

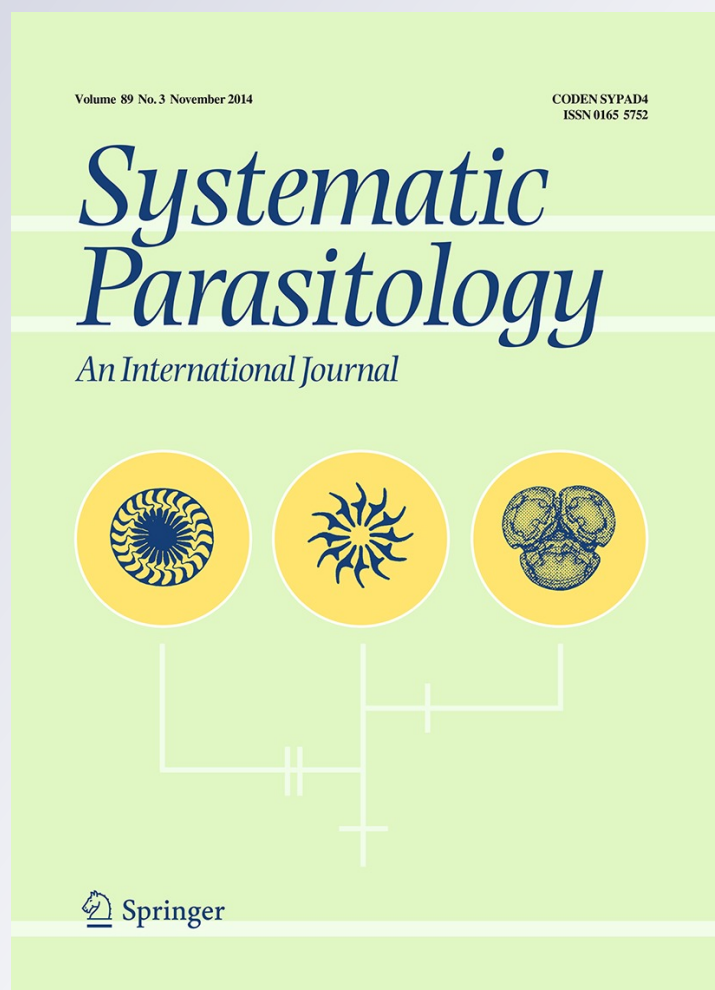
*Lamellodiscus aff. euzeti* Diamanka,  
Boudaya, Toguebaye & Pariselle, 2011  
(Monogenea: Diplectanidae) from the  
gills of *Cheimerus nufar* (Valenciennes)  
(Pisces: Sparidae) collected in the Arabian  
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# ***Lamellodiscus* aff. *euzeti* Diamanka, Boudaya, Toguebaya & Pariselle, 2011 (Monogenea: Diplectanidae) from the gills of *Cheimerius nufar* (Valenciennes) (Pisces: Sparidae) collected in the Arabian Sea, with comments on the distribution, specificity and historical biogeography of *Lamellodiscus* spp.**

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**Abstract** Specimens of *Lamellodiscus* Johnston & Tiegs, 1922 (Monogenea: Diplectanidae) were collected from the gills of *Cheimerius nufar* (Valenciennes) (Sparidae) in the Arabian Sea. All of these parasites belonged to one and the same species, which is morphologically very close to *L. euzeti* Diamanka, Boudaya, Toguebaya & Pariselle, 2011. A different host, distant locality and small morphological differences compared with the original description of *L. euzeti* acted as a stimulus for a detailed redescription. The specimens from the Arabian Sea differ slightly in the details of the male copulatory organ (MCO) from the type-specimens of *L. euzeti*, which were re-examined, and from the respective drawings in its original description. Such differences include a longer

inner process of the large element of the accessory piece associated with the proximal part of the copulatory tube, a longer point on the small element of the accessory piece associated with the distal part of the copulatory tube, and the presence of a smooth or slightly folded inner margin of this element rather than structures resembling spines which occur in the type-specimens of *L. euzeti*. Therefore, the present specimens infecting *C. nufar* in the Indo-Pacific may represent a different, but morphologically very similar species to the Atlantic form *L. euzeti*; consequently, they are recognised here as *Lamellodiscus* aff. *euzeti*. This form belongs to the ‘ignoratus s. str.’ subgroup of the genus. The composition of this subgroup is redefined to comprise 17 species, including *L. coral-linus* Paperna, 1965 but excluding *L. acanthopagri* Roubal, 1981, and the morphology of the MCO of representatives of this group is clarified. A link between the diversity of *Lamellodiscus* species and the ancestral origin of present-day sparid species in the Tethys Sea is suggested. It is shown that *Lamellodiscus* spp. exhibit rather high levels of specificity to their hosts, since half of them parasitise only a single host species and c.90% infect closely related host species. Comparison of the levels of host-specificity of the species of this genus with other narrowly specific genera of the Dactylogryidea revealed that their estimations are comparable. The possibility of intra-host speciation within *Lamellodiscus* is discussed. It is

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shown that a co-evolutionary model is more discernible if it includes data on the occurrence of morphologically similar species from different regions and host taxa.

