ligophorus pilengas* ex *Liza haematocheilus* from Sea of Japan, Posiet Bay, Russia				*Ligophorus mediterraneus* ex *Mugil cephalus* from Black Sea, Kerch Channel, Ukraine			
	Mean	SD	Range	N	Mean	SD	Range	N
Body length	660	101	468–877	15	770	126.3	585–1,090	18
Body width	189	19	164–324	15	125	24.0	82–175	18
Pharynx length	27	2.8	23–32	15	36	6.6	25–50	33
Pharynx width	28	2.2	25–33	15	32	8.3	20–50	33
Testis length	52	4.5	45–60	15	55	14.6	35–90	33
Testis width	31	3.0	25–34	15	31	8.5	20–50	30
Ovary length	65	3.0	60–70	15	77	9.1	60–90	22
Ovary width	30	2.6	25–35	15	36	9.9	25–63	29
Haptor length	83	10.1	70–98	15	51	11.9	30–75	34
Haptor width	109	5.3	100–120	15	118	24.3	80–163	34
VAA	41	2.8	38–47	14	36	2.2	33–41	19
VAB	33	2.5	30–36	14	26	1.4	24–28	19
VAC	11	2.4	8–15	15	12	1.2	11–15	19
VAD	16	1.8	13–18	15	17	1.1	16–20	19
VAE	9	1.0	8–11	15	9	0.4	9–10	19
VAF	22	1.1	20–24	15	18	1.7	16–21	16
VAG	44	4.3	39–52	14	38	2.1	34–41	19
DAA	44	3.4	39–49	15	36	2.5	32–41	19
DAB	32	3.1	28–37	15	26	1.6	24–28	19
DAC	10	0.9	8–11	15	9	1.0	8–11	19
DAD	18	2.4	15–22	15	16	1.4	13–18	19
DAE	9	0.8	8–11	15	9	0.5	9–11	19
DAF	20	1.3	18–22	15	19	2.0	15–22	15
DAG	41	3.3	37–46	15	35	2.2	32–38	19
HTL	13	0.9	11–14	15	13	0.9	10–14	19
VBL	50	4.3	45–59	15	41	2.8	36–48	19
VBDP	14	1.3	11–17	15	10	1.9	8–14	11
DBL	45	3.5	42–54	15	40	3.1	34–48	19
APTL	40	7.2	35–52	15	35	3.3	30–42	21
APML	37	4.9	32–48	15	24	2.3	21–31	21
APMW	4	0.5	3–4	15	2.8	0.3	2–3	21
APSL	9	1.4	8–13	15	27	2.2	23–30	21
COL	93	11.6	76–111	15	90	8.8	79–120	23
COW	1	0.1	0,7–1	15	0.9	0.2	0.5–1	12
VL	46	2.7	43–52	15	41	5.3	36–55	12

* See Material and methods section for abbreviations of metric variables of sclerotized characters.

Redescription

Based on 15 adult worms from the Posiet Bay, Russia. Body fusiform. One terminal and two bilateral cephalic lobes well developed. Cephalic glands posterolateral to pharynx. Testis shape varies from ovate to elongate-ovate; copulatory organ C-shaped, long, thin, enters accessory piece through membranous opening in distal part of main lobe; base of copulatory organ with thick-walled heel; accessory piece claw-shaped, pincerlike, secondary lobe joins main one middistally by simple joint, distal end of secondary lobe slightly deflected or adjoining main one. Main lobe of accessory piece elongated, cylindrical with bowed and slightly tapered distal part, the latter with small terminal mouth; secondary lobe slightly tapered proximally, bowed, shorter than main lobe, extending beyond level of distal end of main lobe. Ovary U-shaped; oviduct and ootype not observed, uterus elongated, Mehlis' glands inconspicuous, occupying intervitellarial body space between pro-

static reservoir and seminal receptacle. Vagina winding or coiled; vaginal aperture mid-ventral; distal end of vagina funnel-shaped, thin-walled. Peduncle broad, short, subequal in length and width. Haptor subhexagonal, wider than long. Pairs of anchors subequal in shape and size; both anchors with sharply bent blade, shaft about 1.5 to 2.6 times longer than point, the latter not reaching level of tip of inner root; outer root and point subequal in length shorter than inner root. Tip of outer root of ventral anchor extending past level of that of inner root, tip of outer root of dorsal anchor varies in range from not reaching tip of inner root to extending its past level. Bars subequal in length; finger-like anterior protuberances of ventral bar situated ventrally, not reaching level of dorsal side of bar; ventral knot and dorsal anteromedian process present or absent; some specimens with posteromedian prolongation of shield extending beyond level of posterior end of bar. Transverse dorsal bar yoke-shaped, small posteromedian process present or absent.

Remarks

The species closely resembles *L. cephali* and *L. cheleus* in the distal position of the copulatory organ entrance in the accessory piece, which is claw-shaped with a cylindrical, distally tapered main lobe and in the shape of anchors. Additionally, *L. pilengas* resembles *L. cephali* in the morphology of the ventral bar, namely finger-like anterior protuberances situated ventrally, not reaching the level of the dorsal side of the bar; ventral knot present or absent. But *L. pilengas* differs from *L. cephali* by having: i) the same width for the proximal and middle region (before the bifurcation) of the main lobe of the accessory piece of copulatory complex (vs. expanded proximally in the latter species); ii) another position of the secondary lobe adjoining the main one (middistal vs. medial in *L. cephali*); iii) the shape of secondary lobe (bowed vs. winding in *L. cephali*); iv) a small, hill-shaped (vs. long, Λ-shaped in *L. cephali*) anteromedian process of the ventral bar (when present) and from *L. cheleus* in the morphology of the secondary lobe of the accessory piece (bowed and slightly tapered proximally vs. straight and expanded proximally in *L. cheleus*), the ventral bar (finger-like anterior protuberances situated ventrally, not reaching the level of the dorsal side of the bar; dorsal anteromedian process present or absent vs a finger-like anterior protuberances form together with a V-shaped structure on the dorsal side of the bar; the anteromedian process on the dorsal side always absent in *L. cheleus*) and larger measurements for VBDP.

The morphology of the haptoral sclerites and the general shape of the accessory piece of *L. pilengas* is similar to that of *L. llewellyni* and *L. triangularis* sp. n., in that all three occur sympatrically on *Lz. haematocheilus* in the NW Pacific region and the first two species in the Azov-Black Sea basin. Both species can be easily distinguished from *L. pilengas* by their characteristic funnel-shaped or triangular expansion of the distal part of the main lobe of the accessory piece, respectively. Further, *L. pilengas* differs from *L. llewellyni* by the shape of the secondary lobe and the position of its distal end in relation to the main lobe (bowed, with its distal end usually turning away from the main lobe vs. spoon-shaped with its distal end adjoining the distal end of the main lobe in *L. llewellyni*).

The synonymy of *L. gussevi* with *L. pilengas* proposed by Balbuena et al. (2006) is accepted herein. Differences in shape and measurements of sclerotized characters between the two forms seem to fall within the normal range of intraspecific variation.

Previous descriptions of *L. pilengas* by Sarabeev and Balbuena (2004) and Miroshnichenko and Maltsev (2004) do not give details of the morphology of the ovary, testis, haptor and peduncle of the worms. In addition, both descriptions do not provide full information on the morphological variability of the ventral bar. Further, Miroshnichenko and Maltsev (2004) depicted the distal end of the accessory piece with a hook-shaped end. We consider that the distal end of the main lobe of the accessory piece bears a small terminal mouth. Dmitrieva et al. (2007) provided new microphotographs, drawings and

measurements of *L. pilengas* from the Black/Azov Sea region that are adequate, but insufficient details were given regarding the exact morphology and the morphological variability of the ventral bar and as to the shape of ovary, testis, haptor and peduncle. The present redescription supplies such information and provides an original drawing and measurements of specimens of *L. pilengas* from the Sea of Japan for comparative purposes. The ranges of variation of all metric characters of the specimens examined fall within the range, or overlap widely, with those reported by Sarabeev and Balbuena (2004), Miroshnichenko and Maltsev (2004), Balbuena et al. (2006), Dmitrieva et al. (2007) except for the slightly smaller measurements of VAF, COL and VL than those provided by Miroshnichenko and Maltsev (2004). These differences in measurements seem to fall within the normal range of intraspecific variation. Comparison of the Pacific specimens with those from the Azov-Black Sea region has not revealed differences in either the shape or measurements.

The present record of *L. pilengas* is the first one from the native range of *Lz. haematocheilus*. All previous records of this parasite refer to the introduced area of its host (Dmitrieva, 1996; Maltsev, Miroshnichenko, 1998; Domnich, Sarabeev, 1999; Domnich, Sarabeev, 2000 a; Domnich, Sarabeev, 2000 b; Sarabeev, 2000; Sarabeev, Domnich, 2000; Gaevskaja et al., 2002; Miroshnichenko, Maltsev, 2004). *L. pilengas* seems to be oioxenic, since it has been recorded on other hosts only sporadically. Thus, we can establish that this species was introduced into the Azov-Black Sea region together with its type-host.

The synonymy of *L. vanbenedenii sensu* Gussev (1985) with *L. pilengas*, proposed by Sarabeev and Balbuena (2004), is not accepted herein. The specimen depicted (fig. 328 Б of Gussev, 1985) does not correspond to *L. vanbenedenii*, since the copulatory complex shows a claw-shaped and short accessory piece (rather than arrow-shaped and long in *L. vanbenedenii*). However, it also differs from *L. pilengas* because of the short, distally-tapered main lobe of the accessory piece of the copulatory complex (rather than long and tubular in *L. pilengas*). Furthermore, we have found on *Lz. haematocheilus* from the Sea of Japan several specimens similar to those of Gussev (1985). A description of a new species is proposed below to accommodate these specimens.

Ligophorus mediterraneus Sarabeev, Balbuena et Euzet, 2005
(fig. 3, *d*; 14, *h-n*; table 10)

Synonyms: *Ligophorus mugilinus* (Hargis, 1955) sensu Euzet and Suriano (1977), Mariniello et al. (2004), and Sarabeev and Balbuena (2004).

Records: 1. Euzet and Suriano (1977); 2. Miroshnichenko and Maltsev (1998); 3. Caillot et al. (1999); 4. Öztürk and Aydoğdu (2003); 5. Mariniello et al. (2004); 6. Sarabeev and Balbuena (2004); 7. Sarabeev et al. (2005); 8. Popjuk (2009); 9. Dmitrieva et al. (2009 a); 10. Present study.

Type host: *M. cephalus* (1–10).

Type locality: Mediterranean Sea, Gulf of Valencia (7, 10), Spain.

Additional localities: Mediterranean Sea: Gulf of Santa Pola (10), Santa Pola Salt Marshes (10), Júcar Estuary (10), Ebro Delta (10), Spain; Sète (1), Thau Lagoon (10), Biguglia Pond, Corsica (3), France; Cabras and Mistras Lagoon, Sardinia (9), Tarquinia Lagoon (5), Italy; Bayramdere Lagoon, Karacabey (4), Turkey. Black Sea: Sozopol Bay (10), Bulgaria; Sevastopol coastal waters (9), Balaklava Bay (10), Kerch Channel (2, 6–8, 10), Ukraine. Azov Sea, Utlyutsky Estuary (10), Ukraine.

Type specimens: holotype and five paratypes (BMNH 2005.1.7.1 and 2005.1.7.2–6, respectively) (7).

Material deposited: voucher material from the Kerch Channel at the IZAN M–1 (3 specimens) and ZNUMZ 11900082–11900083, 11900085–11900088 (12 specimens).

Redescription

Based on 37 adult worms from the Kerch Channel, Ukraine. Body fusiform with maximum width at level of gonads. One terminal and two bilateral cephalic lobes well developed. Cephalic glands posterolateral to pharynx. Testis varies from ovate to elongate-ovate; copulatory organ C-shaped, long, thin, enters accessory piece proximally; base of copulatory organ with thick-walled heel; accessory piece cross-shaped. Main lobe of accessory piece cylindrical, bowed, elongated, wider proximally than distally. Secondary lobe massive, V-shaped with very unequal length branches, subequal in length with main lobe, extending beyond distal end of main lobe; upper branch of secondary lobe hook-shaped, inwardly curved, narrowing distally (rarely straightened hook), about three times longer than lower one, articulated lengthways of distal part of main lobe. Ovary U-shaped; oviduct and ootype not observed, uterus elongated, Mehlis' glands conspicuous, occupying intervitellarial body space between prostatic reservoir and seminal receptacle. Vagina winding; vaginal aperture dextroventral; distal end of vagina scyphoid and narrow. Peduncle broad, slightly longer than wide or length and width subequal. Haptor subhexagonal, wider than long. Pairs of anchors subequal in shape and size; both with sharply bent blade, shaft about 1.5 to 2.4 times longer than point, the latter not reaching level of tip of inner root, outer root and point shorter than inner root; tip of outer root extending to or past level of that of inner root; outer root longer than point in ventral anchor and subequal in dorsal one. Bars subequal in length. Ventral bar with V-shaped knot on ventral shield, anterolateral flaps of the latter connect with pair of finger-like anterior protuberances, forming together V-shaped structure on dorsal side of bar; anteromedian process on dorsal side absent, instead median groove present, which is formed by rising protuberances; some specimens with massive shield, posteromedian margin of shield extending beyond posterior level of bar. Transverse dorsal bar yoke-shaped, posteromedian process absent.

Remarks

L. mediterraneus is very similar to *L. mugilinus* and *L. saladensis* in possessing a C-shaped, long and thin copulatory organ, which enters a cross-shaped accessory piece proximally; a massive secondary lobe, which is subequal in length with the main lobe, extending beyond the distal end of the main one; a longer upper branch of the secondary lobe than lower branch; a scyphoid and narrow distal end of the vagina; and similar anchor shape. However, the secondary lobe of the accessory piece of the male copulatory organ of *L. mediterraneus* has an inwardly curved upper branch, which is about three times longer than the lower branch, whereas in *L. mugilinus* and *L. saladensis* it has a straight or backwardly curved upper branch, which is only two times longer than the lower branch. In addition, the anteromedian process of the ventral bar of *L. mediterraneus* is absent, whereas it is present in *L. mugilinus* and *L. saladensis*. Further, *L. mediterraneus* differs from *L. mugilinus* by having a smaller ratio of VAD to VAC (Sarabeev et al., 2006).

The previous descriptions of this species by Euzet and Suriano (1977) and Sarabeev et al. (2005) lacked information on the detailed morphology of the ventral bar, as well as on the shape and measurements of ovary, testis, peduncle and haptor of this worm. The original measurements of this species were printed in an erratum (Sarabeev et al., 2006) correcting Table II of Sarabeev et al. (2005). Dmitrieva et al. (2009 a) redescribed this species and provided new features on the morphology of the ventral bar, that in general agree with those in the present study, except for the morphological differences between the dorsal and ventral side of the bar. Further, the general shape of the accessory piece and its lobes were misinterpreted in all previous descriptions. Description piece was described as claw-shaped with the small secondary lobe (Euzet, Suriano, 1977; Sarabeev et al., 2005; Dmitrieva et al., 2009 a). The ranges of variation of all metric characters of

the specimens examined fall within the range, or overlap widely, with those reported by Sarabeev et al. (2005) and Dmitrieva et al. (2007).

The present redescription redefines the shape of the ovary and the accessory piece of the copulatory complex and its lobes, as well as supplements the ventral shield with the knot on the ventral bar; the relative position of the roots and point of anchors reported previously.

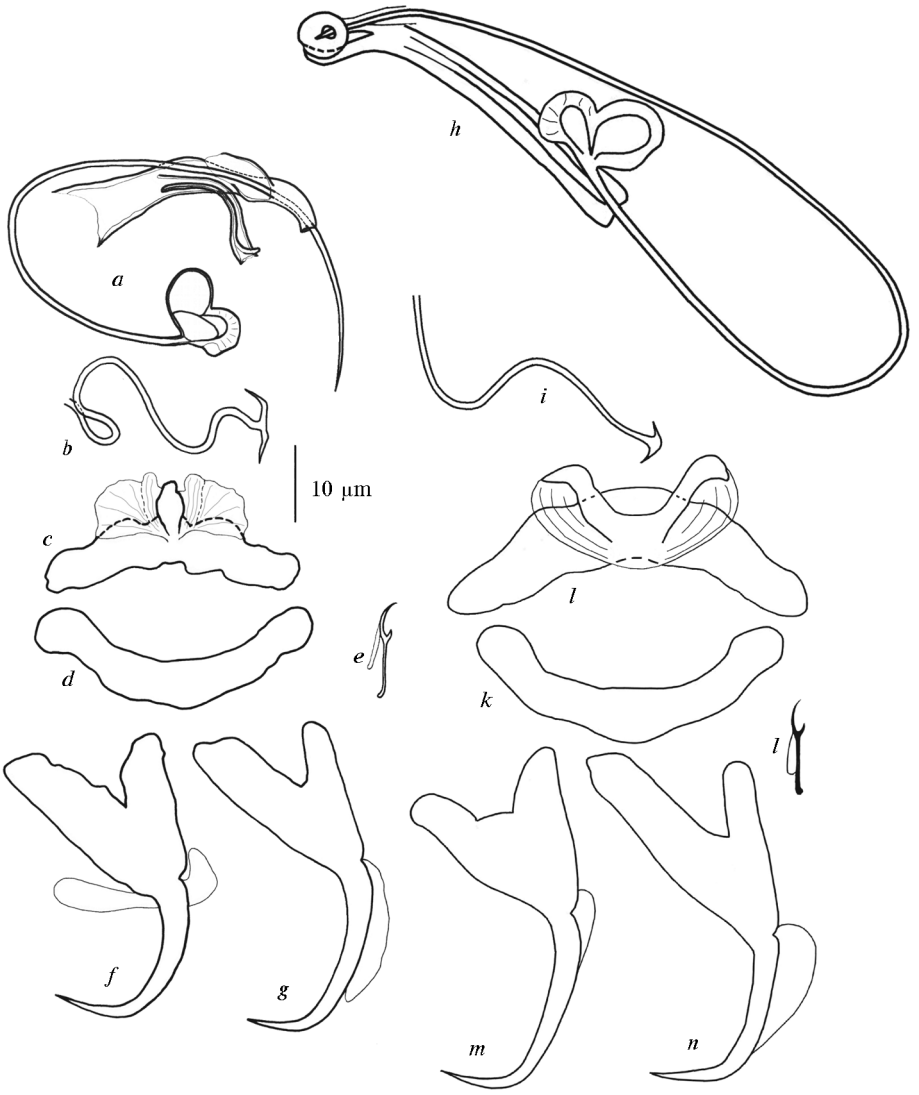

Fig. 15. Haptor and genital sclerotized structures of *Ligophorus cephali* Rubtsova, Balbuena, Sarabeev, Blasco-Costa and Euzet, 2006 (*a-g*) (after Rubtsova et al., 2006, *J. Parasitol.* 92: 486–495 reproduced with permission) and *Ligophorus llewellyni* Dmitrieva, Gerasev and Pron'kina, 2007 (*h-n*): *a*, *h* — male copulatory complex: copulatory organ and accessory piece; *b*, *i* — vagina; *c*, *j* — ventral bar; *d*, *k* — dorsal bar; *e*, *l* — hook; *f*, *m* — ventral anchor; *g*, *n* — dorsal anchor.

Рис. 15. Склеротизированные гапторальные и генитальные структуры *Ligophorus cephali* Rubtsova, Balbuena, Sarabeev, Blasco-Costa et Euzet, 2006 (*a-g*) (по: Rubtsova et al., 2006, *J. Parasitol.* 92: 486–495, воспроизведено с разрешения) и *Ligophorus llewellyni* Dmitrieva, Gerasev et Pron'kina, 2007 (*h-n*): *a*, *h* — мужская копулятивная система: копулятивный орган и вспомогательный аппарат; *b*, *i* — вагина; *c, j* — вентральная пластинка; *d*, *k* — дорсальная пластинка; *e*, *l* — краевой крючок; *f*, *m* — вентральный срединный крючок; *g*, *n* — дорсальный срединный крючок.

Table 11. Metric characters of *L. cephali* and *L. llewellyni*
Таблица 11. Метрические характеристики *L. cephali* и *L. llewellyni*

Characters*	*Ligophorus cephali* ex *Mugil cephalus* from Black Sea, Kerch Channel, Ukraine				*Ligophorus llewellyni* ex *Liza haematocheilus* from Sea of Japan, Artemovka and Razdol`naja Delta, Russia			
	Mean	SD	Range	N	Mean	SD	Range	N
Body length	928	173	526–1,251	57	665	148	420–930	13
Body width	127	47.5	70–351	57	95	15	60–120	13
Pharynx length	35	5.8	20–45	33	26	5.7	22–40	12
Pharynx width	36	9.1	22–55	33	25	6.5	15–40	12
Testis length	51	9.2	30–65	30	47	9.1	40–65	13
Testis width	28	8.0	15–45	29	23	4.1	20–35	13
Ovary length	71	12	50–90	13	52	7.4	40–65	13
Ovary width	35	9.1	20–50	23	27	3.3	20–32	13
Haptor length	62	10.1	45–75	15	62	13.5	40–80	14
Haptor width	131	18.2	90–163	15	100	16.7	80–130	13
VAA	38	2.1	34–43	57	43	2.4	39–48	14
VAB	28	1.5	23–32	57	34	3.1	29–39	14
VAC	12	2.5	8–18	57	11	1.1	9–13	13
VAD	18	1.8	15–24	57	15	2.6	11–20	13
VAE	10	1.0	8–12	57	10	1.1	8–12	23
VAF	20	1.1	17–21	10	24	2.0	21–28	24
VAG	40	2.9	34–48	57	45	3.3	40–51	13
DAA	39	1.9	35–43	57	44	3.8	38–50	14
DAB	30	1.7	23–34	57	32	2.5	27–35	14
DAC	10	1.2	8–12	57	10	0.9	8–11	15
DAD	17	1.4	14–20	57	21	3.5	16–28	12
DAE	9	0.8	7–11	57	9	1.1	8–11	21
DAF	23	1.5	20–24	10	22	1.8	19–24	21
DAG	40	1.5	36–43	57	41	2.6	35–45	14
HTL	14	0.8	12–15	57	12	1.2	10–13	13
VBL	40	4.8	34–51	57	49	3.0	43–53	13
VBDP	8	2.0	5–13	57	12	2.6	7–16	13
DBL	39	5.5	32–52	56	42	2.8	37–45	13
APTL	37	3.5	33–49	57	39	2.7	33–42	15
APML	“	“	“	“	“	“	“	“
APMW	3	0.3	3–4	16	5	1.6	4–8	13
APSL	14	3.5	11–20	18	9	1.3	7–11	11
COL	102	7.9	92–118	25	100	7.8	90–110	14
COW	0.9	0.1	0.7–1	16	1.0	0.1	0.7–1	13
VL	54	10.4	43–85	31	40	4.4	35–47	12

* See Material and methods section for abbreviations of metric variables of sclerotized characters.

Ligophorus cephali Rubtsova, Balbuena, Sarabeev, Blasco-Costa et Euzet, 2006 (fig. 5, *a, f*; 15, *a-g*; table 11)

Synonyms: *Ligophorus chabaudi* Euzet and Suriano, 1977 sensu Dmitrieva (1996); Dmitrieva and Gerasev (1996); Sarabeev and Balbuena (2004); Miroshnichenko and Maltsev (2004); Dmitrieva et al. (2007).

Records: 1. Dmitrieva (1996); 2. Dmitrieva and Gerasev (1996); 3. Sarabeev and Balbuena (2004); 4. Miroshnichenko and Maltsev (2004); 5. Rubtsova et al. (2006 a); 6. Dmitrieva et al. (2007); 7. Popjuk (2009); 8. Dmitrieva et al. (2009 b); 9. Present study.

Type host: *M. cephalus* (1–9).

Other host: *Lz. haematocheilus* (9).

Type localities: Mediterranean Sea: Gulf of Valencia (5, 9), Ebro Delta (5, 9), Spain. Black Sea, Kerch Channel (3–5, 7, 9), Ukraine.

Additional localities: Mediterranean Sea: Gulf of Santa Pola (9) Santa Pola Salt Marshes (9), Spain. Black Sea: Sozopol Bay (9), Bulgaria; Sevastopol coastal waters (1, 2, 6, 8), Balaklava Bay (9), Ukraine. Azov Sea: Utlyutsky Estuary (9), Ukraine.

Type specimens: 35 syntypes at the BMNH 2005.11.4.1–7.

Material deposited: voucher material ex *M. cephalus* from the Kerch Channel at the IZAN M–3.1 (2 specimens) and ZNUMZ 11900082–11900084, 11900086–11900088 (12 specimens).

Redescription

Based on 57 adult worms from the Kerch Channel, Ukraine. Body fusiform with maximum width at level of gonads. One terminal and two bilateral cephalic lobes well developed. Cephalic glands slightly posterior to pharynx. Testis shape varies from ovate to elongate-ovate; copulatory organ C-shaped, long, thin, enters accessory piece through membranous opening in distal part of main lobe; base of copulatory organ with thick-walled heel; accessory piece claw-shaped, pincerlike, secondary lobe joins main lobe medially by simple joint and turns away from the latter. Main lobe of accessory piece cylindrical, slightly bowed, expanded proximally and narrowed distally; secondary lobe winding, shorter than main lobe, may extend to level of tip of distal end of main one. Ovary U-shaped; oviduct and ootype short, uterus elongated, Mehlis' glands inconspicuous. Vagina coiled or winding tube; vaginal aperture dextroventral or midventral; distal end of vagina funnel-shaped, thin-walled. Peduncle broad, slightly longer than wide or length and width subequal. Haptor subhexagonal, wider than long. Pairs of anchors subequal in size and unequal in shape. Both anchors with sharply bent blade, point not reaching level of tip of inner root, the latter longer than outer root and point, outer root and point subequal in length; tip of outer root extending to or past level of that of inner root. Blade of ventral anchor with shaft 1.7 to 2.1 times longer than point, in dorsal anchor 2.3–3.2 times. Bars subequal in length. Ventral bar with Λ-shaped dorsal anteromedian process; knot on ventral shield usually absent; finger-like anterior protuberances situated ventrally, not reaching level of dorsal side of bar; some specimens with posteromedian prolongation of shield extending beyond level of posterior end of bar. Transverse dorsal bar yoke-shaped, posteromedian process small or absent.

Remarks

The species closely resembles *L. pilengas* and *L. cheleus* in the distal position of the copulatory organ entrance in the accessory piece, which is claw-shaped with a cylindrical, distally-tapered main lobe and in the general shape of both anchors (see Remarks for *L. pilengas* for detailed information on resemblance and discrimination among these species). *L. cephali* can be distinguished from *L. cheleus* by having: i) an expanded proximal end of the main lobe of the accessory piece (vs. the same width for the proximal and middle region (before the bifurcation) in *L. cheleus*); ii) a winding and slightly extended distally secondary lobe of the accessory piece (vs. straight and expanded proximally in *L. cheleus*); iii) the dorsal anteromedian process of the ventral bar (vs. absent in *L. cheleus*); iv) finger-like anterior protuberances not reaching the level of the dorsal side of the bar (vs. protuberances forming together a V-shaped structure on the dorsal side of the bar). A differential diagnosis for *L. cephali* and *L. chabaudi*, both species occurring sympatrically on *M. cephalus* in the Mediterranean, is provided in remarks for the latter species.

The original description of *L. cephali* by Rubtsova et al. (2006 a) provided sufficient information on morphological features of this species but lacked a verbal description and metric data of internal organs, details of the position of the vaginal aperture, the exact

structure of the accessory piece, the ventral bar, the blade of anchors, the relative position of the roots and point of anchors, which have been supplied herein. Dmitrieva et al., (2009 b) redescribed this species but with an error in the morphology of the copulatory complex (in spite of the correct drawing on fig. 1F of Dmitrieva et al., 2009 b) and the ventral bar (see explanations above in Description of taxonomically important characters and related terminology). The current redescription redefines the morphology of the copulatory complex and the ventral bar for this species. Reinvestigation of the copulatory organ and vagina length supports Dmitrieva et al., (2009 b) in that the lower limits for the copulatory organ and vagina are higher than originally described by Rubtsova et al. (2006 a) (table 11).

Ligophorus llewellyni Dmitrieva, Gerasev et Pron'kina, 2007
(fig. 3, *f*; 15, *h-n*; table 11)

Records: 1. Dmitrieva et al. (2007); 2. Present study.

Type host: *Lz. haematocheilus* (1).

Type locality: Black Sea, off Sevastopol, Crimean Peninsula (1).

Additional localities: Sea of Japan: Posiet Bay (2), Razdol'naya Delta (2), Artemovka Delta (2), Russia. Black Sea, Kerch Channel (2), Ukraine. Azov Sea, Sivash Lake, Ukraine (2).

Type specimens: holotype (IBSS 509), paratypes (IBSS 509/1–10; ZIN 8195–98; BMNH 2006.5.23.1) (1).

Material deposited: voucher material from the Artemovka Delta at the IZAN M–11 (3 specimens) and ZNUMZ 11900090 (2 specimens), from the Razdol'naya Delta at the ZNUMZ 11900093 and 11900098 (2 specimens).

Redescription

Based on 14 adult worms from the Artemovka Delta and the Razdol'naya Delta, Russia. Body fusiform with maximum width at level of gonads. One terminal and two bilateral cephalic lobes well developed. Cephalic glands posterolateral to pharynx. Testis elongate-ovate; copulatory organ C-shaped, long, thin, enters accessory piece through membranous opening in distal part of main lobe; base of copulatory organ with thick-walled heel; accessory piece claw-shaped, pincerlike, bifurcate middistally, secondary lobe articulated with main one by simple joint, runs along main one; distal ends of both main and secondary lobes adjoin. Main lobe of accessory piece tubular, slightly bowed or straight, its distal end with funnel-shaped expansion; secondary lobe spatulate, much shorter than main lobe, extending to level of tip of distal end of main lobe. Ovary U-shaped; oviduct, ootype and uterus not observed, Mehlis' glands occupying intervitellarial body space between prostatic reservoir and seminal receptacle. Vagina winding, vaginal aperture dextroventral or midventral; distal end of vagina funnel-shaped, thin-walled. Peduncle broad, short, subequal in length and width. Haptor subhexagonal, wider than long. Pairs of anchors subequal in shape and size; both anchors with sharply bent blade, shaft about 1.7 to 3 times longer than point, the latter not reaching level of tip of inner root, outer root and point shorter than inner root, outer root and point subequal in length. Tip of outer root of ventral anchor extending to or past level of that of inner root, tip of outer root of dorsal anchor may extend to level of tip of inner root. Bars subequal in length; finger-like anterior protuberances of ventral bar situated ventrally, not reaching level of dorsal side of bar; ventral knot and dorsal anteromedian process present or absent; some specimens with posteromedian prolongation of shield extending beyond level of posterior end of bar. Transverse dorsal bar yoke-shaped, small posteromedian process present or absent.

Remarks

L. llewellyni differs from all other species of *Ligophorus* in the unique morphology of the accessory piece of the copulatory complex, which is claw-shaped and pincerlike with a funnel-shaped expansion at the distal end of the main lobe perforated by a short tunnel with the opening at the level of the middistal bifurcation of the accessory piece serving the copulatory organ; a spatulate secondary lobe runs along the main one.

In the morphology of the haptoral sclerites and general shape of the accessory piece this species closely resembles *L. pilengas* and *L. triangularis* sp. n. But *L. llewellyni* can easily be distinguished from both species by the shape of the main lobe (with a funnel-shaped expansion in the distal end vs. tapered in *L. pilengas* or with a triangular expansion in *L. triangularis* sp. n.) and secondary one (spoon-shaped vs. bowed in both species) of the accessory piece and their relative position (alongside vs. usually turning away from the main lobe in *L. pilengas*).

The original description of *L. llewellyni* contained inaccuracies in the description of the accessory piece of the copulatory complex, lacking detail on the position of the copulatory organ entrance in the accessory piece, the secondary lobe, which was said to be absent, and the morphology of the distal end, described as "...composed of two well-defined half-rings..." (Dmitrieva et al., 2007), whereas it actually consists of a funnel-shaped expansion with an entire ring, as a terminal structure, and perforated by the tunnel that serves the copulatory organ. Further, the original description lacks information on the variability of the ventral bar structures and provided no data on the anteromedian process and knot. Measurements of the ventral and dorsal pair of anchors were proposed as the main differential character for discrimination from the closely related *L. pilengas*; they are larger in *L. llewellyni* for the dorsal anchor and smaller for the inner length of the proximal part and the length of the main part of the ventral anchor (Dmitrieva et al., 2007). However, according to table 2 of Dmitrieva et al. (2007), the variation ranges of all measurements of *L. llewellyni* except one either fell within or overlapped with those of *L. pilengas*. Only the inner length of the proximal part of the ventral anchor showed non-overlapping ranges (Dmitrieva et al., 2007). The present study sustains the shape and morphometric similarity of the ventral and dorsal anchor/bar complexes of *L. pilengas* and *L. llewellyni*. That seems to be natural because both species are oioxenous parasites of *Lz. haematocheilus*. It has been demonstrated on the phylogenetically close group of *Dactylogyrus* spp. that most specialist parasites have a similar attachment apparatus due to specialisation to their host but marked differences in the form of the copulatory organs (Jarkovsky et al., 2004).

L. llewellyni is the third *Ligophorus* species, which was recognized on *Lz. haematocheilus* after its introduction in the Azov-Black Sea (Dmitrieva et al., 2007 and the present study).

Ligophorus domnichi Rubtsova, Balbuena et Sarabeev, 2007
(fig. 5, *b*, *c*, *g*, *h*; 16, *a-g*)

Records: 1. Gussev (1955); 2. Rubtsova et al. (2007); 3. Dmotrieva et al. (2013); 4. Present study.

Type host: *M. cephalus* (1–4).

Type locality: Sea of Japan, Kiyevka Bay (2, 4), Russia.

Additional localities: Sea of Japan: Posiet Bay (3), Razdol'naya Delta (4), Tumen-Ula River (1, 3), Russia. Yellow Sea, Off Zhifu, Yantai, China (3). East China Sea, Off Ryukyu Islands (3).

Type specimens: four syntypes at the BMNH (2006.6.1.2) (2).

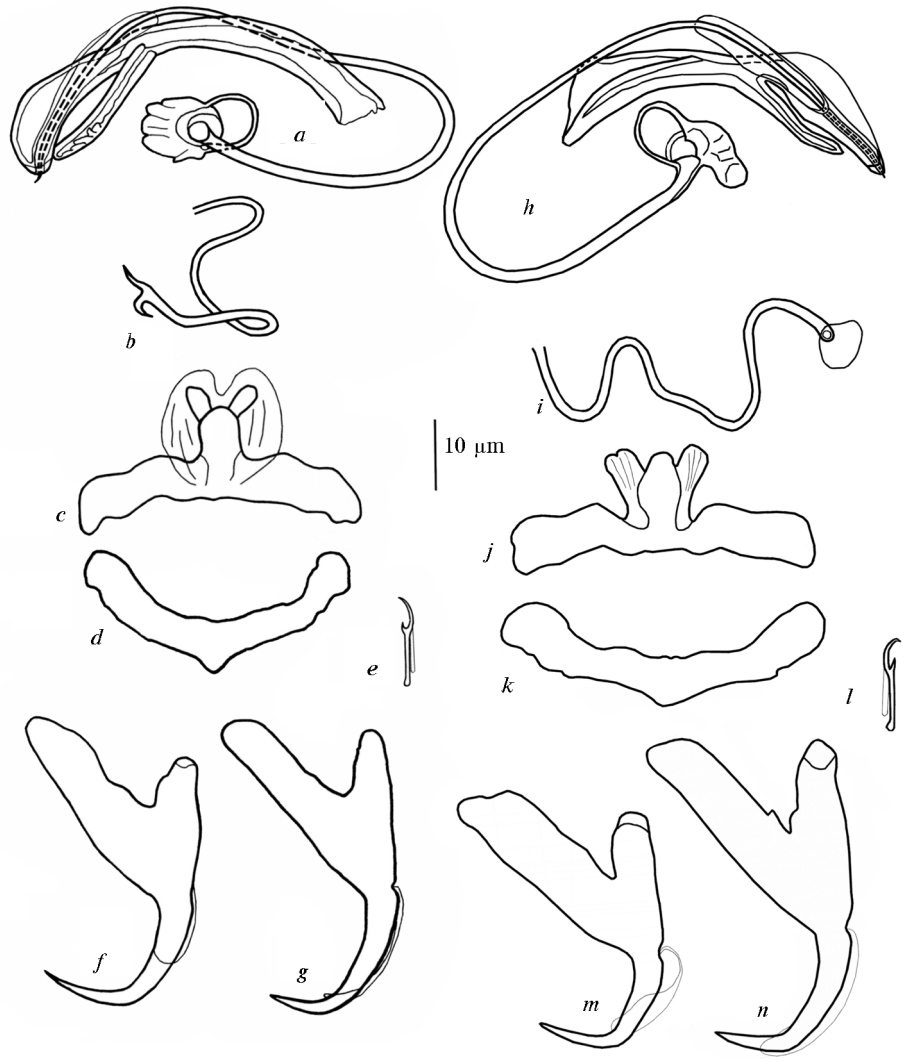

Fig. 16. Haptor and genital sclerotized structures of *Ligophorus domnichi* Rubtsova, Balbuena et Sarabeev, 2007 (*a-g*) and *Ligophorus pacificus* Rubtsova, Balbuena et Sarabeev, 2007 (*h-n*) (after Rubtsova et al., 2007, *J. Parasitol.* 93: 772–780 reproduced with permission): *a*, *h* — male copulatory complex: copulatory organ and accessory piece; *b*, *i* — vagina; *c*, *j* — ventral bar; *d*, *k* — dorsal bar; *e*, *l* — hook; *f*, *m* — ventral anchor; *g*, *n* — dorsal anchor.

Рис. 16. Склеротизированные гапторальные и генитальные структуры *Ligophorus domnichi* Rubtsova, Balbuena et Sarabeev, 2007 (*a-g*) и *Ligophorus pacificus* Rubtsova, Balbuena et Sarabeev, 2007 (*h-n*) (по: Rubtsova et al., 2007, *J. Parasitol.* 93: 772–780, воспроизведено с разрешения): *a*, *h* — мужская копулятивная система: копулятивный орган и вспомогательный аппарат; *b*, *i* — вагина; *c*, *j* — вентральная пластинка; *d*, *k* — дорсальная пластинка; *e*, *l* — краевой крючок; *f*, *m* — вентральный срединный крючок; *g*, *n* — дорсальный срединный крючок.

Remarks

The recent description of this species by Rubtsova et al. (2007), while sufficient, lacks a description of the ventral and dorsal side of the ventral bar, as well as information on the exact position of the vagina aperture, on the variability of the shape of blade and relative position of the roots and the point of anchors. The vaginal aperture opens dextroventrally or midventrally; both anchors with a sharply bent blade, the shaft of the ventral anchor 1.4 to 1.9 times longer than the point, in the dorsal one 1.9 to 2.6 times; the point does not reach the level of the tip of the inner root; the tip of the outer root of the

ventral anchor may extend to the level of the tip of the inner root; the tip of the outer root of the dorsal anchor extends to or past the level of that of the inner root; the ventral bar with the knot on the ventral shield, lateral flaps of the shield contiguous to the anterior protuberances, the latter extending to the dorsal side of the bar, where they are reduced to a pair of small plates; the anteromedian process on the dorsal side between a pair of small plates; a V or T-shaped knot of the ventral shield attached to a Λ-shaped dorsal anteromedian process; the pair of small plates occupies the anterolateral position in relation to the anteromedian process.

In addition to the differential diagnosis of *L. domnichi* provided by Rubtsova et al. (2007) the distinct morphology of the ventral bar of this species should be noted from the most resembling *L. chabaudi*, *L. pilengas*, *L. cephali*, *L. llewellyni* and *L. cheleus* (the anteromedian process and the pair of small plates on the dorsal side of the bar present vs. both structures absent in *L. chabaudi* and *L. cheleus* and the pair of small plates absent in *L. pilengas*, *L. cephali* and *L. llewellyni*).

Ligophorus pacificus Rubtsova, Balbuena et Sarabeev, 2007
(fig. 16, *h-n*)

Records: 1. Rubtsova et al. (2007); 2. Dmitrieva et al. (2013); 3. Present study.

Type host: *M. cephalus* (1–3).

Type localities: Sea of Japan: Kiyevka Bay (1, 3), Razdol'naya Delta (1, 3), Russia.

Additional localities: Sea of Japan: Posiet Bay (2), Tumen-Ula River (2), Russia. Yellow Sea, Off Zhifu, Yantai, China (2). Sunda Sea (2).

Type specimens: four syntypes at the BMNH (2006.6.1.3–4) (1).

Material deposited: two voucher specimens from the Kiyevka Bay at the IZAN M–15.

Remarks

The recent description of this species by Rubtsova et al. (2007), while sufficient, lacks a description of the ventral and dorsal side of the ventral bar, as well as information on the exact position of the vagina aperture, on the variability of the shape of blade and relative position of the roots and the point of anchors. The vaginal aperture opens dextroventrally or midventrally; both anchors with a sharply bent blade, the shaft of the ventral anchor 1.4 to 2.1 times longer than the point, in the dorsal one 1.8 to 2.6 times; the point does not reach the level of the tip of the inner root; the tip of the outer root of the ventral anchor may extend to the level of the tip of the inner root; the tip of the outer root of the dorsal anchor extends to or a past level of that of the inner root; the ventral bar with the knot on the ventral shield, lateral flaps of the shield contiguous to the anterior protuberances, the latter extending to the dorsal side of the bar, where they are reduced to the pair of small plates; the anteromedian process on the dorsal side between the pair of small plates; a V-shaped knot of the ventral shield attached to a Λ-shaped dorsal anteromedian process; the pair of small plates occupies the lateral or anterolateral position in a relation to the anteromedian process.

In addition to the differential diagnosis of *L. pacificus* provided by Rubtsova et al. (2007) the distinct morphology of the ventral bar of this species should be noted from the most resembling *L. chabaudi*, *L. pilengas*, *L. cephali*, *L. llewellyni* and *L. cheleus* (the anteromedian process and the pair of small plates on the dorsal side of the bar present vs. both structures absent in *L. chabaudi* and *L. cheleus* and the pair of small plates absent in *L. pilengas*, *L. cephali* and *L. llewellyni*).

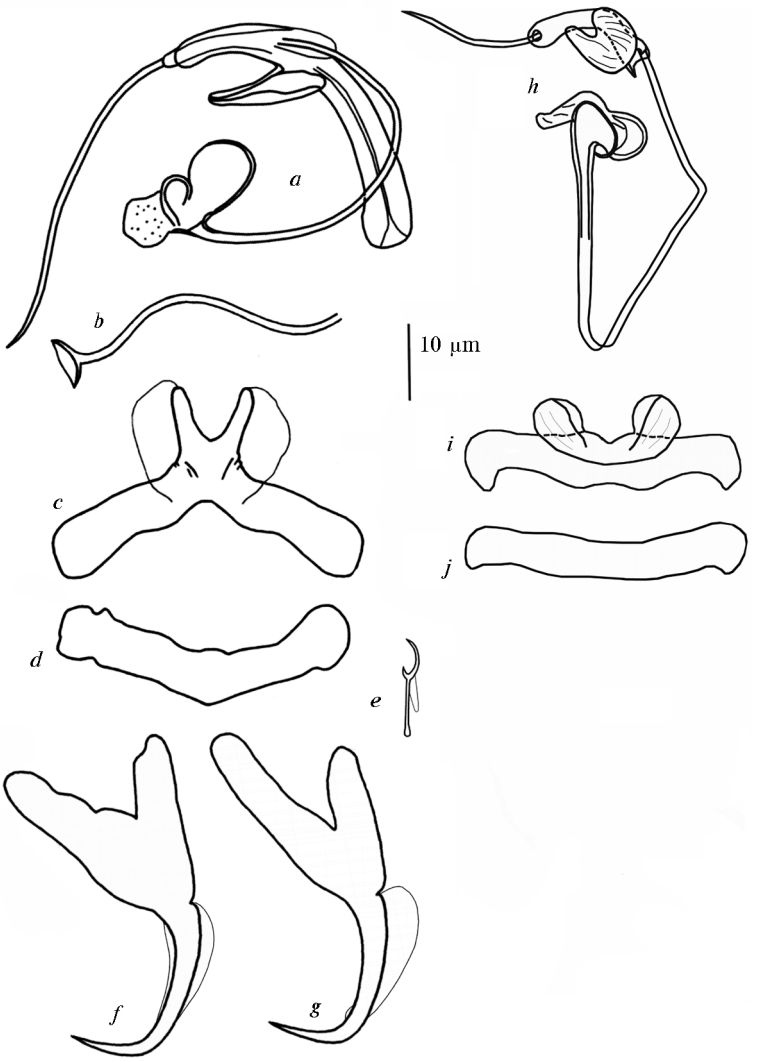

Fig. 17. Haptor and genital sclerotized structures of *Ligophorus cheleus* Rubtsova, Balbuena et Sarabeev, 2007 (*a-g*) (after Rubtsova et al., 2007, J. Parasitol. 93: 772–780 reproduced with permission) and *Ligophorus uruguayense* Failla Siquier et Ostrowski de Núñez, 2009 (*h-j*): *a*, *h* — male copulatory complex: copulatory organ and accessory piece; *b* — vagina; *c*, *i* — ventral bar; *d*, *j* — dorsal bar; *e* — hook; *f* — ventral anchor; *g* — dorsal anchor.

Рис. 17. Склеротизированные гапторальные и генитальные структуры *Ligophorus cheleus* Rubtsova, Balbuena et Sarabeev, 2007 (*a-g*) (по: Rubtsova et al., 2007, J. Parasitol. 93: 772–780, воспроизведено с разрешения) и *Ligophorus uruguayense* Failla Siquier et Ostrowski de Núñez, 2009 (*h-j*): *a*, *h* — мужская копулятивная система: копулятивный орган и вспомогательный аппарат; *b* — вагина; *c*, *i* — вентральная пластинка; *d*, *j* — дорсальная пластинка; *e* — краевой крючок; *f* — вентральный срединный крючок; *g* — дорсальный срединный крючок.

Ligophorus cheleus Rubtsova, Balbuena et Sarabeev, 2007
(fig. 3, *g*; 17, *a-g*)

Records: 1. Rubtsova et al. (2007); 2. Dmitrieva et al. (2013); 3. Present study.

Type host: *M. cephalus* (1–3).

Type localities: Sea of Japan: Kiyevka Bay (1, 3), Razdol'naya Delta (1, 3), Russia.

Additional localities: Sea of Japan: Posiet Bay (2), Tumen-Ula River (2), Russia. Yellow Sea, Off Zhifu, Yantai, China (2).

Type specimens: four syntypes at the BMNH (2006.6.1.1) (1).

Material deposited: two voucher specimens from the Kiyevka Bay at the IZAN M–5.1 and M–5.2.

Remarks

This species was recently adequately described by Rubtsova et al. (2007). However, their description lacks information on the ventral and dorsal side of the ventral bar, as well as on the variability of the shape of blade and relative position of the roots and the point of anchors. Both anchor with a sharply bent blade; the shaft of the ventral anchor 1.7 to 2.3 times longer than the point, in the dorsal one 2.2 to 3.1 times; the point does not reach the level of the tip of the inner root; the tip of the outer root of the ventral anchor extending to or beyond the level of that of the inner root; the tip of the outer root of the dorsal anchor not reaching the level of the tip of the inner root; the ventral bar with a V-shaped knot on the ventral shield, the anterolateral flaps of the latter connect with the pair of finger-like anterior protuberances, forming together a V-shaped structure on the dorsal side of the bar; the anteromedian process on dorsal side absent. A differential diagnosis of *L. cheleus* can be found in Rubtsova et al. (2007), supplementary information on the discrimination of this species can be found in the Remarks for *L. cephali*, *L. domnichi* and *L. pacificus* of the present study.

Ligophorus uruguayense Failla Siquier et Ostrowski de Núñez, 2009
(fig. 17, *h-j*; table 12)

Record: Failla Siquier and Ostrowski de Núñez (2009).

Type host: *Mugil platanus* Günther.

Type locality: Southwest Atlantic, Laguna de Rocha (34°33'–34°41' S and 54°02'–54°22' W), Rocha Department, Uruguay.

Additional locality: Southwest Atlantic, Las Flores (34°50' S and 55°25' W), Maldonado Department, Uruguay.

Type specimens: syntypes at the CHFC AP/12192–12196; and at the Helminthological Collection of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina, MACN–Pa 477/1–4.

Redescription

Based on two syntypes [CHFC AP/12196] from Las Flores, Maldonado Department, Uruguay. Description, figures and measurements are provided only for clearly visible structures. Body oblong with maximum width at level of gonads. Two terminal and bilateral cephalic lobes. Cephalic glands posterolateral to pharynx. Copulatory organ C-shaped, long, thin, its distal end enters accessory piece proximally; base of copulatory organ with thick-walled heel; accessory piece claw-shaped; secondary lobe articulated with main one lengthways along proximal part of the latter. Main lobe of accessory piece cylindrical, bowed, relatively short, slightly extended to both proximal and distal end, distal and with small bulb-shaped expansion. Secondary lobe V-shaped plate with equal branches, shorter than main lobe, not reaching level of distal tip of main lobe; secondary lobe articulates with main one along proximal part of the latter; both distal ends of V-shaped plate connected with main lobe. Ovary U-shaped; Mehlis' glands comprising several elongated glandular cells. Vagina winding; vaginal aperture dextroventral; distal end of vagina scyphoid and narrow. Peduncle short, wider than long, slightly tapering posteriorly. Haptor subhexagonal, wider than long. Pairs of anchors subequal in shape and size; both anchors with sharply bent blade, shaft about 1.7 and 1.9 times longer than point in ventral and dorsal anchor, respectively; point not reaching level of tip of inner root, outer root and

point shorter than inner root, outer root and point subequal in length. Inner root of ventral anchor with process. Bars subequal in length. Ventral bar with ventral shield culminating in widely-separated protuberances, the latter forming together V-shaped structure on dorsal side of bar; knot and anteromedian process absent. Transverse dorsal bar yoke-shaped with enlarged extremities.

Remarks

L. uruguayense differs from all other species of *Ligophorus* in the unique morphology of the accessory piece of the copulatory complex, which is claw-shaped with a V-shaped, plate-like secondary lobe that joins the main lobe along the proximal portion. This species closely resembles *L. huitrempe* in the morphology of the accessory piece and the ventral bar. Both species share a relatively short accessory piece (15–20 μm) (Failla Siquier, Ostrowski de Núñez, 2009 and the present study) with an expanded distal end

Table 12. Metric characters of *L. uruguayense* and *L. tainhae*
Таблица 12. Метрические характеристики *L. uruguayense* и *L. tainhae*

Characters*	*Ligophorus uruguayense* ex *Mugil platanus* from Southwest Atlantic, Las Flores, Department of Maldonado, Uruguay		*Ligophorus tainhae* ex *Mugil liza* *from Southwest Atlantic, Guandu River, State of Rio de Janeiro, Brazil*			
	Range	N	Mean	SD	Range	N
Body length	323, 468	2	789	40.2	743–815	3
Body width	114, 166	2	129	26.5	106–158	3
Pharynx length	28, 32	2	–	–	41	1
Pharynx width	21, 30	2	–	–	35	1
Ovary length	46, 66	2	98	15.0	81–108	3
Ovary width	26, 36	2	45	25.6	21–72	3
Haptor length	106	1	64	9.7	56–75	3
Haptor width	42	1	105	18.2	89–125	3
VAA	39	1	39	1.2	38–41	6
VAB	23	1	30	1.5	28–32	6
VAC	11	1	11	1.2	10–13	6
VAD	16	1	16	2.5	13–20	6
VAE	9	1	11	0.5	11–12	6
VAF	15	1	20	0.5	20–21	6
VAG	36	1	42	1.0	41–43	6
DAA	37	1	41	0.9	39–42	6
DAB	26	1	31	1.2	30–33	6
DAC	9	1	8	1.4	6–10	6
DAD	20	1	17	1.8	15–19	6
DAE	10, 11	2	10	0.5	10–11	6
DAF	19	1	23	1.2	22–25	6
DAG	35	1	39	1.0	38–41	6
HTL	12	2	12	1.0	11–13	4
VBL	36, 40	2	47	5.9	43–54	3
VBDP	6, 7	2	5	0	5	3
DBL	36, 41	2	40	4.2	37–45	3
APTL	15	1	82	3.8	79–86	3
APML	“	“	47	2.5	45–50	3
APMW	3	1	6	0.6	6–7	3
APSL	6	1	78	2.1	76–80	3
COL	88	1	116	4.2	113–121	3
COW	1	1	1	0	1	3
VL	–	–	41	0.7	40–41	2

* See Material and methods section for abbreviations of metric variables of sclerotized characters.

of the main lobe and a V-shaped secondary lobe. *L. uruguayense* can be easily distinguished from *L. huitrempe* by the claw-shaped accessory piece of the copulatory complex (vs. cross-shaped in *L. huitrempe*), slightly expanded (vs. massive in *L. huitrempe*) distal end of the main lobe of the accessory piece and by the smaller measurements for DAE, APMW and ratio of the shaft to the point of the dorsal anchor (1.9 vs. 2.3–2.9 in *L. huitrempe*).

We examined two specimens of the name-bearing types but they were not well enough positioned so as to ascertain the exact shape of the vagina and the ventral and dorsal pair of anchors. The original description of haptoral structures of this species is adequate (figure 4 A and B of Failla Siquier, Ostrowski de Núñez (2009)), but the variation range of many morphological characteristics is very wide. The lower limits are about two times (or more) smaller than the upper ones for the following measurements: VAC, VAD, DAC, DAD and DAE. This may indicate that the measured specimens represented more than one species. The drawing of the accessory piece (fig. 3, E of Failla Siquier, Ostrowski de Núñez, 2009) does not provide sufficient information for the discrimination of this species. Further, the ovary shape was depicted as pyriform, whereas it is U-shaped, and the vaginal sclerotized tube was described as a structure that possesses "transverse annulations at distal end" (Failla Siquier, Ostrowski de Núñez, 2009). Our observation reveals that this feature corresponds to a muscular or fibrous sheath surrounding the sclerotized vaginal tube. So the sclerotized vagina of *L. uruguayense* is similar to that of other species of *Ligophorus*, especially those with a scyphoid distal end.

The present redescription redefines the shape of the ovary, vagina and the accessory piece of the copulatory complex and its lobes, as well as supplying new information on the morphology of the ventral bar. The measurements of morphological characteristics of the type specimens studied herein fall within the range of those provided in the original description with the exception of the body length (323–468 vs. 650–2689 in Failla Siquier, Ostrowski de Núñez, 2009)

Ligophorus tainhae Abdallah, Azevedo et Luque, 2009 (fig. 18, *a-g*; table 12)

Record: Abdallah et al. (2009).

Type host: *Mugil liza* Valenciennes.

Type locality: Southwest Atlantic, Guandu River (22°48'32" S, 43°37'35" W), State of Rio de Janeiro, Brazil.

Type specimens: holotype at the CHIOC 37179 a, paratypes at the CHIOC 37179 b-d.

Voucher specimens: three specimens from the Guandu River at the UFRRJ LTG01–03

Redescription

Based on three adult worms from type-locality UFRRJ LTG01–03. Body fusiform with maximum width at level of gonads. One terminal and two bilateral cephalic lobes well developed. Testis elongate-ovate; copulatory organ C-shaped, long, thin, enters accessory piace distally; base of copulatory organ with thick-walled heel; accessory piece claw-shaped, pincerlike, secondary lobe joins main lobe proximally by simple joint, turning away from the latter, upwardly curved and crossing main lobe distally. Main lobe of accessory piece cylindrical, bowed, expanded medially and distally with median opening for copulatory organ entrance; secondary lobe narrowing medially and expanding to proximal and distal end, proximal part massive, shaft-shaped; secondary lobe longer than main one, not extending to level of tip at distal end of main lobe. Ovary U-shaped; oviduct, ootype, uterus, Mehlis' glands not observed. Vagina winding tube; vaginal aperture dextroventral; distal end of vagina funnel-shaped, thin-walled. Peduncle tapered distally, longer than wide. Haptor subhexagonal, wider than long. Pairs of anchors subequal in shape and

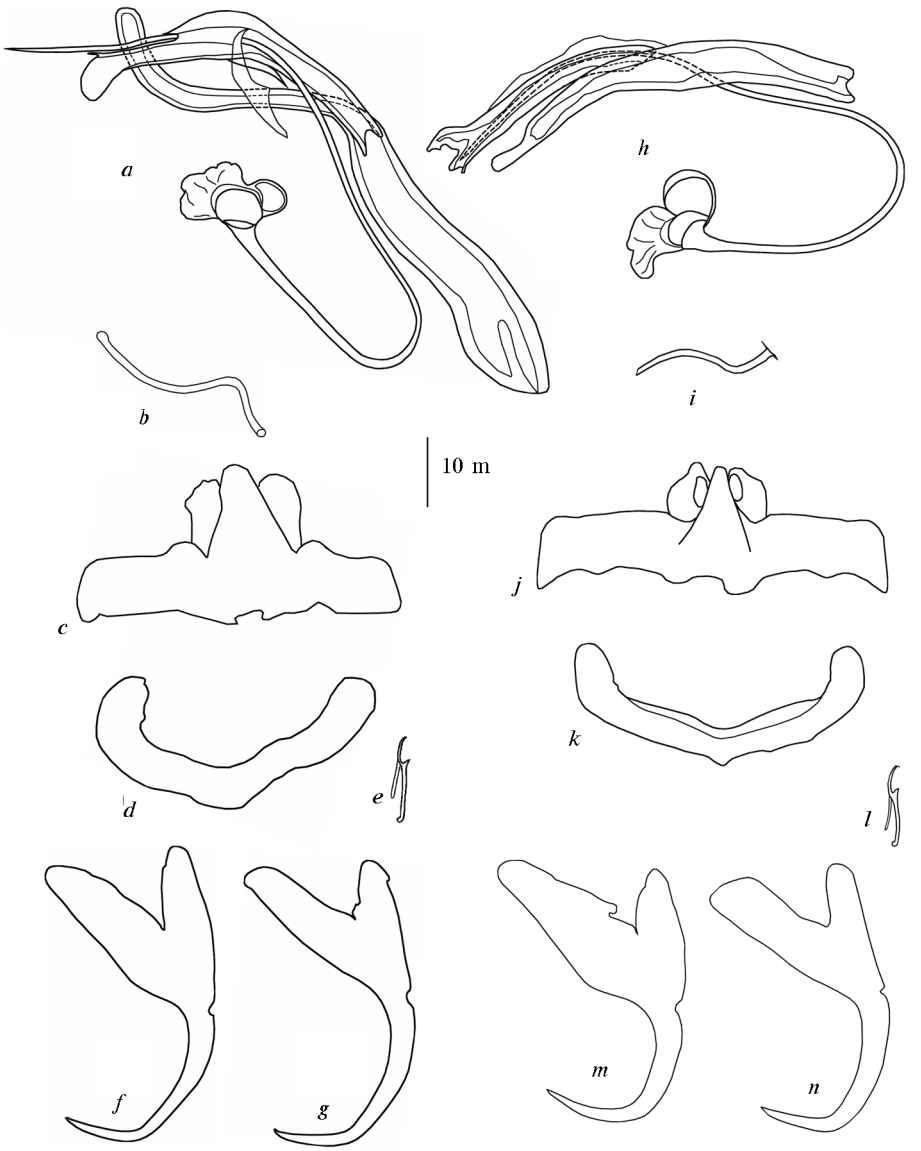

Fig. 18. Haptor and genital sclerotized structures of *Ligophorus tainhae* Abdallah, Azevedo et Luque, 2009 (*a-g*) and *Ligophorus brasiliensis* Abdallah, Azevedo et Luque, 2009 (*h-n*): *a*, *h* — male copulatory complex: copulatory organ and accessory piece; *b*, *i* — vagina; *c*, *j* — ventral bar; *d*, *k* — dorsal bar; *e*, *l* — hook; *f*, *m* — ventral anchor; *g*, *n* — dorsal anchor.

Рис. 18. Склеротизированные гаптоpальные и генитальные структуры *Ligophorus tainhae* Abdallah, Azevedo et Luque, 2009 (*a-g*) and *Ligophorus brasiliensis* Abdallah, Azevedo et Luque, 2009 (*h-n*): *a*, *h* — мужская копулятивная система: копулятивный орган и вспомогательный аппарат; *b*, *i* — вагина; *c*, *j* — вентральная пластинка; *d*, *k* — дорсальная пластинка; *e*, *l* — краевой крючок; *f*, *m* — вентральный срединный крючок; *g*, *n* — дорсальный срединный крючок.

size. Both anchors with sharply bent blade, point not reaching level of tip of inner root, the latter longer than outer root and point, length difference more apparent in dorsal anchor; tip of outer root extending to or past level of that of inner root. Blade of ventral anchor with shaft 1.7 to 1.9 times longer than point, in dorsal anchor 2–2.5 times. Bars subequal in length. Ventral bar with dorsal anteromedian process and ventral knot, both Λ-shaped; finger-like anterior protuberances reducing dorsally to the pair of small plates, the latter occupying lateral position in relation to anteromedian process. Transverse dorsal bar yoke-shaped, small posteromedian process present.

Remarks

L. tainhae differs from all other species of *Ligophorus* in the unique morphology of the accessory piece of the copulatory complex, as follows: i) a larger secondary lobe than main one of a claw-shaped accessory piece (except *L. brasiliensis*); ii) a main lobe expanding medially and distally with a median opening for the copulatory organ entrance; iii) a secondary lobe narrowing medially and expanding to proximal and distal end of secondary lobe, with a massive, shaft-shaped proximal part. Further, it was pointed out that this species has the largest accessory piece of the male copulatory complex (Abdallah et al., 2009). The species closely resembles *L. brasiliensis*. Both species share a claw-shaped accessory piece of the copulatory complex with a larger secondary lobe than main one and similar morphology of the ventral bar, which possesses a massive anteromedian process and protuberances reaching the level of the dorsal side of the bar. In addition to the above-listed unique characteristics *L. tainhae* can be distinguished from *L. brasiliensis* by the absence of the process of the inner root in the ventral anchor (vs. present in *L. brasiliensis*), a larger ratio of shaft to point of dorsal anchor and measurements for DAB and APML, and smaller DAC, DAE and VL.

The original description of *L. tainhae* while adequate, did not agree with the present study in the range of some metric characters. Namely, Abdallah et al. (2009) reported larger measurements for VAB, VAF, DAF, HTL, DBL, COL with smaller ones for VL. The present redescription clarifies the morphology of the accessory piece of the copulatory complex and the ventral bar and redefines the range of measurements for the mentioned characters.

Ligophorus brasiliensis Abdallah, Azevedo et Luque, 2009
(fig. 18, *h-n*; table 13)

Record: Abdallah et al. (2009).

Type host: *M. liza*.

Type locality: Southwest Atlantic, Guandu River (22°48'32" S, 43°37'35" W), State of Rio de Janeiro, Brazil.

Type specimens: holotype at the CHIOC 37180 a, paratypes at the CHIOC 37180 b-d.

Voucher specimens: three specimens from the Guandu River at the UFRRJ LBG01–03

Redescription

Based on three adult worms from type-locality UFRRJ LBG01–03. Body fusiform with maximum width at level of gonads. One terminal and two bilateral cephalic lobes well developed. Cephalic glands posterior to pharynx. Copulatory organ C-shaped, long, thin, enters accessory piece medially; base of copulatory organ with thick-walled heel; accessory piece claw-shaped, pincerlike, secondary lobe joins main lobe proximally by simple joint, parallel to the latter. Main lobe cylindrical, with distal spine-shaped expansion, slightly bowed with proximal opening for copulatory organ entrance; secondary lobe expanded medially and narrowing at proximal and distal end, in the latter end tapered up to point; secondary lobe longer than main one, may extend to level of tip of distal end of main one. Ovary U-shaped; oviduct, ootype, uterus, Mehlis' glands not observed. Vagina winding tube; vaginal aperture dextroventral; distal end of vagina funnel-shaped, thin-walled. Peduncle broad, slightly longer than wide or long and width subequal. Haptor subhexagonal, wider than long. Pairs of anchors slightly unequal in shape and size. Ventral anchor with sharply bent blade, shaft 1.1 to 1.7 times longer than point, point not reaching level of tip of inner root, the latter longer than outer root and point, outer root shorter than point; tip of outer root not extending to level of that of inner root; inner root with process, reaching to outer root in one specimen. Dorsal anchor with sharply bent blade, shaft 1.7 to 1.8 times longer than point, point not reaching level of tip of inner

Table 13. Metric characters of *L. brasiliensis*, *L. saladensis* and *L. abditus*
Таблица 13. Метрические характеристики *L. brasiliensis*, *L. saladensis* и *L. abditus*

Characters*	*Ligophorus brasiliensis* ex *Mugil liza* from Southwest Atlantic, Guandu River, State of Rio de Janeiro, Brazil				*Ligophorus saladensis* ex *Mugil platanus* from Southwest Atlantic, Samborombyn Bay, Buenos Aires, Argentina	*Ligophorus abditus* ex *Mugil cephalus* from Sea of Japan: Kiyevka Bay, Russia			
	Mean	SD	Range	N	N=1	Mean	SD	Range	N
Body length	625	7.1	620, 630	2	660	677	156	450–900	12
Body width	135	12	126, 143	2	180	87	22	70–150	12
Pharynx length	–	–	60	1	46	34	4.6	25–40	10
Pharynx width	–	–	56	1	43	33	6.8	22–4	10
Testis length	–	–	–	–	–	48	7	40–55	7
Testis width	–	–	–	–	–	25	5.2	20–35	7
Ovary length	–	–	70	1	91	53	5.7	45–60	7
Ovary width	–	–	29	1	57	34	6.9	25–45	7
Haptor length	–	–	63	1	54	60	7.4	50–70	10
Haptor width	–	–	103	1	100	98	17.1	70–120	10
VAA	42	0.6	41–42	3	36	41	3.0	35–45	14
VAB	–	–	27, 28	2	26	29	2.7	23–33	14
VAC	–	–	8	2	12	10	1.5	7–12	14
VAD	20	1.2	19–21	3	16	20	1.4	17–22	14
VAE	13	1.8	11–15	4	9	10	1.0	9–12	14
VAF	18	1.5	17–20	3	18	20	1.2	19–23	14
VAG			35, 36	2	38	39	3.7	32–43	14
DAA	39	1	38–40	3	31	44	3.4	37–48	13
DAB	29	0.6	28–29	3	24	31	3.4	25–35	12
DAC	10	2	8–12	3	9	11	1.1	9–12	12
DAD	16	0	16	3	12	21	2.1	18–24	12
DAE	12	0	12	3	9	9	1.3	7–11	13
DAF	21	1	20–22	3	16	22	2.1	18–25	13
DAG	39	1.5	38–41	3	32	42	3.1	37–46	12
HTL	–	–	12	2	11	13	1.0	12–14	13
VBL	–	–	47, 48	2	38	42	3.2	35–46	14
VBDP	–	–	4.5, 6	2	6	10	1.4	8–12	13
DBL	–	–	43, 44	2	35	41	2.8	34–44	14
APTL	50	9.3	44–61	3	22	46	2.6	42–50	14
APML	25	4.4	22–30	3	19	“	“	“	“
APMW	4	0.6	4–5	3	4	8	1.2	7–10	13
APSL	46	6.4	42–53	3	21	11	1.3	9–13	12
COL	109	4.4	104–112	3	95	105	11.0	90–120	14
COW	1	0	1	3	1	1	0.1	0.7–1	10
VL	–	–	54, 55	2	55	46	6.4	42–60	6

* See Material and methods section for abbreviations of metric variables of sclerotized characters.

root, the latter longer than outer root and point, outer root and point subequal; tip of outer root extending to or past level of that of inner root. Bars subequal in length. Ventral bar with dorsal anteromedian process and ventral knot, both Λ-shaped; finger-like anterior protuberances reduced dorsally to the pair of small plates, the latter occupies lateral position in relation to anteromedian process. Transverse dorsal bar yoke-shaped, small posteromedian process present.

Remarks

L. brasiliensis can be easily distinguished from other species of *Ligophorus* by: i) a distal spine-shaped expansion of the main lobe of the accessory piece of the copulatory complex; ii) a larger secondary lobe than the main one of a claw-shaped acces-

sory piece. The second and third features are shared with *L. tainhae*. A differential diagnosis from this species is provided in Remarks for *L. tainhae*.

The present study provides details on the morphology of the accessory piece of the male complex organ and clarifies the shape of its lobes. In contrast with the original description (Abdallah et al., 2009) no terminal bifurcation of the secondary lobe was observed and a distal spine-shaped expansion of the main lobe is revealed by the present study. Further, metric features for VAA, VAB, VAD, DAB, DAD, DAF, HTL, VBL, DBL and VL in the original description were smaller and beyond the range of those obtained in the present study.

Ligophorus guanduensis Abdallah, Azevedo et Luque, 2009

Record: Abdallah et al. (2009).

Type host: *M. liza*.

Type locality: Southwest Atlantic, Guandu River (22°48'32" S, 43°37'35" W), State of Rio de Janeiro, Brazil.

Type specimens: holotype at the CHIOC 37181 a, paratypes at the CHIOC 37181b-d.

Remarks

Unfortunately no types of *L. guanduensis* could be obtained to verify the original description. The morphology of the main and secondary lobe of the accessory piece is not clearly defined in the original description. But, based on microphotographs presented by Abdallah et al. (2009, fig. 4 A) it seems that the accessory piece of the copulatory complex is similar to that of *L. tainhae* and *L. brasiliensis*. We assume that the male copulatory complex of *L. guanduensis* possesses a claw-shaped accessory piece, a larger secondary lobe than main one and a distal entrance of the copulatory organ in the accessory piece. This species differs from both *L. tainhae* and *L. brasiliensis* in the position of the distal tip of the secondary lobe of the accessory piece, which extends beyond the level of the distal end of the main lobe (vs. crossing or not reaching the distal end of the main lobe in *L. tainhae* and *L. brasiliensis*, respectively). In addition, *L. guanduensis* can be distinguished from *L. tainhae* by the smaller accessory piece of the copulatory complex and from *L. brasiliensis* by the absence of a distal spine-shaped expansion of the main lobe of the accessory piece, as well as by larger measurements for VAC.

Ligophorus lizae Abdallah, Azevedo et Luque, 2009

Record: Abdallah et al. (2009).

Type host: *M. liza*.

Type locality: Southwest Atlantic, Guandu River (22°48'32" S, 43°37'35" W), State of Rio de Janeiro, Brazil.

Type specimens: holotype at the CHIOC 37178 a, paratypes at the CHIOC 37178 b.

Remarks

Specimens of this species were not available for the present study. The original description and drawing of the accessory piece of the copulatory complex did not include the middistal expansion of the main lobe that is visible on the microphotograph (Abdallah et al., 2009, fig. 4 D). In addition, it is difficult to define the exact position of the copulatory organ entrance in the accessory piece because the drawing and microphotograph of the copulatory complex do not agree with each other (compare figures 5 A and 4 D of Abdallah et al., 2009). According to the drawing, it enters the accessory piece proxi-

mally and passes inside the main lobe (figure 5 A of Abdallah et al., 2009), while the microphotograph suggests that a certain part of the copulatory organ is located under the accessory piece and enters through its distal part (fig. 4 D of Abdallah et al., 2009). Based on the microphotograph of the copulatory complex, *L. lizae* is characterized by a claw-shaped duck-billed accessory piece (the main lobe with middistal and distal expansion, the latter partially covers secondary lobe). This shape of the accessory piece of the copulatory complex is unique and clearly distinguishes *L. lizae* from other species of *Ligophorus*.

Ligophorus saladensis Marcotegui et Martorelli, 2009
(fig. 19, *a-g*; table 13)

Record: Marcotegui and Martorelli (2009).

Type host: *M. platanus*.

Type locality: Southwest Atlantic, Samborombón Bay, between Punta Piedras (32°57' S; 57°08' W) and Punta Rasa (36°18' S; 56°48' W), Buenos Aires, Argentina.

Type specimens: holotype at the MLP 5933, paratypes at the MLP 5934.

Redescription

Based on single paratype MLP 5934. Body fusiform with maximum width at level of gonads. One terminal and two bilateral cephalic lobes well developed. Cephalic glands posterolateral to pharynx. Testis ovate; copulatory organ C-shaped, long, thin, enters accessory piece proximally; base of copulatory organ with thick-walled heel; accessory piece cross-shaped. Main lobe of accessory piece bowed, elongated, cylindrical, with dilated distal end. Secondary lobe massive, trident-shaped with unequal branches, subequal in length with main lobe, extending beyond distal end of main lobe; medial branch of secondary lobe of accessory piece the smallest one, upper branch about two times longer than lower one, straight, articulated with main lobe by suture joint. Ovary U-shaped; oviduct, ootype and uterus not observed, Mehlis' glands conspicuous, comprising elongated glandular cells, occupying space between prostatic reservoir and seminal receptacle. Vagina winding; vaginal aperture dextroventral; distal end of vagina scyphoid and narrow. Peduncle broad, short, wider than long, tapering posteriorly. Haptor subhexagonal, wider than long. Pairs of anchors subequal in shape, ventral anchor longer than dorsal anchor. Both anchors with sharply bent blade, shaft 2 or 1.8 times longer than point in ventral and dorsal anchor, respectively, point not reaching level of tip of inner root, outer root shorter than inner root. Tip of outer root of ventral anchor not reaching level of that of inner root; inner root longer than point and outer root. Tip of outer root of dorsal anchor extending to or past level of that of inner root; inner root longer than point and outer root, the latter two equal in length. Bars equal in length. Ventral bar with Λ-shaped dorsal anteromedian process; knot on ventral shield not observed; finger-like anterior protuberances situated ventrally, not reaching level of dorsal side of bar. Transverse dorsal bar yoke-shaped with enlarged and rounded extremities, posteromedian process poorly developed or absent.

Remarks

L. saladensis differs from all species of *Ligophorus* in the unique morphology of the secondary lobe of the accessory piece of the copulatory complex, which is trident-shaped with a large upper part. This species is very similar to *L. mugilinus* and *L. mediterraneus* in the shape of the accessory piece and the distal end of the vagina. For discrimination of these three species see Remarks for *L. mugilinus* and *L. mediterraneus*.

The present redescription redefines the shape of the accessory piece of the copulatory complex and its lobes, as well as clarifying the morphology of the ventral bar. In the original description, accessory piece was described as claw-shaped with a small secondary lobe, while it is cross-shaped with a cylindrical main lobe and a massive, trident-shaped secondary lobe. The distal end of the vagina, described as funnel-shaped, is, according to the present re-examination, scyphoid. All metric characters of the examined specimens fall within the range of those reported by Marcotegui and Martorelli (2009), except for the length of the ventral bar and the accessory piece of the copulatory complex.

Ligophorus abditus Dmitrieva, Gerasev et Gibson, 2013
(fig. 19, *h-n*; table 13)

Records: 1. Dmitrieva et al. (2013); 2. Present study.

Type host: *M. cephalus* (1, 2).

Type locality: Sea of Japan: Posiet Bay (1), Russia.

Additional localities: Sea of Japan, Kiyevka Bay (2), Russia.

Type specimens: holotype at the ZIN 12292, nine paratypes at the ZIN, two at the BMNH 2013.3.28.1–2 and five at the IBSS 523/1–5 (1).

Material deposited: voucher material from the Kiyevka Bay at the BMNH NHMUK 2012.10.1.4–12.

Redescription

Based on 14 voucher specimens from the Kiyevka Bay. Body fusiform with maximum width at level of gonads. One terminal and two bilateral cephalic lobes, well developed. Testis shape varies from ovate to elongate-ovate; copulatory organ C-shaped, long, thin, enters accessory piece distally; base of copulatory organ with thick-walled heel; accessory piece claw-shaped, pincerlike, secondary lobe joins main lobe middistally by simple joint, turning away from the latter. Main lobe of accessory piece cylindrical, expanded distally, slightly bowed; distal part of main lobe beak-shaped with characteristic membranous opening at level of terminal bifurcation of accessory piece reaching to ovate or round thin-walled expansion and terminating in round "labium"; secondary lobe straight or bowed, shorter than main lobe, not reaching level of tip of distal end of main lobe. Ovary U-shaped; oviduct and ootype short, uterus elongated, Mehlis' glands inconspicuous. Vagina winding tube; vaginal aperture dextroventral; distal end of vagina funnel-shaped, thin-walled. Peduncle broad, longer than wide. Haptor subhexagonal, wider than long. Pairs of anchors subequal in shape and size. Both anchors with sharply bent blade, point not reaching level of tip of inner root, the latter longer than outer root and point, outer root and point subequal in length. Shaft of ventral anchor 1.7 to 2.4 times longer than point, tip of outer root extending to or past level of that of inner root; shaft of dorsal anchor 2–3.6 times longer than point, tip of outer root may extend to level of tip of inner root. Bars subequal in length. Ventral bar with knot on ventral shield, lateral flaps of shield contiguous to anterior protuberances, the latter not reaching level of dorsal side of bar; V-shaped knot of ventral shield attached to Λ-shaped dorsal anteromedian process. Transverse dorsal bar yoke-shaped, posteromedian process present.

Remarks

L. abditus is distinguished from all other species of the genus by the unique morphology of the main lobe of the accessory piece of the copulatory complex, which has a beak-shaped distal part with characteristic membranous opening at the level of the terminal bifurcation of the accessory piece, reaching an ovate or round thin-walled expansion and terminating in a round "labium".

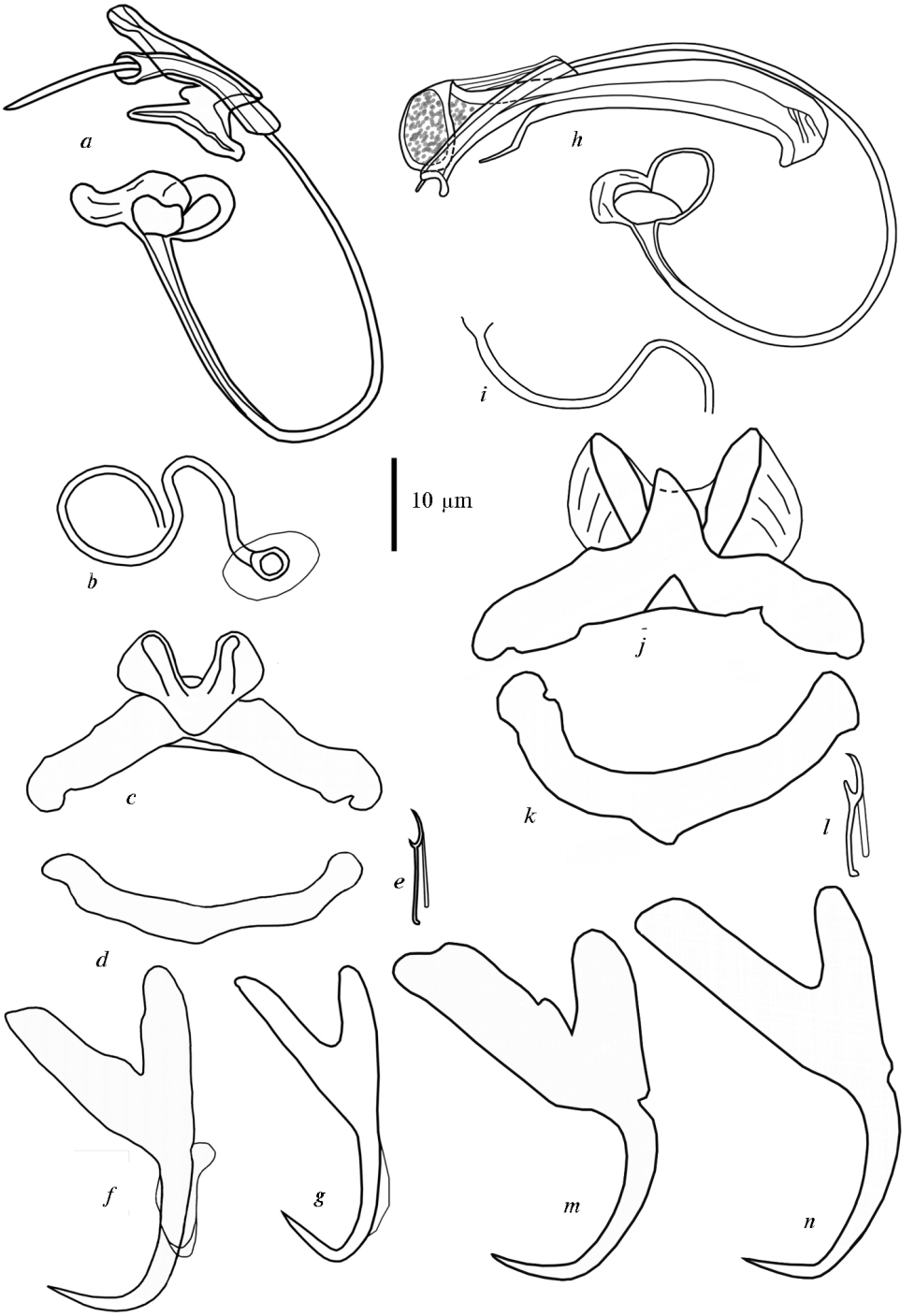

Fig. 19. Haptor and genital sclerotized structures of *Ligophorus saladensis* Marcotegui et Martorelli, 2009 (*a-g*) and *Ligophorus abditus* Dmitrieva, Gerasev et Gibson, 2013 (*h-n*): *a*, *h* — male copulatory complex: copulatory organ and accessory piece; *b*, *i* — vagina; *c*, *j* — ventral bar; *d*, *k* — dorsal bar; *e*, *l* — hook; *f*, *m*— ventral anchor; *g*, *n* — dorsal anchor.

Рис. 19. Склеротизированные гаптоpальные и генитальные структуры *Ligophorus saladensis* Marcotegui et Martorelli, 2009 (*a-g*) и *Ligophorus abditus* Dmitrieva, Gerasev et Gibson, 2013 (*h-n*): *a*, *h* — мужская копулятивная система: копулятивный орган и вспомогательный аппарат; *b*, *i* — вагина; *c*, *j* — вентральная пластинка; *d*, *k* — дорсальная пластинка; *e*, *l* — краевой крючок; *f*, *m*— вентральный срединный крючок; *g*, *n* — дорсальный срединный крючок.

This species closely resembles *L. chabaudi*, *L. pacificus, L. domnichi* and *L. triangularis* sp. n., all parasites of *M. cephalus* (except the latter species) in the Japan Sea, in having a claw-shaped accessory piece with an main lobe expanded distally, bowed or straight secondary lobe and the distal position of the copulatory organ entrance into the accessory piece; a similar shape of the ventral anchor blade. Further, it resembles *L. pacificus, L. domnichi* and *L. triangularis* sp. n., through the presence of the anteromedian process on the dorsal side of the ventral bar. In addition to the unique features *L. abditus* differs from *L. chabaudi*, *L. pacificus* and *L. domnichi* in the position of the protuberances of the ventral bar, which do not reach the level of the dorsal side of the bar, further from *L. pacificus* and *L. domnichi* in the absence of the pair of small plates of the ventral bar and from *L. chabaudi* in smaller measurements for VAC and larger APTL and APML. Moreover, *L. abditus* can be distinguished from *L. triangularis* sp. n. by the position of the distal tips of the secondary and main lobe of the accessory piece of the copulatory complex (the secondary lobe not reaching the level of the distal tip of the main lobe vs. extending to or past the level of the distal tip of the main lobe in *L. triangularis* sp. n.). This species was initially proposed as new herein, but during the production of the manuscript it was described by Dmitrieva et al. (2013). The present redescription is based on our own material and provides new information on the shape of the ovary and of the measurements of the testis, ovary, haptor and hooks. It also clarifies the shape of the accessory piece of the copulatory complex and its lobes, and the morphology of the ventral bar.

***Ligophorus triangularis* sp. n.**
(fig. 20; table 14)

Type host: *Lz. haematocheilus.*

Type localities: Sea of Japan: Posiet Bay, Razdol'naya Delta, Artemovka Delta, Russia.

Material deposited: syntypes from the Posiet Bay at the IZAN Kt-M1.1, Kt-M1.2 (2 specimens) and ZNUMZ 11900092, 11900099 (4 specimens); from the Razdol'naya Delta at the BMNH NHMUK 2012.10.1.1–2 (2 specimens), IZAN Kt-M1. 3 (1 specimen) and ZNUMZ 11900095–1190097 (3 specimens) and from the Artemovka Delta at the IZAN Kt-M1.4 (1 specimen) and BMNH NHMUK 2012.10.1.3 (6 specimens).

Etymology: From Latin (triangularis = triangular) refers to the triangular expansion of the distal part of the main lobe of the accessory piece of the copulatory complex.

Description

Based on 19 adult worms, including the syntypes from the Posiet Bay, the Razdol'naya Delta and the Artemovka Delta, Russia. Body fusiform with maximum width at level of gonads. One terminal and two bilateral cephalic lobes, well developed. Cephalic glands posterolateral to pharynx. Testis elongated to ovate; copulatory organ C-shaped, elongated, thin, enters accessory piece through membranous opening in distal part of main lobe; base of copulatory organ with thick-walled heel; accessory piece claw-shaped, pincerlike, secondary lobe joins main lobe middistally by simple joint. Main lobe of accessory piece cylindrical, bowed, elongated with subtriangular heavy-sclerotized expansion at distal part; secondary lobe bowed, shorter than main lobe, extending to or past level of distal tip of main lobe. Ovary U-shaped; oviduct and, ootype short, uterus elongated, Mehlis' glands occupying intervitellarial body space between seminal vesicle and seminal receptacle. Vagina winding or coiled; vaginal aperture dextroventral, distal end of vagina funnel-shaped, thin-walled. Peduncle broad, short, subequal in length and width. Haptor subhexagonal, wider than long. Pairs of anchors subequal in shape and size; both anchors with sharply bent blade shaft about 1.8 to 3.1 times longer than point, the latter not reaching level of tip of inner root, outer root and point shorter than inner root, outer root and point subequal in length. Tip of outer root of ventral anchor extending past level of that

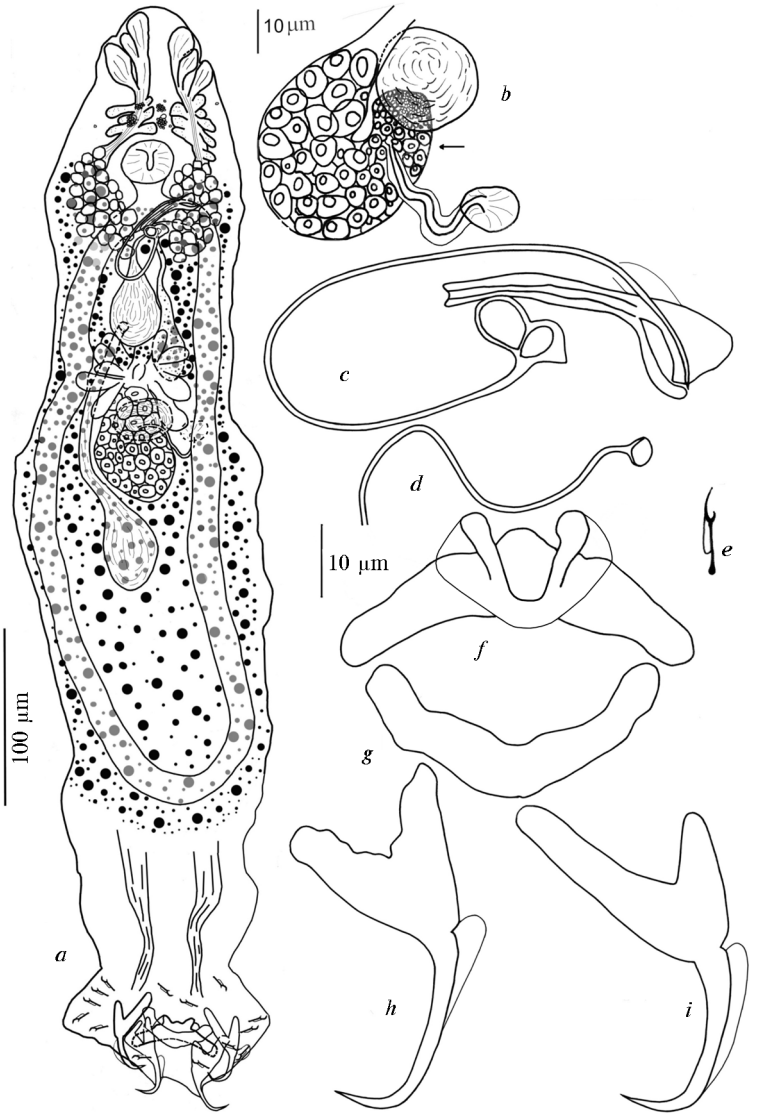

Fig. 20. *Ligophorus triangularis* sp. n.: *a* — whole mount, dorsal view; *b* — ovary, lateral view, with adjoining organs of female complex (proximal limb (arrowed) ventral to distal one of U-shaped ovary shown); *c* — male copulatory complex: copulatory organ and accessory piece; *d* — vagina; *e* — hook; *f* — ventral bar; *g* — dorsal bar; *h* — ventral anchor; *i* — dorsal anchor. Scale bars: *a* — 100 μm, *b* — 10 μm, *c*-*i* — 10 μm.

Рис. 20. *Ligophorus triangularis* sp. n.: *a* — общий вид, дорсально; *b* — яичник, латеральный вид, с прилежащими органами женской половой системы (показано проксимальную ветку, расположенную вентрально (обозначен стрелкой) по отношению к дистальной ветке U-образного яичника); *c* — мужская копулятивная система: копулятивный орган и вспомогательный аппарат; *d* — вагина; *e* — краевой крючок; *f* — вентральная пластинка; *g* — дорсальная пластинка; *h* — вентральный срединный крючок; *i* — дорсальный срединный крючок. Масштабные линейки: *a* — 100 мм, *b* — 10 мм, *c*-*i* — 10 мм.

of inner root, tip of outer root of dorsal anchor may extend to level of tip of inner root. Bars subequal in length. Ventral bar widest at middle and laterally tapered; dorsal anteromedian process present or absent; finger-like anterior protuberances situated ventrally, not reaching level of dorsal side of bar; some specimens with posteromedian prolongation of shield extending beyond level of posterior end of bar. Transverse dorsal bar yoke-shaped, small posteromedian process present or absent.

Table 14. Metric characters of *L. triangularis* sp. n. and *L. miroshnichenki* sp. n.
Таблица 14. Метрические характеристики *L. triangularis* sp. n. и *L. miroshnichenki* sp. n.

Characters*	*Ligophorus triangularis* sp. n. ex *Liza haematocheilus* from Sea of Japan, Posiet Bay, Artemovka and Razdol`naja Delta, Russia				*Ligophorus miroshnichenki* sp. n. ex *Liza haematocheilus* from Sea of Japan, Posiet Bay, Russia			
	Mean	SD	Range	N	Mean	SD	Range	N
Body length	580	136	400–900	18	650	57.7	550–700	7
Body width	97	25	50–136	19	81	12.1	70–100	7
Pharynx length	30	5	25–40	19	26	4.0	22–30	3
Pharynx width	26	4	15–32	19	26	3.5	22–28	3
Testis length	45	9	30–60	16	42	1.5	40–43	3
Testis width	28	5	20–36	16	23	3.1	20–26	3
Ovary length	47	6	35–60	18	59	8.5	50–70	4
Ovary width	31	5	20–40	18	24	6.8	17–30	4
Haptor length	60	12	40–90	18	55	13.8	40–80	6
Haptor width	100	23	60–150	18	84	8.5	75–100	7
VAA	45	3	40–50	18	41	1.6	38–43	7
VAB	35	3	30–42	18	33	2.1	30–37	7
VAC	11	2	9–15	18	9	2.2	6–12	7
VAD	16	2.2	13–22	18	14	3.3	10–19	7
VAE	10	1	9–12	18	9	1.1	7–10	7
VAF	24	2	21–27	18	22	0.8	21–23	7
VAG	44	3	40–50	18	42	1.6	39–44	7
DAA	44	4	36–50	18	44	1.6	41–45	7
DAB	30	3	22–35	18	31	0.8	30–32	7
DAC	10	2	7–14	18	8	1.5	7–10	7
DAD	20	3	15–25	18	19	1.3	18–21	7
DAE	9	1	6–11	18	9	0.9	8–10	7
DAF	21	1	19–24	18	22	1.2	20–24	7
DAG	41	2	37–43	17	42	2.3	39–45	7
HTL	11	1.1	10–13	18	12	0.8	11–13	7
VBL	51	3	47–55	18	40	1.5	38–43	7
VBDP	11	2	7–14	18	8	1.6	6–10	7
DBL	43	2	40–47	18	38	2.5	34–41	7
APTL	38	3.4	32–43	19	24	2.6	20–27	7
APML	“	“	“	“	“	“	“	“
APMW	7	1	6–8	19	3	0.6	2–4	7
APSL	13	2	10–15	19	9	1.6	7–11	7
COL	103	11	85–120	19	114	19.9	98–152	7
COW	1	0	1	15	1	0	1	7
VL	50	6	38–60	15	26	2.4	22–29	7

* See Material and methods section for abbreviations of metric variables of sclerotized characters.

Remarks

L. triangularis sp. n. is distinguished from all other species of the genus by the unique morphology of the main lobe of the accessory piece of the copulatory complex, which has a distal subtriangular, heavy-sclerotized expansion.

L. triangularis sp. n. is similar to *L. chabaudi*, *L. pacificus* and *L. domnichi* by having a claw-shaped accessory piece with a main lobe expanded distally, bowed or straight secondary lobe and the distal position of the copulatory organ entrance into the accessory piece. In addition to its unique features, *L. triangularis* sp. n. differs from these three species in the position of the distal tips of the secondary and main lobe of the accessory piece of the copulatory complex (the secondary lobe extending to or past the level of the distal tip of the main lobe vs. not reaching the level of the distal tip of the main lobe in *L. chabaudi* and *L. pacificus* or extending or not to the level of the distal tip of the

main lobe in *L. domnichi*) and the morphology of the ventral bar (finger-like anterior protuberances not reaching level of dorsal side of the ventral bar vs. extending to level of the dorsal side of the ventral bar in all compared species). Further, the new species differs from these three species by the larger measurements of VAF, additionally from *L. chabaudi* and *L. domnichi* by larger VAA, and from *L. domnichi* by larger VBL and VBAP. Differences in the shape of the ventral anchor have also been observed between *L. pacificus* and *L. triangularis* sp. n. namely, the tip of the outer root of *L. triangularis* sp. n. extends past the level of that of the inner root, while in *L. pacificus*, it may extend to the level of the tip of the inner root.

In the morphology of the haptoral sclerites and general shape of the accessory piece, this species closely resembles *L. pilengas* and *L. llewellyni*. All three species parasitise *Lz. haematocheilus* in the NW Pacific region. For discrimination of *L. triangularis* sp. n. from *L. pilengas* and *L. llewellyni* see Remarks for these species.

***Ligophorus miroshnichenki* sp. n.**
(fig. 21, *a-g*; table 14)

Synonym: *Ligophorus vanbenedenii* sensu Gussev (1985).
Record: 1. Gussev (1985); 2. Present study.
Type host: *Lz. haematocheilus* (1, 2).
Type locality: Sea of Japan: Posiet Bay, Russia (2).
Additional locality: Yellow Sea, Liao-Ho River (1), China.
Material deposited: holotype at the IZAN Kt-XX, and six paratypes at the IZAN Kt-XX.
Etymology: The species is named for Dr. Anatoliy Miroshnichenko, Vernardskiy Tavricheskiy National University, Ukraine in recognition to his contribution to taxonomy and ecology of Monogenea from Ukrainian fish.

Description

Based on seven adult worms, including the holotype and six paratypes. Body fusiform with maximum width at level of gonads. One terminal and two bilateral cephalic lobes well developed. Cephalic glands posterolateral to pharynx. Testis elongated; copulatory organ C-shaped, elongated, thin, enters accessory piece medially through membranous opening; base of copulatory organ with thick-walled heel; accessory piece claw-shaped, pincerlike, secondary lobe joins main lobe middistally by simple joint. Main lobe of accessory piece cylindrical, bowed, widest at middle and tapering proximally, relatively short; secondary lobe turns away from main lobe, bowed, shorter than main lobe, extending past level of distal tip of main lobe. Ovary U-shaped; oviduct and, ootype short, uterus elongated, Mehlis' glands occupying intervitellarial body space between seminal vesicle and seminal receptacle. Vagina winding; vaginal aperture dextroventral, distal end of vagina funnel-shaped, thin-walled. Peduncle broad, short, subequal in length and width or longer than wide. Haptor subhexagonal, wider than long. Pairs of anchors subequal in shape and size, ventral anchor heavier than dorsal one; both anchors with sharply bent blade shaft of ventral anchor 2.5 to 3.1 times longer than point and dorsal one 2 to 3 times longer, point not reaching level of tip of inner root, outer root and point shorter than inner root, outer root and point subequal in length; tip of outer root extending past level of that of inner root. Bars subequal in length. Ventral bar widest at middle and laterally tapered; dorsal anteromedian process present or absent; finger-like anterior protuberances situated ventrally, not reaching level of dorsal side of bar; some specimens with posteromedian prolongation of shield extending beyond level of posterior end of bar. Transverse dorsal bar yoke-shaped, small posteromedian process present or absent.

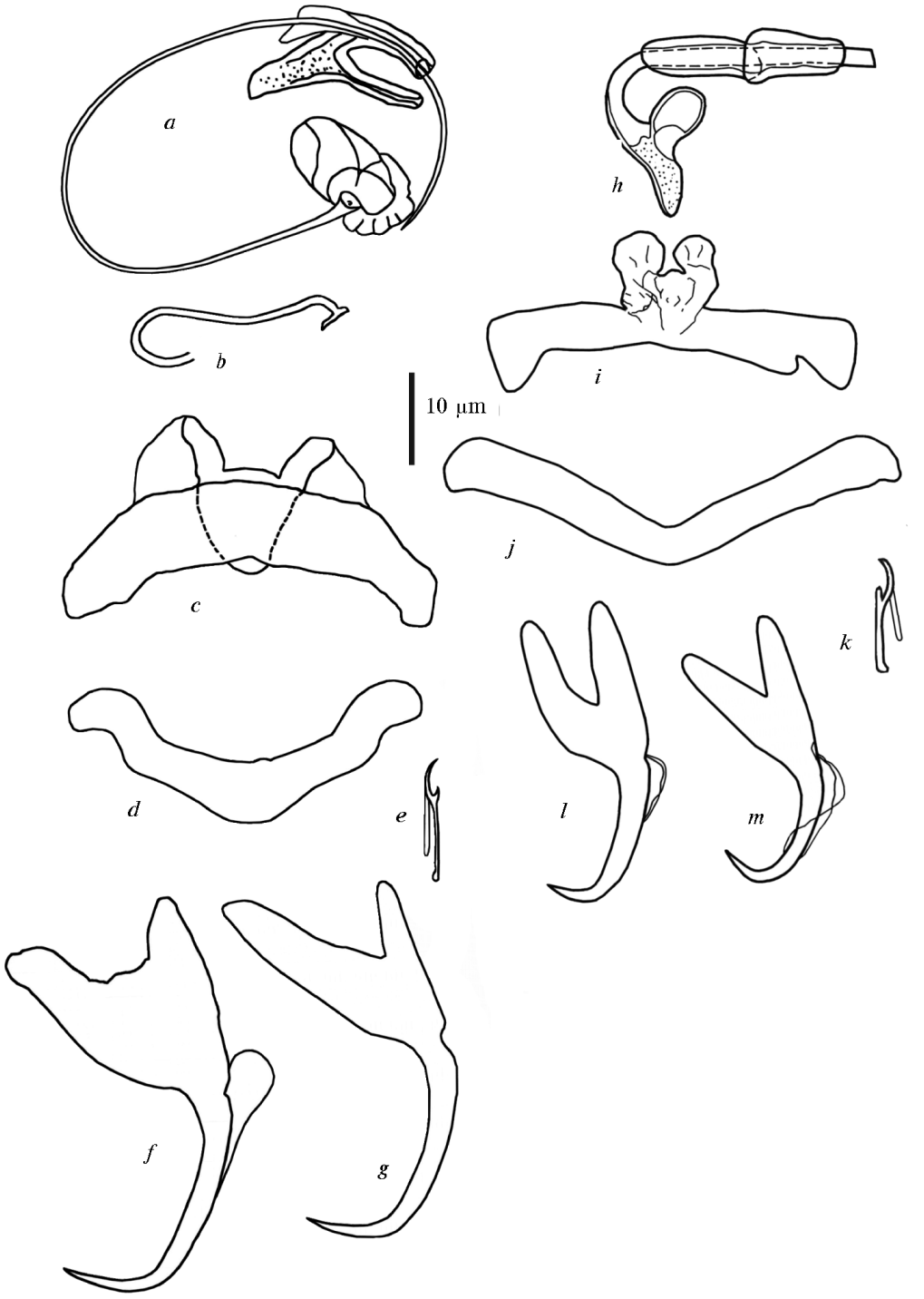

Fig. 21. Haptor and genital sclerotized structures *Ligophorus miroshnichenki* sp. n. (*a-g*) and *Ligophorus rectus* sp. n. (*h-m*): *a*, *h* — male copulatory complex: copulatory organ and accessory piece; *b* — vagina; *c*, *i* — ventral bar; *d, j* — dorsal bar; *e*, *k* — hook; *f*, *l* — ventral anchor; *g*, *m* — dorsal anchor.

Рис. 21. Склеротизированные гапторальные и генитальные структуры *Ligophorus miroshnichenki* sp. n. (*a-g*) and *Ligophorus rectus* sp. n. (*h-m*): *a*, *h* — мужская копулятивная система: копулятивный орган и вспомогательный аппарат; *b* — вагина; *c*, *i* — вентральная пластинка; *d*, *j* — дорсальная пластинка; *e*, *k* — краевой крючок; *f*, *l* — вентральный срединный крючок; *g*, *m* — дорсальный срединный крючок.

Remarks

L. miroshnichenki sp. n. is distinguished from other species of the genus by the medial position of the copulatory organ entrance in the accessory piece, which is short (20–27 μm) claw-shaped, pincerlike and tapered proximally. There are another four species of *Ligophorus* with a short accessory piece, *L. minimus*, *L. acuminatus*, *L. huitrempe* and *L. uruguayense*. The new species is easily distinguished from the latter three species by the position of the copulatory organ entrance in the accessory piece (medial vs. proximal in *L. acuminatus*, *L. huitrempe* and *L. uruguayense*) and in the shape of the accessory piece (claw-shaped vs. rod-shaped in *L. acuminatus* and cross-shaped in *L. huitrempe* and *L. uruguayense*). Further *L. miroshnichenki* sp. n. differs from *L. huitrempe* and *L. uruguayense* in the shape of the distal end of the vagina (funnel-shaped *vs.* scyphoid in compared species). *L. miroshnichenki* sp. n. differs from *L. minimus* in the shape of the main lobe of the accessory piece (cylindrical *vs.* triangle-shaped in *L. minimus*) and the texture of the distal end of the vagina (thin-walled vs. thick-walled in *L. minimus*). The species closely resembles *L. cephali, L. cheleus* and *L. pilengas* by having a claw-shaped, pincerlike accessory piece without an expansion in the distal part of the main lobe and a similar shape of the ventral anchor. *L. miroshnichenki* sp. n. differs from these three species in the shape of the accessory piece of the copulatory organ (tapered proximally vs. expanded proximally in *L. cephali* and *L. cheleus* or cylindrical without narrowing in *L. pilengas*) and shorter APTL, APML and VL; further from *L. cephali* and *L. cheleus* in the position of the distal tips of the secondary and main lobe of the accessory piece (the secondary lobe extending past the level of the distal tip of the main lobe vs. not reaching the level of the distal tip of the main lobe in *L. cheleus* or extending or not to the level of the distal tip of the main lobe in *L. cephali*) and from *L. pilengas* in shorter VBL.

The form redrawn as *L. vanbenedenii* from *Lz. haematocheilus* in Liao-Ho River, China by Gussev (1985) seems to correspond to *L. miroshnichenki* sp. n. because it possesses a short claw-shaped, pincerlike accessory piece of the male copulatory complex with a tapered proximal end and the similar shape of the anchor/bar complex conforms to that of the new species and not to that of *L. vanbenedenii* (fig. 328 B in Gussev (1985)). But the vagina depicted by Gussev (1985) is slightly longer than that in specimens studied herein.

The description of *L. triangularis* sp. n. and *L. miroshnichenki* sp. n. raises the number of *Ligophorus* species from *Lz. haematocheilus* in the NW Pacific to five, namely, *L. kaohsianghsieni*, *L. pilengas*, *L. llewellyni*, *L. triangularis* sp. n. and *L. miroshnichenki* sp. n. Only three of those species, all described earlier, were recorded from this host in the region of introduction, the Azov-Black Sea.

***Ligophorus rectus* sp. n.**
(fig. 21, *h-m*; table 15)

Type host: *Lz. tade*.

Type locality: South China Sea, Zhanjiang, Guangdong Province, China.

Material deposited: holotype and three paratypes at the BMNH 2008.8.16.41–44.

Etymology: From Latin (rectus = straight) refers to the straight shape of the accessory piece of the copulatory complex.

Description

Based on four type specimens. Body fusiform with maximum width at level of ovary. One terminal and two bilateral cephalic lobes well developed. Cephalic glands posterolateral to pharynx. Testis elongate-ovate, vas deferens winding, runs to small seminal vesicle; copulatory organ J-shaped, short, thick, enters accessory piece proximally; base of copulatory organ with thick-walled heel; accessory piece rod-shaped, straight, bilobed, lobes lying in line one behind other and articulated by simple joint, both serve to sup-

Table 15. Metric characters of *L. rectus* sp. n. and *K. ellochelon* comb. n.
Таблица 15. Метрические характеристики *L. rectus* sp. n. and *K. ellochelon* comb. n.

Characters*	*Ligophorus rectus* sp. n. ex *Liza tade* from South China Sea, Zhanjiang coastal waters, Guangdong Province, China				*Kriboetrema ellochelon* comb. n. ex *Liza vaigiensis* from South China Sea, Zhanjiang coastal waters, Guangdong Province, China			
	Mean	SD	Range	N	Mean	SD	Range	N
Body length	713	59.7	670–800	4	995	83.5	900–1,100	4
Body width	133	15	120–150	4	211	13.2	192–220	4
Pharynx length	40	4.8	35–45	4	78	11.1	69–94	4
Pharynx width	38	5.2	33–44	4	69	16.8	59–94	4
Testis length	145	16.8	125–165	4	94	15.5	80–110	4
Testis width	56	5.7	48–60	4	62	15.9	40–75	4
Ovary length	105	15	90–120	3	141	19.6	120–167	4
Ovary width	43	3.5	39–45	3	83	16.7	68–101	3
Haptor length	51	5	45–56	4	105	9.5	95–115	4
Haptor width	103	7.6	93–110	4	140	23.5	110–165	4
VAA	31	0.6	30–31	4	34	1.3	32–34.5	3
VAB	22	0.7	20.5–22	4	21	0.8	20.5–22	3
VAC	11	0.3	10.5–11	3	7	1.2	6–8	4
VAD	11	0.9	9.5–11.5	4	19	0.3	19–19.5	4
VAE	6	0	6	4	10	0.6	9–10	3
VAF	17	1	16–18	3	16	0.6	15–16	3
VAG	33	0	32.5	3	28	1.3	26.5–29	3
DAA	26	1	25–27	4	55	2.4	52.5–58	4
DAB	20	0.5	19–20	4	36	1.3	34–37	4
DAC	9	0.6	8.5-10	4	13	1.3	11–14	4
DAD	11	2.2	9–14	4	26	2.8	22.5–28	4
DAE	4	0.3	4–4.5	4	21	0.9	20–22	4
DAF	16	1	15–17	4	25	0.6	24.5–26	4
DAG	29	0.9	28–30	4	48	1.9	47–51	4
HTL	12	0.9	11–13	4	13	0	13	2
VBL	37	2.4	33–38	4	48	5.4	41–54	4
VBDP	7	0.5	7–8	4	11	3.1	8–11	3
DBL	46	3.4	43–50	4	65	6.9	58–74	4
APTL	20	0.5	20–21	4	58	6.9	49–64	4
APML or APPL	14	1.5	13–16	4	“	“	“	“
APMW or APPW	4	0	4	4	5	1.5	3–6	3
APSL or APDL	9	0.8	8–10	4	17	1	16–18	3
COL	39	0.6	38–39	3	133	5.6	125–138	4
COW	2	0.2	1.5–2	4	2	0.3	1.5–2	4
VL	–	–	–	–	41	8.2	36–53	4

* See Material and methods section for abbreviations of metric variables of sclerotized characters.

port copulatory organ; both lobes cylindrical, distal lobe slightly tapered distally. Ovary J-shaped; oviduct and ootype not observed, uterus elongated, Mehlis' glands inconspicuous, occupying intervitellarial body space between prostatic reservoir and seminal receptacle. Vagina non sclerotized; vaginal aperture midventral. Peduncle thin, elongated, longer than wide, tapering posteriorly. Haptor subhexagonal, wider than long. Pairs of anchors subequal in shape, ventral anchor larger than dorsal one. Both anchors with sharply bent blade, shaft 2.7 to 3 times longer than point, the latter short, not reaching level of tip of inner root, outer root slightly shorter than inner root, both inner and outer root longer than point; tip of outer root extending past level of that of inner root. Dorsal bar longer than ventral one, the latter straight or slightly bowed with wedge-like lateral ends directed perpendicularly from main axis of bar; dorsal anteromedian process Λ-shaped; lateral flaps of shield contiguous to anterior protuberances, which extend to dorsal side of ven-

tral bar, where they are reduce to pair of small plates and occupy anterolateral position in relation to anteromedian process. Dorsal bar V-shaped with extended extremities.

Remarks

This species is unique among all valid species of *Ligophorus* in having a rod-shaped accessory piece with the lobes lying in a line one behind the other, both supporting the copulatory organ.

L. rectus sp. n. resembles six other species by having a thick (larger than 1.5 μm) and relatively short copulatory organ (less than 65 μm), namely, *L. parvicirrus, L. hamulosus*, *L. bykhowskyi*, *L. zhangi*, *L. simpliciformis* and *L. bipartitus.* Moreover, the new species is similar to *L. hamulosus* and *L. bipartitus* in having a longer ventral anchor than the dorsal one, a shorter transverse ventral bar than the dorsal one, and to *L. parvicirrus*, *L. bykhowskyi*, *L. zhangi* and *L. bipartitus* in having a non sclerotized vagina. The new species differs from *L. parvicirrus* in: i) the texture of the heel of the base of the copulatory organ (thick-walled vs. thin-walled in *L. parvicirrus*); ii) the relative size of the ventral and dorsal bar (dorsal bar longer vs. subequal in *L. parvicirrus*); iii) the presence of the anteromedian process (rather than absence in *L. parvicirrus*) and the absence of a massive, lobular posteromedian process on the ventral bar (rather than presence in *L. parvicirrus*); iv) having one terminal cephalic lobe (rather than two lobes in *L. parvicirrus*) and iv) smaller measurements for VAA, VAB, VAD, VAF, VAF, VAG, DAA, DAB, DAE, DAF, DAG and APML and larger ones for the ovary and testis length; VAC and DBL. *L. rectus* sp. n. differs from *L. hamulosus*, *L. bykhowskyi* and *L. zhangi* in having a different pattern of connection of the copulatory organ with the accessory piece. In the new species the copulatory organ enters the accessory piece proximally and passes inside of it, while in the compared species, the copulatory organ is outside of the accessory piece and connected predominantly with its distal part. Further, *L. rectus* sp. n. differs from *L. hamulosus, L. bykhowskyi* and *L. zhangi* in having a bilobed rod-shaped, straight and slightly tapered distally accessory piece of the copulatory organ with articulated lobes (rather than bowed with an expanded proximal end in *L. hamulosus*; a single gutter-shaped, bowed lobe with an expanded proximal end in *L. bykhowskyi* and *L. zhangi*); from *L. hamulosus*, *L. bykhowskyi* and *L. simpliciformis* in the J-shaped copulatory organ (rather than C-shaped in *L. hamulosus*, and straight or slightly bowed in *L. bykhowskyi* and *L. simpliciformis*); from *L. hamulosus* and *L. simpliciformis* in the non-sclerotized vagina (rather than sclerotized in these two species). Substantial metric differences are also noted between the compared species and *L. rectus* sp. n. The new species differs from *L. hamulosus* in larger measurements for the pharynx length and width, VAA, VAC, VAE, DAA, DAB, DAC, DAE and smaller COL; from *L. bykhowskyi*, *L. zhangi*, *L. simpliciformis* and *L. bipartitus* in smaller DAA and VBL; further from *L. bykhowskyi* in smaller length and width of the body and haptor, VAA, VAD, DAB, DAD, DAE, DAG, DBL, COL, COW, APTL, APMW and larger VAF, VBDP, and larger ratio of the shaft to the point of both anchor pairs; from *L. zhangi* in smaller VAA, VAE, DAE, COL, COW, APTL, APMW and larger VAF, DAF; from *L. simpliciformis* in smaller VAA, VAF, VAE, DAF, DAE, COL; from *L. bipartitus* in smaller DBL and APTL (comparative data for *L. hamulosus* from Pan, 1999 and for *L. zhangi*, *L. simpliciformis* and *L. bipartitus* from Dmitrieva et al., 2012).

The new species resembles *L. parvicopulatrix* in having a similar shape ovary, anchor/bar complex and the thick (larger than 1.5 μm) copulatory organ. *L. rectus* sp. n. differs from *L. parvicopulatrix* in the shape of the accessory piece (bilobed and tubular vs. one concave lobe in *L. parvicopulatrix*) and shorter measurements for COL, VAA, VAC, VAG, DAA, DAG and longer for DBL.

Species inquirendae

Ancyrocephalus leporinus Zhang et Ji, 1981

Synonym: *Ligophorus leporinus* (Zhang and Ji, 1981) Gussev, 1985.

Records: 1. Zhang and Ji (1981); 2. Wu et al. (1991); 3. Zhang (2001).

Type host: *M. cephalus* (1, 2).

Other hosts: *Lz. vaigiensis* (3); *L. macrolepis* (3); and *Liza affinis* (3) (= *Osteomugil ophuiseni* (Bleeker) in Zhang (2001)).

Type locality: East China Sea, Chongwu, Huian, Fujian (?) Province (1), China.

Additional localities: East China Sea, Jimei, Huian, Fujian Province (1), Zhejiang Province (2), China. South China Sea: Yangjiang, Guangdong Province (3), Shuixi, Guangdong Province (3), Chenghai, Guangdong Province (3), Haikou, Hainan Province (3), Baimajing, Hainan Province (3), China.

Type specimens: at the Department of Biology, South China Teacher's College, Guangzhou, China (1) accession number not available.

Remarks

No type specimens of *A. leporinus* were available for the present study. Gussev (1985) transferred this species to *Ligophorus* making the following remark: "Undoubtedly, due to the large diameter of the tube of the copulatory complex and the weakly developed roots of one pair of the anchors, it strongly differs from other species of mullets, but according to all available information it should be transferred to *Ligophorus* as comb. n.". This transfer seems correct if we consider only the sclerotized structures of *A. leporinus* provided in the original description by Zhang and Ji (1981). However, available for the present study specimens of very similar form (described below as new species in the proposed new genus) to *A. leporinus* enable us to reject Gussev's (1985) transfer of this species to *Ligophorus*. Both forms share a similar shape of the anchor/bar complex, a coiled copulatory organ, a simple concave accessory piece of the copulatory complex and a large body size. But, the unique external and internal morphology revealed in new form are the key features that justify its allocation within the new genus (see below).

Additional material is needed to establish the taxonomic position of *A. leporinus* and it should, therefore, be considered *incertae sedis*.

Ligophorus chongmingensis Hu et Li, 1992

Record: 1. Hu and Li (1992).

Type host: *M. cephalus* (1).

Type locality: Yellow Sea, Chongming Island, Shanghai (1), China.

Type specimens: holotype deposited at DBSTU (1), accession number not available.

Remarks

Specimens of this species were not available for the present study. Hu and Li (1992) indicated that *L. chongmingensis* "is similar to *L. kaohsianghsieni* Gussev, 1962 and *L. vanbenedenii* Gussev, 1955, in the shape of the middle anchors and supporting apparatus, but it differs from the latter by the shape of the ventral connective plate and the copulatory tube". However, the form of *Ligophorus* presented by Gussev (1955) was later described as *L. domnichi*, and differs from *L. chongmingensis* in many morphological features (e. g. the shape of the vaginal aperture of the anchors and of the accessory piece of the male copulatory complex) (Rubtsova et al., 2007). The shape of the trans-

verse ventral bar and accessory piece of *L. chongmingensis* corresponds to that of *L. kaohsianghsieni* without the laminae on the ventral bar and thin membrane on distal ends of the accessory piece (fig. 329 of Gussev, 1985; fig. 2 of Dmitrieva, 1996; and redescription of *L. kaohsianghsieni* in the present study), which are indistinguishable on some specimens. *L. kaohsianghsieni* has a winding copulatory tube, which usually does not attain any particular shape and, therefore, the copulatory tube cannot be a useful trait for the discrimination of these two species. The shape of the accessory piece of the copulatory complex and the ventral bar is similar in both species, but the original description of *L. chongmingensis* does not reveal key details of the structure of the accessory piece, such as the presence and shape of the main and secondary lobe and their articulation. A comparison of metric characters of *L. chongmingensis* and *L. kaohsianghsieni* showed their ranges as overlapping (Hu, Li, 1992. and table 3 of the present study). Both species have been reported from the same host and sea. The type-locality for both species is the Yellow Sea (Hu, Li, 1992; Gussev, 1985). *L. kaohsianghsieni* has also been recorded on *M. cephalus*, in the East China Sea (Wu et al., 1991). Due to the lack of type-specimens and of a satisfactory description of the accessory piece of the copulatory complex and given the similarity of *L. chongmingensis* to *L. kaohsianghsieni*, it is currently impossible to determine whether they represent one variable species, or two closely related species. Thus, *L. chongmingensis* is here considered a *species inquirendae*.

***Kriboetrema* gen. n.**

Type species: *K. ellochelon* (Zhang, 2001) comb. n.

Other species: *K. rectangulus* sp. n.

Etymology: The genus is named after Drs. Delane C. Kritsky and Walter A. Boeger in recognition of their substantial contribution to research on monogeneans. The generic designation is formed by an acronym of their family names followed by the commonly used suffix -trema.

Diagnosis

Large dactylogyrid worms with body flattened dorsoventrally, comprising cephalic region, trunk, peduncle and haptor. Tegument smooth. Two terminal and two or four bilateral cephalic lobes; three pairs of head organs; cephalic glands unicellular, abundant, posterolateral to pharynx. Mouth subterminal, midventral; pharynx a muscular, glandular bulb; oesophagus short; intestinal caeca two, simple, confluent posterior to gonads, lacking diverticula. Two pairs of eyes, each eye with lens. Anterior pair closer together and with smaller eyes than posterior pair. Gonads intercaecal, testis postovarian or partially overlapping ovary, medial, ovate or elongate-ovate. Vas deferens on left side not encircling intestinal caeca, runs anterosinistrally; one or two seminal vesicles, dactylogyrid-type. Two prostatic reservoirs. Copulatory complex comprising tubular, counterclockwise, coiled, sclerotized, copulatory organ and accessory piece; base of copulatory organ expanded to form sclerotized bulb; accessory piece articulated or not with base of copulatory organ. Accessory piece serving as guide for distal portion of copulatory organ, comprised of either simple concave or bilobed structure; when accessory piece bilobed, one tube-like lobe directly serving copulatory organ, while other lobe adjoins the first one and unconnected with copulatory organ. Ovary medial, subovate or pyriform; seminal receptacle preovarian or at level of ovary, ventral; vaginal aperture midventral, vagina sclerotized, distal end of vagina funnel-shaped or scyphoid. Genital pore midventral near level of intestinal bifurcation. Vitellaria in trunk, absent from regions of other reproductive organs. Haptor globose or subrectangular with poorly developed lateral flaps, dorsal, ventral anchor/bar complex and seven pairs of similar hooks. Hook distribution normal; hooks similar in shape and size, each with upright acute thumb, domus, slender shank comprised of one subunit; ventral

and dorsal anchors similar in shape, with filament, inner and outer roots, base and blade, base markedly thicker than blade, separated by notch. Transverse ventral and dorsal bar present. Bars dissimilar, transverse ventral bar inverted, V-shaped with anteromedian process, shield on ventral side and anterior pair of protuberances. Dorsal bar straight or yoke-shaped, shield absent. Parasites of gills of mugilid fishes.

Remarks

Currently, the Dactylogyridae includes about 220 genera, representing marine, brackish and freshwater worms occurring on fish throughout the world. *Kriboetrema* gen. n. is diagnosed by: i) a large dactylogyrid worm with a body flattened dorsoventrally; ii) the vas deferens on the left side not encircling the intestinal caeca; iii) two prostatic reservoirs; iv) a copulatory complex comprising a counterclockwise coiled copulatory organ; v) the base of the copulatory organ expanded to form a sclerotized bulb; vi) the midventral vaginal aperture; vii) the haptor globose or rectangular with poorly developed lateral flaps, the dorsal and ventral anchor/bar complex, seven pairs of hooks, each with an upright acute thumb, domus, a slender shank composed of one subunit; viii) ventral and dorsal anchors similar in shape; bars dissimilar in shape; ix) the ventral bar with the anteromedian process, the shield on the ventral side and an anterior pair of protuberances.

Based on the comparative morphology of the genital and haptoral structures, *Kriboetrema* gen. n. is similar to *Ligophorus*, whose species also parasitise the gills of mugilids. Both genera are characterised by possessing: two simple intestinal caeca, confluent posteriorly; a sinistral, not looping around caeca vas deferens, a dorsal and ventral anchor/bar complex, seven pairs of similar hooks; ventral and dorsal anchors similar in shape, dissimilar transverse bars and an inverted V-shaped ventral bar with the anteromedian process, the shield on the ventral side and the anterior pair of protuberances. *Kriboetrema* gen. n. differs from *Ligophorus* in: i) the morphology of the base of the copulatory organ that expands in a sclerotized bulb (rather than bilobed base, expanding to form a bulb and a heel in *Ligophorus*); ii) having a dorsoventrally flattened body (rather than fusiform in *Ligophorus*); iii) possessing a coiled copulatory organ (rather than uncoiled in *Ligophorus*); iv) having two prostatic reservoirs (rather than one in *Ligophorus*); v) a subovate or piryform ovary (rather than U- or J-shaped in *Ligophorus*) and vi) the inconspicuous or poorly developed lateral flaps of the haptor (rather than well developed in *Ligophorus*).

Kriboetrema ellochelon (Zhang, 2001) **comb. n.**
(fig. 22; table 15)

Synonym: *Ligophorus ellochelon* Zhang, 2001.

Record: Zhang (2001).

Type host: *L. vaigiensis.*

Type locality: South China Sea, Zhanjiang (21°2' N, 110°3' E), Guangdong Province, China.

Type specimens: holotype (GDZJ 20000308) and paratypes (GDZJ 20000308–2–8).

Redescription

Based on four paratypes GDZJ 20000313–2, 2000313–3. Body fusiform, robust; greatest width at level of ovary. Two terminal and two bilateral cephalic lobes well developed. Oesophagus short. Members of anterior pair of eyes smaller and closer together than members of posterior pair. Testis ovate, overlapping ovary ventrally. Vas deferens dilating twice to form two tandem seminal vesicles, first vesicle elongated, (43 ± 8.3 [33–53] (4) × 17 ± ± 2.5 [16–21] (4)) and smaller than the second vesicle; the latter pyriform (74 ± ± 8.7 [66–86] (4) × 38 ± 7.6 [32–49] (4)). Two pyriform prostatic reservoirs; copula-

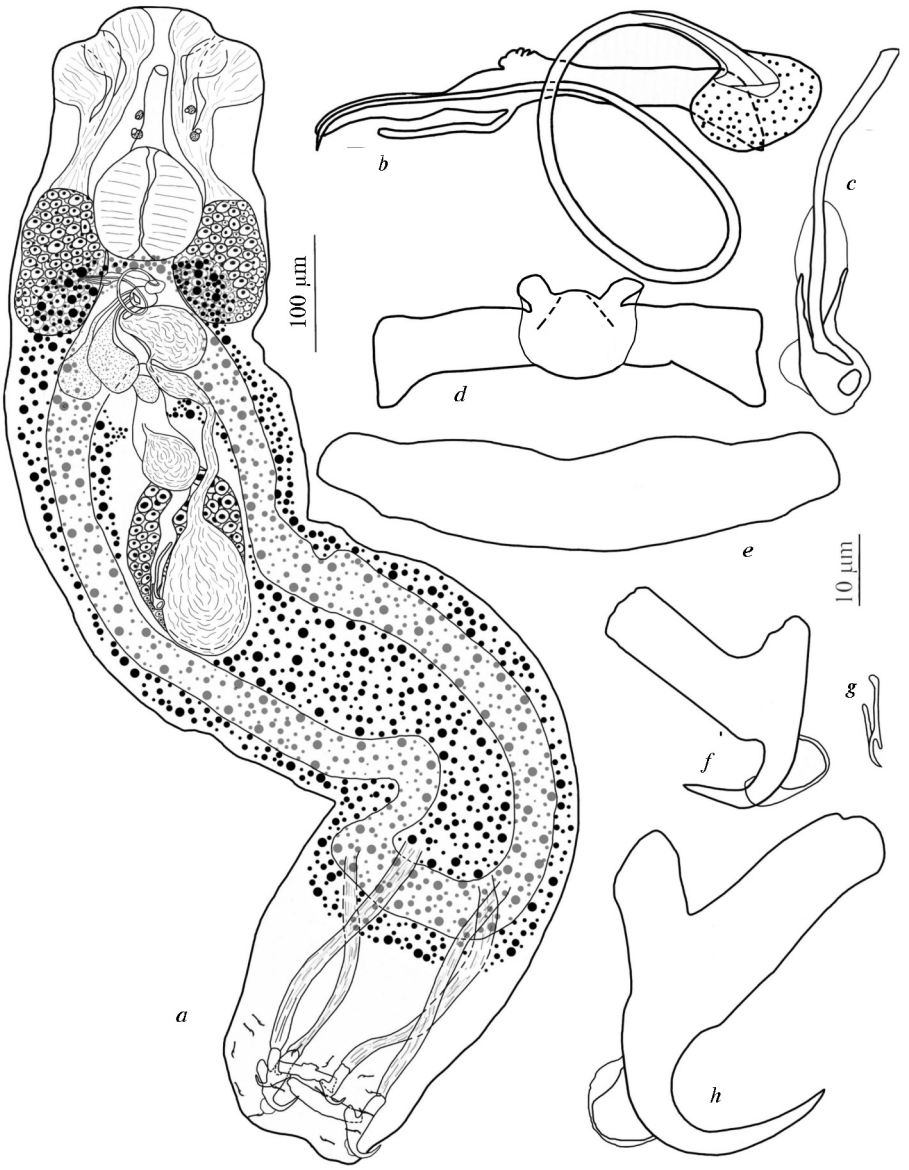

Fig. 22. *Kriboetrema ellochelon* (Zhang, Yang, Liu, 2001) comb. n.: *a* — whole mount, ventral view; *b* — male copulatory complex: copulatory organ and accessory piece; *c* — sclerotized part of vagina; *d* — ventral bar; *e* — dorsal bar; *f* — ventral anchor; *g* — hook; *h* — dorsal anchor. Scale bars: *a* — 100 μm, *b-h* — 10 μm.

Рис. 22. *Kriboetrema ellochelon* (Zhang, Yang, Liu, 2001) comb. n.: *a* — общий вид, вентрально; *b* — мужская копулятивная система: копулятивный орган и вспомогательный аппарат; *c* — склеротизированная часть вагины; *d* — вентральная пластинка; *e* — дорсальная пластинка; *f* — вентральный срединный крючок; *g* — краевой крючок; *h* — дорсальный срединный крючок. Масштабные линейки: *a* — 100 мкм, *b-h* — 10 мкм.

tory organ sclerotized, coiled tube of slightly more than one counterclockwise ring, long, thin, enters accessory piece medially; base of copulatory organ expanded to form heavily sclerotized bulb; accessory piece claw-shaped, pincerlike, bifurcate middistally, secondary lobe articulated with main one by joint. Main lobe of accessory piece tubular, straight, long, expanded medially and clearly narrowing distally, articulated with base of copulatory organ; secondary lobe bowed, shorter than main lobe, not reaching level of tip of main lobe. Ovary subovate, broadly overlapping testis; oviduct, ootype, Mehlis' glands

not observed; uterus thick-walled, runs dorsomedially to common slit-like genital pore; vaginal aperture sclerotized, midventral, scyphoid with bulb and two additional sclerites; vaginal tube muscular, partially sclerotized, winding, thin-walled; seminal receptacle at ovary level or slightly preovarian. Peduncle broad, shorter than width or subequal in length and width. Haptor not distinctly set off from body proper with poorly developed lateral flaps, subhexagonal, wider than long. Pairs of anchors unequal in shape and size, dorsal anchor larger and heavier than ventral one; length difference between roots more apparent in ventral anchor, point of dorsal anchor elongated and two times longer than that of ventral anchor. Both ventral and dorsal anchors with elongated inner root, the latter longer and heavier than outer root and point, outer root shorter than point, the latter not reaching level of tip of inner root, base markedly thicker than blade, separated by notch; ventral anchor with sharply bent blade, shaft 1.6 to 1.7 times longer than point; dorsal anchor with smoothly bent blade, shaft 1.1 to 1.3 times longer than point. Ventral anchors connected by transverse ventral bar; the latter massive, slightly bowed with wedge-like lateral ends directed perpendicularly from main axis of bar and Λ-shaped dorsal anteromedian process: finger-like anterior protuberances of ventral bar situated ventrally, not reaching level of dorsal side of bar; posteromedian prolongation of shield extending beyond level of posterior end of bar. Dorsal anchors connected by straight transverse dorsal bar, larger than ventral one, with slightly narrowing lateral extremities.

Remarks

Kriboetrema ellochelon comb. n. is the type species of the genus. This species is unique in possessing two tandem seminal vesicles, the articulation of the accessory piece with the base of copulatory organ, the medial position of the copulatory organ entrance in a claw-shaped, pincerlike, bifurcate middistally accessory piece, a scyphoid distal end of vagina with the bulb and two additional sclerites and a massive, straight dorsal bar.

Zhang (2001) described this species based on seven mounted specimens and deposited one holotype and paratypes at the GDZJ. Reexamination of the paratypes revealed previously unreported two tandem seminal vesicles and prostatic reservoirs and the ventral shield with anterior protuberances on the ventral bar, as well as inaccuracies in the description of the morphology of both the proximal and distal ends of the accessory piece. We observed that the accessory piece is claw-shaped, middistally bilobed (rather than trilobed, according to Zhang (2001)), the main lobe is tubular, straight, long, and clearly narrowing distally; the secondary lobe is trigger-shaped, shorter than the main lobe, and not reaching the level of the distal end of the main lobe. The present redescription illustrates for the first time an in toto view and supplies new, detailed information on the shape and measurements of the pharynx, ovary, testis, seminal vesicles, haptor, genital and haptoral sclerotized structures.

***Kribotrema rectangulus* sp. n.**
(fig. 23; table 16)

Type host: *V. cunnesius*.

Type locality: South China Sea, Zhanjiang, Guangdong Province, China.

Material deposited: holotype and two paratypes at the BMNH 2008.8.19.1–2 and 2008.8.16.45.

Etymology: From Latin (rectangulus = rectangular) refers to the rectangular shape of haptor.

Description

Based on three type specimens from the South China Sea, Zhanjiang, Guangdong Province. Large dactylogyrid worm with dorsoventrally flattened, robust body and great-

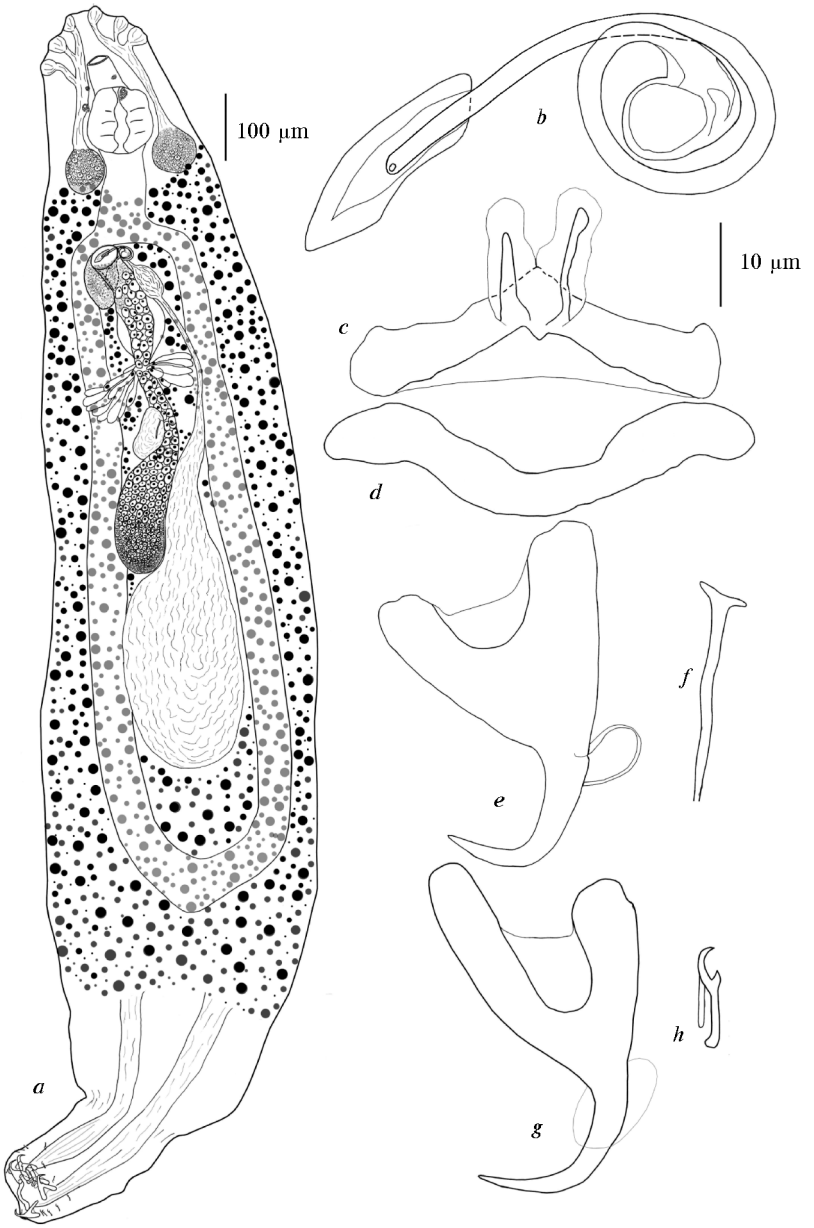

Fig. 23. *Kriboetrema rectangulus* sp. n.: *a* — whole mount, ventral view; *b* — male copulatory complex: copulatory organ and accessory piece; *c* — ventral bar; *d* — dorsal bar; *e* — ventral anchor; *f* — vagina; *g* — dorsal anchor; *h* — hook. Scale bars: *a* — 100 μm, *b-h* — 10 μm.

Рис. 23. *Kriboetrema rectangulus* sp. n.: *a* — общий вид, вентрально; *b* — мужская копулятивная система: копулятивный орган и вспомогательный аппарат; *c* — вентральная пластинка; *d* — дорсальная пластинка; *e* — вентральный срединный крючок; *f* — вагина; *g* — дорсальный срединный крючок; *h* — краевой крючок. Масштабные линейки: *a* — 100 мкм, *b-h* — 10 мкм.

est width at level of gonads. Two terminal and two pairs of bilateral cephalic lobes, each lobe comprising head organ. Pharynx ovate; oesophagus elongated. Gonads tandem or slightly overlapping. Testis elongate-ovate; copulatory organ coil of about one and half counterclockwise ring, thick. Base of copulatory organ expanded to form bulb; accessory piece comprises simple concave, straight, distally tapered lobe, not articulated with base of copulatory organ. Ovary medial, pyriform to elongated. Oviduct and ootype short, thick-walled; Mehlis' glands conspicuous, comprising elongated glandular cells; uterus thick-

Table 16. Metric characters of *K. rectangulus* sp. n.
Таблица 16. Метрические характеристики *K. rectangulus* sp. n.

Characters*	*Kriboetrema rectangulus* sp. n. ex *Valamugil cunnesius* from South China Sea, Zhanjiang coastal waters, Guangdong Province, China			
	Mean	SD	Range	N
Body length	1,897	196	1,710–2,000	3
Body width	385	192	190–574	3
Pharynx length	97	20.2	75–115	3
Pharynx width	87	18	67–102	3
Testis length	325	128	205–460	3
Testis width	178	72.5	105–250	3
Ovary length	238	47	184–270	3
Ovary width	88	37.6	57–130	3
Haptor length	190	85.4	110–280	3
Haptor width	105	47.7	50–135	3
VAA	37	1.0	36–38	4
VAB	30	0.6	30–31	3
VAC	10	0.6	9–10	3
VAD	9	0.6	9–10	3
VAE	10.7	0.6	10–11	3
VAF	17	1.5	16–19	3
VAG	40	0.5	40–41	4
DAA	41	0.6	40–41	3
DAB	30	0.6	30–31	3
DAC	8	2.5	6–11	3
DAD	11	1.2	10–12	3
DAE	11.5	0.7	11–12	2
DAF	17	1.5	16–19	3
DAG	39	2.5	36–41	3
HTL	17	1.5	16–19	3
VBL	44	0.7	43–44	2
VBDP	8	2.1	6–9	2
DBL	54	5.7	50–58	2
APTL	21	2.3	20–24	3
APMW	8	1.0	7–9	3
COL	87	17.7	75–107	3
COW	2.5	0.2	2.3–2.6	3
VL	25	5.9	18–29	3

* See Material and methods section for abbreviations of metric variables of sclerotized characters.

walled, elongated, runs dorsomedially to common ovate genital pore. Vagina sclerotized, straight or winding; vaginal aperture midventral, funnel-shaped; seminal receptacle ovate, thick-walled at ovary level. Peduncle broad, short, tapered posteriorly. Haptor subrectangular, longer than wide, well diferentiated from body proper. Pairs of anchors subequal in shape, inner length of dorsal anchor longer than that of ventral anchor; length of main part of ventral and dorsal anchors equal; ventral anchor with subequal weakly developed roots; inner root of dorsal anchor longer than outer root; tip of outer root of ventral anchor extending past level of that of inner root, tip of outer root of dorsal anchor extending to level of tip of inner root; both anchors with sharply bent blade, shaft of ventral anchor 1.5 to 1.9 times longer than point and that of dorsal anchor 1.4 to 1.6; shaft of ventral and dorsal anchors equal; point of both anchors not reaching level of tip of inner root. Ventral anchors connected by inverted V-shaped transverse ventral bar with extended extremities, membranous plate on posterior margin, ventral shield with two anterior finger-like protuberances and Λ-shaped anteromedian process. Anterior protuberances

situated ventrally, not reaching level of dorsal side of bar. Dorsal anchors connected by yoke-shaped transverse dorsal bar, longer than ventral bar, with rounded extremities.

Remarks

This species is unique in having a simple concave, straight, distally tapered accessory piece; two pairs of bilateral cephalic lobes; a piryform ovary; subrectangular haptor; subequal weakly developed roots of the ventral anchor and the membranous plate on the posterior margin of the ventral bar.

Due to the above-declared high similarity in sclerotized structures of *K. rectangulus* sp. n. and *A. leporinus,* we provide differential diagnosis for these two species. The new species differs from *A. leporinus* by having a sclerotized vagina; same width for proximal and middle region of the accessory piece of the copulatory complex and the membranous plate on the posterior margin of the ventral bar (in *A. leporinus* the vagina seems not to be sclerotized, the accessory piece expanded proximally (Zhang, Ji, 1981) and the membranous plate of the ventral bar is absent); a shorter copulatory organ, dorsal and ventral bars; and a longer inner length of the dorsal anchor.

Key to genera and species of Dactylogyridae from Atlantic and Pacific mullets

Таблица для определения родов и видов Dactylogyridae от атлантических и тихоокеанских кефалевых рыб

1a. Copulatory organ uncoiled, its base expanded to form bilobed structure with bulb and heel; one prostatic reservoir; ovary U or J-shaped; body fusiform; haptor with well developed lateral flaps. .... *Ligophorus* (2)

1b. Copulatory organ coiled; its base expanded to form sclerotized bulb; two prostatic reservoirs; ovary subovate or piryform; body dorsoventrally flattened; haptor with poorly developed lateral flaps. .... *Kriboetrema* gen. n. (34)

2a. Copulatory organ thick (2 μm or more at middle portion) and short (65 μm and less). ..... (3)

2b. Copulatory organ thin (about 1 μm at middle portion) and long (greater than 66 μm). ..... (5)

3a. Vagina sclerotized, accessory piece of copulatory complex consisting of single lobe with expanded proximal end, copulatory organ 55 μm and longer, outer root and point 5 and 3 μm and less, respectively, of both ventral and dorsal anchor pairs. ..... *L. hamulosus*

3b. Vagina non sclerotized, accessory piece of copulatory complex consisting of two lobes, claw or rod-shaped, copulatory organ less than 54 μm in length, outer root and point greater than 6 and 4 μm, respectively, of both ventral and dorsal anchor pairs. ..... (4)

4a. Heel of base of copulatory organ thin-walled, accessory piece claw-shaped, roots of both anchor pairs unequal in length, ventral and dorsal bar subequal in length, shaft of both ventral and dorsal anchor greater than 20 μm, ventral bar with massive and lobular posteromedian process, anteromedian process absent. ..... *L. parvicirrus*

4b. Heel of base of copulatory organ thick-walled, accessory piece rod-shaped or bowed with expanded proximal end, roots of both anchor pairs subequal in length, shaft of both ventral and dorsal anchor less than 19 μm, ventral bar smaller than dorsal one, anteromedian process of ventral bar present, massive and lobular posteromedian process absent. ..... *L. rectus* sp. n.

5a. Distal end of vagina scyphoid, accessory piece of copulatory organ cross-shaped (except *L. uruguayense*), secondary lobe articulates with the main one by suture lengthways along full its length or only with its distal/proximal part. ..... (6)

5b. Distal end of vagina funnel-shaped accessory piece of copulatory organ claw or rod-shaped, secondary lobe articulates with the main one by joint. ..... (12)

6a. Copulatory organ winding, 131 μm in length and greater, secondary lobe of the accessory piece longer than main lobe, articulates with the latter lengthways along full its length, proximal tip of secondary lobe extending beyond that of main lobe, vagina 86 μm in length and longer. ..... (7)

6b. Copulatory organ C-shaped, shorter than 130 μm, secondary lobe of the accessory piece shorter or subequal with main lobe, articulates with the latter lengthways along distal or proximal part, proximal tip of secondary lobe extending, or not to that of main lobe, vagina shorter than 85 μm. ..... (8)

7a. Body, pharynx, ovary and accessory piece relatively large (larger than 1,100 μm, 55 μm, 180 μm and 31 μm in length, respectively), secondary lobe of accessory piece of copulatory complex with membranous plates at distal ends, distal end of vagina broad 7–9 μm, blade of both anchors smoothly bent, shaft 1–1.9 times larger than point. ..... *L. kaohsianghsieni*

7b. Body, pharynx, ovary and accessory piece relatively small (less than 940 μm, 46 μm, 130 μm and 30 μm in length, respectively), membranous plates at distal ends of secondary lobe of accessory piece of copu-

latory complex absent, distal end of vagina narrow, less than 6 μm, blade of both anchors sharply bent, shaft about 1.9–3.2 times larger than point. ..... *L. macrocolpos*

8a. Accessory piece of copulatory complex 20 μm and shorter, its main lobe with distal bulb-shaped expansion, secondary lobe V-shaped with equal branches, shorter than main lobe, articulates with the latter lengthways along its proximal part, proximal tip of secondary lobe extending to level of that of main lobe. ..... (9)

8b. Accessory piece of copulatory complex 21 μm and longer, bulb-shaped distal expansion of main lobe of accessory piece absent, secondary lobe trident or V-shaped with unequal branches, subequal in length with main lobe, articulates with the latter lengthways of its distal part, proximal tip of secondary lobe not reaching level of that of main lobe. ..... (10)

9a. Distal end of the main lobe of the accessory piece of copulatory complex slightly expanded (less than 4 μm wide), both distal ends of V-shaped secondary lobe connected with main lobe, ratio of shaft to point of dorsal anchor less than 2, inner root of ventral anchor with process. ..... *L. uruguayense*

9b. Distal end of the main lobe of the accessory piece of copulatory complex massive (5 μm and greater wide), only upper end of V-shaped secondary lobe connected with main lobe, ratio of shaft to point of dorsal anchor greater than 2.1, process of inner root of ventral anchor absent. ..... *L. huitrempe*

10a. Secondary lobe of accessory piece with inwardly curved upper branch, which is about three times longer than lower branch. ..... *L. mediterraneus*

10b. Secondary lobe of accessory piece with straight or backwardly curved upper branch, which is about two times longer than lower branch. ..... (11)

11a. Secondary lobe of accessory piece V-shaped, ratio of inner root to outer one of both anchor pairs 1.6 and greater. ..... *L. mugilinus*

11b. Secondary lobe of accessory piece trident shaped, ratio of inner root to outer one of both anchor pairs less than 1.5. ..... *L. saladensis*

12a. Accessory piece of copulatory complex rod-shaped with ovate and short main lobe (12 μm and less). ..... *L. acuminatus*

12b. Accessory piece of copulatory complex claw-shaped with cylindrical or triangle-shaped and long main lobe (greater than 13 μm in length). ..... (13)

13a. Accessory piece of copulatory organ bifurcate distally to form duck-billed claw. ..... *L. lizae*

13b. Accessory piece of copulatory organ bifurcate distally to form pincerlike or arrow-like claw. ..... (14)

14a. Accessory piece of copulatory complex with triangle-shaped main lobe, distal end of vagina thick-walled. ..... *L. minimus*

14b. Accessory piece of copulatory complex with cylindrical main lobe, distal end of vagina thin-walled. .... (15)

15a. Copulatory organ enters accessory piece proximally. ..... (16)

15b. Copulatory organ enters accessory piece distally or medially. ..... (21)

16a. Ratio of shaft to point of ventral anchor 1.4 and less, point length of both anchor pairs 11 μm and greater, pair of small plates of ventral bar present. ..... (17)

16b. Ratio of shaft to point of ventral anchor greater than 1.5, point length of both anchor pairs less than 10 μm, pair of small plates of ventral bar absent. ..... (19)

17a. Main lobe of accessory piece of copulatory complex tapered distally and expanded proximally, secondary lobe C-shaped, point of ventral anchor extending to level of tip of inner root. ..... *L. szidati*

17b. Main lobe of accessory piece of copulatory complex expanded distally and proximally, secondary lobe J or scoop-shaped, point of ventral anchor not reaching level of tip of inner root. ..... (18)

18a. Distal end of main lobe of the accessory piece of copulatory complex represents hemispherical dome-shaped expansion, secondary lobe massive, gutter-shaped and spatulate, point of ventral anchor 14 μm and less, length of dorsal anchor shaft less than 16 μm, ventral bar 38 μm and less in length. .... *L. angustus*

18b. Distal end of main lobe of the accessory piece of copulatory complex culminating in cordate hemispherical expansion, secondary lobe J-shaped, point of ventral anchor greater than 15 μm, length of dorsal anchor shaft greater than 16 μm, ventral bar 39 μm and greater in length. ..... *L. confusus*

19a. Accessory piece of copulatory organ distally bifurcate forming arrow-like claw, secondary lobe beak-shaped with characteristic distal auricle and double joining of secondary lobe with main one, ratio of shaft to point of both anchor pairs less than 2.4. ..... *L. vanbenedenii*

19b. Accessory piece of copulatory organ distally bifurcate forming pincer-like claw, secondary lobe J-shaped, connected once with main lobe by simple joint, ratio of shaft to point of both anchor pairs greater than 2.5. ..... (20)

20a. Secondary lobe of accessory piece of copulatory complex extending beyond level of distal tip of main lobe, finger-like anterior protuberances on ventral side of ventral bar. ..... *L. heteronchus*

20b. Secondary lobe of accessory piece of copulatory complex extending to level of distal tip of main lobe, finger-like anterior protuberances, forming together V-shaped structure on dorsal side of bar. .... *L. imitans*

21a. Secondary lobe of accessory piece of copulatory complex larger than main lobe, its length greater by 42 μm and larger. ..... (22)

21b. Secondary lobe of the accessory piece of copulatory complex smaller than main lobe, its length less than 41 μm. ..... (24)

22a. Copulatory organ enters main lobe of accessory piece medially, the latter with medial and distal expansion, secondary lobe of accessory piece 76 μm and greater in length, crossing distal end of main lobe, total length of accessory piece greater than 77 μm. ..... *L. tainhae*

22b Copulatory organ enters main lobe of accessory piece proximally, the latter with distal spine-shaped or elongated irregularly in shape expansion, secondary lobe shorter than 75 μm crossing distal end of main lobe, total length of accessory piece less than 76 μm. ..... (23)

23a. Secondary lobe of accessory piece of copulatory complex with elongated irregularly in shape expansion, extending beyond level of distal end of main lobe, outer root of ventral anchor 10 μm and greater. .... *L. guanduensis*

23b. Secondary lobe of accessory piece of copulatory complex with distal spine-shaped expansion, not reaching distal end of main lobe, outer root of ventral anchor less than 10 μm. ..... *L. brasiliensis*

24a. Copulatory organ enters accessory piece medially, the latter short, less than 28 μm in length, tapered proximally. ..... *L. miroshnichenki* sp. n.

24b. Copulatory organ enters main lobe of accessory piece distally, the latter long, greater than 29 μm in length, expanded proximally or with same width for proximal and middle region. ..... (25)

25a. Main lobe of accessory piece of copulatory complex narrowing distally or with same width for distal and middle region. ..... (26)

25b. Main lobe of accessory piece of copulatory complex expanded distally. ..... (29)

26a. Main lobe of accessory piece of copulatory complex with inwardly curved distal end, secondary lobe extending beyond level of distal end of main lobe along more than one-third of its length, copulatory organ less than 74 μm. ..... *L. chenzhenensis*

26b. Main lobe of accessory piece of copulatory complex straight or slightly bowed, secondary lobe not reaching level of distal end of main lobe or slightly extending beyond it, length of copulatory organ 75 μm and greater. ..... (27)

27a. Secondary lobe of accessory piece straight, expanded proximally, anteromedian process of ventral bar absent, finger-like anterior protuberances form V-shaped structure on dorsal of ventral bar. ..... *L. cheleus*

27b. Secondary lobe of accessory piece bowed or winding, expanded distally, anteromedian process of ventral bar present or absent, finger-like anterior protuberances situated ventrally, not reaching level of dorsal side of ventral bar. ..... (28)

28a. Main lobe accessory piece of copulatory complex with same width for proximal and middle region (before the bifurcation), secondary lobe bowed, joins main lobe middistally, anteromedian process of ventral bar present or absent; when present it is small, knoll-shaped. ..... *L. pilengas*

28b. Main lobe accessory piece of copulatory complex expanded proximally, secondary lobe bowed, joins main lobe medially, anteromedian process of ventral bar present, Λ-shaped. ..... *L. cephali*

29a. Finger-like anterior protuberances situated ventrally, not reaching level of dorsal side of bar. ..... (30)

29b. Finger-like anterior protuberances extending to level of dorsal side of bar. ..... (32)

30a. Distal end of main lobe accessory piece of copulatory complex with funnel-shaped expansion, secondary lobe spatulate. ..... *L. llewellyni*

30b. Distal end of main lobe accessory piece of copulatory complex with beak-shaped or subtriangular, heavily-sclerotized expansion, distal expansion of secondary lobe absent. ..... (31)

31a. Distal end of main lobe accessory piece of copulatory complex beak-shaped with characteristic membranous opening at level of terminal bifurcation of accessory piece that reaches ovate or round thin-walled expansion and terminates in round “labium”, ventral bar, length 46 μm and less, distance between protuberances of ventral bar less than 12 μm, anteromedian process ventral bar present, Λ-shaped. .... *L. abditus*

31b. Distal end of main lobe accessory piece of copulatory complex with subtriangular, heavily-sclerotized expansion, ventral bar 47 μm and greater, distance between protuberances of ventral bar 12 μm and greater, anteromedian process of ventral bar present or absent; when present it is small, knoll-shaped. .... *L. triangularis* sp. n.

32a. Distal end of main lobe of accessory piece of copulatory complex with membranous and bulb-shaped expansion, anteromedian process and pair of small plates on dorsal side of ventral bar absent. .... *L. chabaudi*

32b. Distal end of main lobe accessory piece of copulatory complex with heavily-sclerotized and bulb-shaped or membranous and subtriangular expansion, anteromedian process and pair of small plates on dorsal side of ventral bar present. ..... (33)

33a. Distal end of main lobe of accessory piece of copulatory complex heavily-sclerotized and with bulb-shaped expansion. ..... *L. domnichi*

33b. Distal end of main lobe of accessory piece of copulatory complex with membranous and subtriangular expansion. ..... *L. pacificus*

34a Accessory piece claw-shaped, pincerlike, bifurcate middistally, articulated with base of copulatory organ, two tandem seminal vesicles, distal end of vagina scyphoid with bulb and two additional sclerites, roots of the ventral anchor well developed, membranous plate on posterior margin of ventral bar absent, dor-

sal bar massive, straight, body relatively small about 1 mm long, haptor globose, two bilateral cephalic lobes, ovary ovate. ..... *K. ellochelon* comb. n.

34b Accessory piece simple concave, straight, tapered distally, nonarticulated with base of copulatory organ, one seminal vesicle, distal end of vagina funnel-shaped, roots of the ventral anchor weakly developed, membranous plate on posterior margin of ventral bar present, dorsal bar yoke-shaped, body large, about 2 mm long, haptor subrectangular, two pairs of bilateral cephalic lobes, ovary piryform. .... *K. rectangulus* sp. n.

Summary on geographic and host records

Euzet and Suriano (1977) and Euzet and Sanfilippo (1983) recognized 12 species of *Ligophorus* (*L. vanbenedenii*, *L. mugilinus*, *L. szidati*, *L. chabaudi*, *L. macrocolpos*, *L. acuminatus*, *L. minimus*, *L. heteronchus*, *L. angustus*, *L. imitans*, *L. confusus* and *L. parvicirrus*) from five mullet hosts, *M. cephalus*, *Lz. aurata*, *Lz. saliens*, *Lz. ramada* and *C. labrosus*, off the Mediterranean and northwest Atlantic coast. Gussev (1985) added two species to the list (*L. kaohsianghsieni*, *L. leporinus*), one from *Lz. haematocheilus* from the Yellow Sea and another from *M. cephalus* from the East China Sea. Subsequently 21 new species (*L. huitrempe*, *L. chenzhenensis*, *L. chongmingensis, L. hamulosus*, *L. euzeti, L. ellochelon, L. pilengas*, *L. gussevi, L. mediterraneus*, *L. cephali*, *L. llewellyni*, *L. domnichi, L. pacificus*, *L. cheleus*, *L. uruguayense*, *L. tainhae*, *L. brasiliensis*, *L. guanduensis*, *L. lizae*, *L. saladensis* and *L. abditus*) have been added to the genus from Atlantic and Pacific localities, expanding the host range to ten species (*M. platanus*, *M. liza*, *Lz. macrolepis* and *Lz. vaigiensis* registered as new hosts of *Ligophorus* species) and the geographical distribution to the Azov-Black Sea, southwest Atlantic, South China Sea, Sea of Japan and the South East Pacific (Fernández, 1987; Dmitrieva, Gerasev, 1996; Zhang, 2001; Sarabeev, Balbuena, 2004; Miroshnichenko, Maltsev, 2004; Sarabeev et al., 2005; Rubtsova et al. , 2006 a; Dmitrieva et al., 2007; Rubtsova et al., 2007; Failla Siquier, Ostrowski de Núñez, 2009; Abdallah et al., 2009; Marcotegui, Martorelli, 2009; Dmitrieva et al., 2013). Finally, Anderson (1981) and Llewellyn and Anderson (1984) reported *L. angustus* from *C. labrosus* off the northeast Atlantic coast; Mikailov and Seidli (1989) recorded several *Ligophorus* species from mullets introduced into the Caspian Sea; Zhang et al. (1991) recorded *L. vanbenedenii* and *L. leporinus* from a new host, *Lz. affinis*, from the South China Sea; and Dmitrieva et al. (2009 b; 2013) reported *L. chabaudi* from the Sea of Japan and the Yellow Sea. To complete the taxonomic list of *Ligophorus,* 17 species should be mentioned from the Indian Ocean, *L. fluviatilis* (Bychowsky, 1949) from *Liza abu* (Heckel) (= *Mugil abu zarudnyi* Berg in Bychkowsky (1949)), *L. bykhowskyi* and *L. zhangi* from *Crenimugil crenilabris* (Forsskal), *L. simpliciformis*, *L. bipartitus*, *L. campanulatus*, *L. mamaevi*, *L. lebedevi*, *L. surianoae* from *Liza carinata* (Valenciennes) and *L. navjotsodhii*, *L. chelatus*, *L. funnelus*, *L. parvicopulatrix*, *L. bantingensis*, *L. careyensis* from *Liza subviridis* Valenciennes, *L. kedahensis* and *L. fenestrum* from *Valamugil buchanani* Bleeker (see Bychowsky, 1949; Dmitrieva et al., 2012; Soom, Lim, 2012). So, before the present study, 51 nominal species of Dactylogyridae worms from 16 species of mullets were related with *Ligophorus*.

Table 17 and 18 summarises the current host and geographical arrangement of the Atlantic and Pacific species assigned to *Ligophorus*. The present study recognises 33 species of *Ligophorus* in this region from ten mullet species: The host range includes *Lz. tade* as new host, revealed in this study, but leaves out *Lz. affinis* and *Lz. vaigiensis*, whose parasites were transferred herein to another genus or considered as invalid records (see Remarks to species).

The species distribution of *Ligophorus* spp. on mullets is heterogeneous and varies from 1 to 13 species. The cosmopolitan host species, *M. cephalus*, harbours the most diverse

Table 17. Host/parasite list of the 33 valid species of *Ligophorus* from the Atlantic and Pacific waters with information on the geographical distribution based on our own and literature data (see Records for each species)

Таблица 17. Список хозяев с указанием встречающихся на них 33 валидных видов *Ligophorus* из бассейнов Атлантического и Тихого океанов с данными по географическому распределению, основанные на наших и литературных данных (см. Регистрации для каждого вида)

Host	Parasite*	Locality	Host	Parasite*	Locality
C. labrosus	*L. angustus*	NE Atlantic and Mediterranean Sea	*Lz. tade*	*L. rectus* sp. n.	South China Sea
Lz. aurata	*L. szidati*	Mediterranean, Black and Azov Sea	*M. cephalus*	*L. cephali*	Mediterranean, Black and Azov Sea
	L. vanbenedenii	" and Caspian Sea		*L. abditus*	Sea of Japan
Lz. haematocheilus	*L. kaohsianghsieni*	Yellow, Japan, Black and Azov Seas		*L. mediterraneus*	"
	L. llewellyni	Black, Azov Seas and Sea of Japan		*L. chabaudi*	Mediterranean, Yellow Sea and Sea of Japan
	L. pilengas	"		*L. domnichi*	Yellow, East China Sea and Sea of Japan
	L. triangulari sp. n.	Sea of Japan		*L. cheleus*	Yellow Sea and Sea of Japan
	L. miroshnichenki sp. n.	Sea of Japan		*L. pacificus*	"
				L. chenzhenensis	Yellow Sea
Lz. macrolepis	*L. hamulosus*	South China Sea		*L. mugilinus*	NW Atlantic
				L. huitrempe	SE Pacific
Lz. ramada	*L. confusus*	Mediterranean Sea, Sea of Marmara	*M. platanus*	*L. uruguayense*	SW Atlantic
	L. imitans	Mediterranean Sea		*L. saladensis*	"
	L. parvicirrus	"			
Lz. saliens	*L. acuminatus*	Mediterranean and Black Sea	*M. liza*	*L. tainhae*	SW Atlantic
	L. macrocolpos	"		*L. brasiliensis*	"
	L. minimus	"		*L. guanduensis*	"
	L. heteronchus	" and Caspian Sea		*L. lizae*	"

* Only registrations on typical hosts are considered.

parasite assemblage (typical host for 10 (30 %) species and atypical host for 3 (9 %)), followed by *Lz. saliens* (typical and atypical host for 4 (12 %) species each), *Lz. haematocheilus* (5 (15 %) and 1 (3 %) species, respectively), *M. liza* (typical host for 3 (9 %) species), *Lz. aurata* (2 (6 %) species each), *Lz. ramada* (typical host for 3 (9 %) species), *M. platanus* (typical host for 2 (6 %) species) *C. labrosus* (1 (3 %) each), and *Lz. macrolepis* and *Lz. tade* are typical host for 1 (3 %) species each (see tables 17 and 18).

Seventeen (52 %) species are currently recorded in the Mediterranean region as parasitizing six of the eight mullet species known there. The Mediterranean shares one species, *L. chabaudi*, with the Pecific region occurring on *M. cephalus* and three species, *L. kaohsianghsieni*, *L. pilengas* and *L. llewellyni*, that were introduced into the Black and the Azov Seas from the western Pacific together with their typical host, *Lz. haematocheilus* in the 1970s. Three Mediterranean species of *Ligophorus* were reported in the Caspian

Table 18. Parasite/host list of the 33 valid species of *Ligophorus* from the Atlantic and Pacific waters based on our own and literature data (see Records for each species)

Таблица 18. Список 33 валидных видов *Ligophorus* с указанием их распределения на типичных и атипичных хозяевах из бассейнов Атлантического и Тихого океанов, основанные на наших и литературных данных (см. Регистрации для каждого вида)

Parasite name	Typical host	Atypical hosts
L. abditus	*M. cephalus*	–
L. acuminatus	*Lz. saliens*	–
L. angustus	*C. labrosus*	–
L. brasiliensis	*M. liza*	–
L. cephali	*M. cephalus*	*Lz. haematocheilus*
L. chabaudi	*M. cephalus*	–
L. cheleus	*M. cephalus*	–
L. chenzhenensis	*M. cephalus*	–
L. confusus	*Lz. ramada*	*Lz. saliens*, *M. cephalus*
L. domnichi	*M. cephalus*	–
L. guanduensis	*M. liza*	–
L. hamulosus	*L. macrolepis*	–
L. heteronchus	*Lz. saliens*	–
L. huitrempe	*M. cephalus*	–
L. imitans	*Lz. ramada*	–
L. kaohsianghsieni	*Lz. haematocheilus*	*Lz. aurata*, *M. cephalus*
L. lizae	*M. liza*	–
L. llewellyni	*Lz. haematocheilus*	–
L. macrocolpos	*Lz. saliens*	–
L. mediterraneus	*M. cephalus*	–
L. minimus	*Lz. saliens*	–
L. miroshnichenki sp. n.	*Lz. haematocheilus*	–
L. mugilinus	*M. cephalus*	
L. pacificus	*M. cephalus*	–
L. parvicirrus	*Lz. ramada*	–
L. pilengas	*Lz. haematocheilus*	*Lz. aurata*, *Lz. saliens*
L. rectus sp. n.	*Lz. tade*	–
L. saladensis	*M. platanus*	–
L. szidati	*Lz. aurata*	*Lz. saliens*
L. tainhae	*M. liza*	–
L. triangularis sp. n.	*Lz. haematocheilus*	–
L. uruguayense	*M. platanus*	–
L. vanbenedenii	*Lz. aurata*	*M. cephalus*, *C. labrosus*, *Lz. saliens*

Sea after introduction of their typical hosts (*Lz. aurata* and *Lz. saliens*). Ten (30 %) species occur in the Sea of Japan on two host species, sharing at least five species, *L. kaohsianghsieni*, *L. chabaudi*, *L. domnichi*, *L. cheleus*, and *L. pacificus* with the Yellow Sea and one species, *L. domnichi*, with the East China Sea. Eight (24 %) species are currently known in the southwest Atlantic region from two hosts, four species (12 %) occur in the Yellow Sea and two species (6 %) in the South China Seas from different host species, and one species (3 %) each in the southeast Pacific and the northwest Atlantic and the East China Sea on M. cephalus (table 17). It can be stated that the Mediterranean with the Black and the Azov Seas remain the best studied areas that account for more than fifty percent of currently known species diversity of *Ligophorus* in the Atlantic and Pacific regions.

The known geographical distributions of the 15 previously described species of *Ligophorus* (*L. vanbenedenii*, *L. kaohsianghsieni*, *L. szidati*, *L. chabaudi*, *L. macrocolpos*, *L. acuminatus, L. minimus*, *L. heteronchus*, *L. angustus*, *L. imitans, L. confusus*, *L. parvicirrus*, *L. pilengas*, *L. llewellyni* and *L. abditus*) were extended herein based on the material from the new samples. These new geographical records, as well as the discovery of

new *Ligophorus* species, have added the following localities to the known geographical distribution of the genus: the Gulf of Santa Pola and the Santa Pola Salt Marshes of the Mediterranean Sea, Spain; the Sozopol Bay of the Black Sea, Bulgaria; the Berdyansk Bay of the Azov Sea, Ukraine; the Posiet Bay, Kiyevka Bay and the Artemovka Delta of the Sea of Japan, Russia.

The species of *Ligophorus* are completely restricted to the members of the Mugilidae, suggesting a long association between the parasite genus and the host family. When the host-parasite associations are analyzed at the species level, evidence indicates that a given species of *Ligophorus* occurs mostly in a single host species. For instance, *L. mugilinus*, *L. mediterraneus* and *L. chabaudi* occur on *M. cephalus*; *L. macrocolpos*, *L. acuminatus*, *L. minimus* and *L. heteronchus* are found typically on *Lz. saliens* in the Mediterranean, and so on (table 17). Thus, all the recognized species of *Ligophorus* seem fairly oixenous. However, a number of records (see above taxonomic summary of individual species) report putative straggling infections (i. e., occurrences on the wrong host (Ryzsa, 1993)) with *Ligophorus* spp. It is difficult to establish, unambiguously, the nature of these atypical records, because some subjectivity is involved in determining whether or not a given host is typical for a given species. In addition, most previous works lack information on the number of specimens found, as well as on the structure and distribution of other sympatric mugilid populations in the studied areas (see below). However, we found in our material numerous instances that probably represent straggling infections, given that the abundance of specimens on those fish was much lower than on the common host species and their prevalence was less than 10 % in a particular locality and sampling season. Single-specimen infections include *L. szidati* on *Lz. haematocheilus* from the Kerch Channel and on *Lz. saliens* from the Ebro Delta, *L. vanbenedenii* on *C. labrosus* both from the Ebro Delta, *L. confusus* on *M. cephalus* from the Gulf of Valencia, *L. cephali* on *Lz. haematocheilus* from the Sivash Lake and the Kerch Channel, and *L. pilengas* on *Lz. saliens* from the Sozopol Bay, as well as 5-specimen infections with *L. confusus* on *Lz. saliens* from the Ebro Delta. These records seem to represent genuine straggling episodes that can be explained by the occurrence and high abundance of typical hosts (i. e., other mullets) in each locality (see table 1).

The importance of sympatric hosts for straggling was particularly well illustrated in the present study by the species of *Ligophorus* on *Lz. saliens* from the Kerch Channel and the Sivash Lake. In 2005, specimens of *Lz. saliens* were rare, whereas the catches of *Lz. aurata* were abundant in these localities. The three individuals of *Lz. saliens* that could be examined (table 1) lacked the common *Ligophorus* species of these hosts, whereas they harboured 13 specimens of *L. szidati* and one specimen of *L. vanbenedenii*, which are specific to *Lz. aurata*.

The present revision ascertains two episodes of host introductions that resulted in successful colonization of species of *Ligophorus* in the new areas: *Lz. haematocheilus* introduced into the Black Sea and the Sea of Azov from the western Pacific, and *Lz. aurata* and *Lz. saliens* introduced into the Caspian Sea from the Black Sea. The species transferred have adapted well to the new environments and currently dominate the parasite communities of the introduced hosts, probably due to an absence of other specific parasite helminths, e. g. digeneans, nematodes and acanthocephalans (Sarabeev, Domnich, 2000 and our unpublished data). However, it appears that not all species of *Ligophorus* could colonize the new areas. Only three of the five species currently known from *Lz. haematocheilus* in the native area have been recorded in the Black Sea and the Sea of Azov and only one of four and one of two species known on *Lz. saliens* and *Lz. aurata*, respectively, from the Mediterranean Sea have been found in the Caspian Sea (Mikailov, Seidli, 1989). These two patterns of dispersion of *Ligophorus* agree well with the general hypothesis of introduced hosts and their parasite communities (Torchin, Lafferty, 2009).

Thus, the rather strict host specificity and the composition of sympatric mullet populations seem important factors in accounting for the occurrence of species of *Ligophorus* in each host in a given locality. For instance, *L. szidati*, *L. vanbenedenii*, *L. mediterraneus*, *L. cephali*, *L. pilengas* and *L. kaohsianghsieni* were reported in the Azov Sea, where the populations of *Lz. haematocheilus*, *M. cephalus* and *Lz. aurata* are large and *Lz. saliens* is rare. In the same vein, *L. pilengas*, *L. kaohsianghsieni*, *L. triangularis* sp. n., *L. miroshnichenki* sp. n., *L. chabaudi*, *L. domnichi*, *L. pacificus*, *L. cheleus* and *L. abditus* occurred in the Russian part of the Sea of Japan where their usual hosts (*Lz. haematocheilus* and *M. cephalus*) historically occur. This conclusion is congruent with Esch and Fernández's (1993) view about the shaping of the parasite faunas of *M. cephalus* studied at that time in the world: "...the distribution and composition of parasite communities is greatly influenced by the contact between host populations. In this case, dispersal of the definitive host and phylogenetic relationships among the parasites seem to be much more significant for parasite distribution than vicariant events".

However, current data and the present study indicate that in addition to parasite exchange between disjoint populations, vicariance may also explain the occurrence of some species of *Ligophorus* on *M. cephalus*. For example, this host from the Mediterranean Sea and the Sea of Japan harbour *L. chabaudi* that is common in both seas, but two additional species occur only in the Mediterranean: *L. mediterraneus* and *L. cephali*, and three species, *L. pacificus*, *L. cheleus* and *L. abditus* only in the Pacific. Likewise, the disjoint populations of this fish in the NW Atlantic and the SE Pacific harbour different species (*L. mugilinus* and *L. huitrempe*, respectively) (table 17). However, recent molecular studies of *M. cephalus* from different geographic areas indicate that it may represent a species complex that includes at least 14 species (Durand et al., 2012; Whitfield et al., 2012). If we accept this molecular hypothesis (all these species morphologically, still have not been defined), then we should conclude that cospeciation and not vicariance is a leading event in species evolution and their diversity.

A salient pattern from examination of host-parasite records is that at least 30 of the recognized species typically co-occur on a given host species with at least another congener (Euzet, Suriano, 1977; Euzet, Sanfilippo, 1983; Radujković, Euzet, 1989; Hassan et al., 1990; D'Amelio et al., 1996; Caillot et al., 1999; Merella, Garippa, 2001; Mariniello et al., 2004; table 17 of the present study). The only exceptions seem to be *L. angustus*, *L. hamulosus* and *L. rectus* sp. n. on *C. labrosus*, *L. macrolepis* and *Lz. tade*, respectively. As was shown by Blasco-Costa et al. (2012) in examples of the Mediterranean species, these co-occurrences can be accounted for by both host-switching and lineage duplications.

Beyond the species level, it also seems common to find representatives of several dactylogyrid genera on a single host (Anderson, 1981; Llewellyn, Anderson, 1984; Radujković, Euzet, 1989; D'Amelio et al., 1996; Merella, Garippa, 2001). In the present study, members of *Ligophorus* co-occurred with species of *Ergenstrema* Paperna, 1964 on *C. labrosus* and *Lz. ramada*. A molecular phylogenetic hypothesis provided by Blasco-Costa (2012) clearly indicates the close relationship between these two genera.

Conclusion

The present study has revealed 33 valid species of *Ligophorus* in the surveyed region, including *L. triangularis* sp. n., *L. miroshnichenki* sp. n. and *L. rectus* sp. n., described in this study from the Pacific region but excluding *L. ellochelon*, which was transferred to another genus; *L. euzeti* and *L. gussevi* are considered as junior synonyms; *L. leporinus* as *incertae sedis*; and *L. chongmingensis* as *species inquirendae*. A new genus of Dactylogyridae *Kriboetrema* is proposed for a species morphologically similar to *Ligophorus* spp, but which differs from those in having a large dorsoventrally flattened body, a coiled

copulatory organ with a bulbous base, two prostatic reservoirs, a subovate or piryform ovary and inconspicuous or poorly developed lateral flaps of the haptor. Two species are proposed for allocation in the new genus, *K. ellochelon* comb. n. and *K. rectangulus* sp. n.

The erection of *Kriboetrema* gen. n. raises the number of Dactylogyridae genera from the grey mullets to three. Among them, *Ligophorus* is the most diverse and widely distributed genus, while *Ergenstrema* and *Kriboetrema* gen. n., represented by two species in each, seem to have a geographical distribution restricted to the NE Atlantic and the NW Pacific region, respectively (Paperna, 1964; Lambert, Sanfilippo, 1977; Anderson, 1981; the present study). The recent molecular study of phylogenetic relationships of *Ligophorus* spp. with other Dactylogyridae genera, based on partial 28S rDNA sequences, also indicates the presence of at least three genera from mullets in the Atlantic and Pacific regions (Blasco-Costa et al., 2012).

The examination of specimens of *Ligophorus*, using phase and differential interference contrast in the present and other recent studies (Sarabeev, Balbuena, 2004; Sarabeev et al., 2005; Rubtsova et al., 2006 a; Rubtsova et al., 2007; Rubtsova, 2009) has resulted in a better understanding of the composition of this genus. It has become evident that, because of the small size of *Ligophorus* species, certain features such as the genital sclerotized structures, processes on ventral and dorsal bars, exact number of head organs and ovary shape are extremely difficult to determine unless phase and differential interference contrast optics are used. In particular, the present study reveals or clarifies a number of morphological features of the genus.

Details of the base and shape of the copulatory organ, which are useful for generic discrimination within the Dactylogyridae (Kritsky, Boeger, 2002; Plaisance, Kritsky, 2004), are given herein. This provides a base for distinguishing *Ligophorus* from morphological similar dactylogyrids, such as *Haliotrema*, *Euryhaliotrema* and *Kriboetrema* gen. n. All *Ligophorus* species possess a base of the copulatory organ expanded into a complex structure, comprising a heel and a bulb. Such structure was depicted in all previous figures of *Ligophorus* spp.

The main morphological types for sclerotized structures are defined herein. These concern the shape of the copulatory organ and the position of its entrance in the accessory piece, the shape of the accessory piece and the distal end of the vagina, the morphology of the ventral bar and anchors.

A shield on the ventral side of the ventral bar is shared by all *Ligophorus* species and can be a useful synapomorphy to distinguish this genus from other genera of the Dactylogyridae.

We provided fuller descriptions of the accessory piece of the copulatory complex. This structure is a key feature for species discrimination because its morphology is unique for each species of *Ligophorus*. We established that all species of the genus treated in the present study share a bilobed accessory piece of the copulatory complex; its unequal parts join each other in a different manner in the case of each species, leading to the formation of a unique shape, which can vary from rod-shaped to cross-shaped (e. g. *L. rectus* sp. n. and *L. kaohsianghsieni*). The description of the accessory piece is clarified herein or in our recent studies (Sarabeev, Balbuena, 2004; Sarabeev et al., 2005; Rubtsova et al., 2006 a; Rubtsova et al., 2007) for all available species.

All studied herein representatives of the genus possess an elongated ovary, which is U- or J-shaped (the latter only in *L. rectus* sp. n.) (e. g. fig. 1 B in Rubtsova et al. (2007) and fig. 20 B of the present study). All previous descriptions of *Ligophorus,* except for Abdallah et al. (2009) and Soo and Lim (2012), have reported oval ovaries, for instance, fig. 2 in Euzet and Suriano (1977) concerning *L. vanbenedenii*; fig. 1 in Euzet and Sanfilippo (1983) concerning *L. parvicirrus*; fig. 1 in Hassan et al. (1990) concerning *L. imitans*; fig. 4 in Fernández (1987) concerning *L. huitrempe*; fig. 1 in Hu and Li (1992) concerning *L. chongmingensis*; and fig. 1 A in Sarabeev and Balbuena (2004) concerning

L. pilengas. The ovary elongation is a useful synapomorphy that clearly distinguishes representatives of the genus from many other genera of the Dactylogyridae. This character is most easily revealed when the worm or ovary lies in lateral view, whereas the latter generally appears oval in both ventral and dorsal views.

Although Euzet and Suriano (1977), Euzet and Sanfilippo (1983), Hassan et al. (1990) and Fernández (1987) noted that only the posterior pair of eyes have lenses, the present study indicates that all eyes have lenses in all the *Ligophorus* species. However, the lenses can be inconspicuous in the anterior pair.

Finally, the morphology and measurements of the pharynx, testis and haptor were provided for each redescribed species. It was done because numerous studies on the Dactylogyridae included this information in the descriptions of new species, e. g. Kritsky and Boeger (2002), Viozzi and Brugni (2004), Plaisance and Kritsky (2004) and Řehulková and Gelnar (2005). However, the shape and range of the metric characters of these organs are highly variable depending on fixation methods and degree of flattening. So these characteristics might be of little use for species discrimination, but can be useful for worm identification beyond the species level.

Consequently, a new generic diagnosis is issued, and a key to species is provided herein for the first time, to incorporate the new characteristics listed above, in order to facilitate species discrimination and differentiation of *Ligophorus* from morphological similar taxa. The key to species of *Ligophorus* furnished herein is predominantly based on features of the accessory piece of the copulatory complex, following the copulatory organ, anchors, ventral bar and vagina.

We consider that the morphology of the accessory piece is of paramount importance for species identification. However, care should be exercised when examining this character; as we showed for *L. heteronchus* and *L. euzeti*, its apparent shape varies with its orientation in space. The morphology of the anchors is also a useful character for species discrimination, although some species of *Ligophorus* have relatively uniform shapes and sizes. However, morphological similarity in the anchor/bar complex is not usually coupled with shape similarity of the copulatory complex. For example, *L. szidati*, *L. angustus* and *L. confusus* are similar in the shape of both anchor pairs and the ventral bar and considerably differ in the morphology of the accessory piece. The same pattern can be observed for *L. acuminatus*, *L. minimus* and *L. heteronchus*. Furthermore, as has been shown in *L. vanbenedenii* and *L. imitans,* morphometric characters of the anchors may depend on the size of the host (Caltran et al., 1995; Rubtsova et al., 2005). Thus, it is advisable that a series of specimens, known to be from hosts of different sizes, be studied when describing new species.

The present study provides hundreds of voucher specimens sampled in the Mediterranean and Azov-Black Sea region that were deposited in three main museums: BMNH, IZAN and ZNUMZ. Therefore, it compensates the lack of type specimens for most species described from this region, namely for *L. vanbenedenii*, *L. szidati*, *L. macrocolpos*, *L. acuminatus*, *L. minimus*, *L. heteronchus*, *L. angustus*, *L. imitans* and *L. confusus*

Ligophorus is a speciose taxon, whose species are oioxenous, restricted to mugilids, and show intriguing host-parasite patterns of association. Presented herein, the detailed description of each studied species is going to be used for a phylogenetic analysis based on the morphological data in our next paper. The understanding of evolutionary patterns is important for aquaculture where monogeneans can be a serious problem. Uncovering ecological and cophylogenetic interactions of hosts with their parasites can help in disease prediction (Desdevises, 2007). For instance, colonization of a host by new parasite can lead to the formation of unbalanced host-parasite relationships causing the death of the host (e. g. Sanz, 1992; Sasal et al., 1999). This study adds to the accumulating evidence, indicating the importance of abundant host population in sharing its specific species of *Ligophorus* with other sympatric hosts. In addition, all species of mullets sampled in

the present study, from 18 localities of five seas of the NE Atlantic and NW Pacific region, harboured species of *Ligophorus* (table 1). The prevalence in most samples were high, reaching 100 % in some localities (table 1) and the abundance of these parasites was usually in the range of several hundred individuals per fish. Because members of *Ligophorus* exhibit high host-specificity and are common and abundant, it is likely that many additional species remain to be discovered. In fact, most species of Mugilidae (over 80 %) have not been systematically surveyed for monogeneans and, thus, the present review might well have shown just the tip of the iceberg of *Ligophorus* biodiversity.

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Наукове видання

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Таксономічна ревізія атлантичних та тихоокеанських видів *Ligophorus* (Monogenea, Dactylogyridae) від кефалевих риб (Teleostei, Mugilidae) з пропозицією нового роду й описом чотирьох нових видів

Монографічна серія

Таксономічна ревізія атлантичних та тихоокеанських видів *Ligophorus* (Monogenea, Dactylogyridae) від кефалевих риб (Teleostei, Mugilidae) з пропозицією нового роду й описом чотирьох нових видів. Сарабєєв В., Рубцова Н., Янг Т., Бальбуена Х. А. — Київ, 2013

У роботі представлена ревізія видів *Ligophorus* Euzet and Suriano, 1977 з басейнів Атлантичного та Тихого океанів, яка базується на численному нещодавно зібраному матеріалі від кефалевих риб із Середземного, Японського й Південно-Китайського морів, а також на доступних для дослідження типових та ваучерних колекційних матеріалах. Всі 35 номінальних видів *Ligophorus*, відомі з басейнів Атлантичного й Тихого океанів критично переглянуті. З них 30 визнані валідними, один incertae sedis (*L. leporinus*), один species inquirendae (*L. chongmingensis*), два молодшими синонімами (*L. euzeti* та *L. gussevi*) та один вид перенесений до іншого роду. Описано три нових види роду *Ligophorus*: *L. triangularis*, *L. miroshnichenki* та *L. rectus*. Надано розширений діагноз роду *Ligophorus* та критично переглянуто попередні визначальні ознаки роду. Надано описи основних морфологічних типів копулятивного органу, допоміжного апарату копулятивного комплексу, дистального кінця вагіни, вентральної пластинки та серединних гачків. Обговорено таксономічну значущість склеротизованих частин у відповідності до їхньої функціональної морфології. Для кожного виду вказано попередні та теперішні знахідки на хазяях та їх географічне поширення. Для видів, які морфологічно подібні до *Ligophorus* spp., але відрізняються великим стиснутим у дорзовентральному напрямку тілом, звивистим копулятивним органом із шароподібною базою, двома простатичними пухирцями, грушоподібним або субовальним яєчником й малопомітними або слаборозвиненими бічними виростами гаптору, засновано новий рід *Kriboetrema*. Два види з басейну Тихого океану віднесено до нового роду — *K. ellochelon* comb. n. та *K. rectangulus* sp. n., від *Liza vaigiensis* та *Valamugil cunnesius* відповідно. Надано ключ родів та валідних видів з досліджених регіонів.

Ключові слова: Середземне море, Чорне море, Азовське море, Південно-Китайське море, склеротизовані структури, морфологія, видове визначення, специфічність.

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