## Introduction

The santer seabream *Cheimerius nufar* (Valenciennes) is widely distributed along coast of the Indian Ocean, including the Red Sea and Arabian Gulf, and is also found in the Eastern Atlantic off the southern coast of Africa (Froese & Pauly, 2011). However, there is currently little information available on its helminth parasites, since it appears that only one species, a digenean, has previously been early reported from this fish (Bray, 1986). During the present investigations, three monogenean species were collected, two members of the Microcotylidae Taschenberg, 1879, one of which has been recently described (Machkewskyi et al., 2013), and one species of the diplectanid genus *Lamellodiscus* Johnston & Tiegs, 1922.

Most species of *Lamellodiscus*, i.e. 53 of the 59 currently accepted species (Domingues & Boeger, 2008; Gibson et al., 2013), are strictly specific parasites of sparid hosts, which makes them of great interest for the study of host-parasite co-evolution and speciation (e.g. Desdevises, 2001, 2006; Desdevises et al., 2001, 2002a, b; Poisot & Desdevises, 2010; Poisot et al., 2011).

Twelve species of this genus are currently known from the Indian Ocean, Red Sea and Arabian Gulf (Paperna, 1965; Roubal, 1981; Byrnes, 1986; Oliver, 1987; Byrnes & Rohde, 1992; Kritsky et al., 2000; Aquaro et al., 2009). Most of these (eight species) were described from species of *Acanthopagrus* (Sparidae), the other hosts being species of *Diplodus*, *Epinephelus*, *Evynnis*, *Rhabdosargus* and *Crenidens* (Sparidae), *Dascyllus* (Pomacentridae) and *Centropyge* (Pomacanthidae). Consequently, *Cheimerius nufar* is an additional (ninth) host and the parasite, considered to have a close affinity to *L. euzeti* Diamanka, Boudaya, Toguebaye & Pariselle, 2011, is a new record (thirteenth) for a *Lamellodiscus* species in the Indian Ocean region.

## Materials and methods

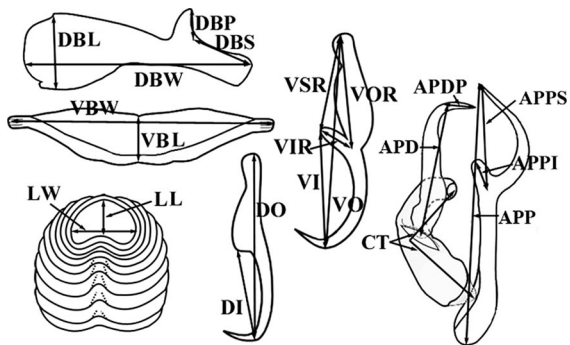
Thirteen specimens of *Cheimerius nufar*, identified according to Randall (1995) and Al-Abdessalaam

(1995), 30–34 cm in total length, were caught in the Arabian Sea off Shuweymiyah (17°54'N, 55°55'E) and Sharbithat (17°39'N, 56°32'E). Some fish were examined fresh and the remainder were frozen immediately upon collection and processed later. All monogeneans were collected from the gills, some of them immediately mounted in glycerine jelly (prepared with 0.5 g of carbolic acid) and others stained with acetocarmine or Mayer's paracarmine as described in Machkewskyi et al. (2013).

Type-material of *Lamellodiscus euzeti* BMNH [British Museum (Natural History) Collection at the Natural History Museum, London] No. 2011.2.17.1-3, *L. falcus* BMNH No. 2005.7.12.1-2, *L. neifari* BMNH No. 2005.7.12.3-4, *L. confusus* BMNH No. 2007.10.17.1-3, *L. toguebayei* BMNH No. 2010.8.11.1-3, 2010.8.11.4-9, *L. vicinus* BMNH No. 2010.8.11.10, *L. triacies* BMNH No. 2010.8.11.11-16 and 15 specimens of *L. fraternus* Bychowsky, 1957 newly collected from *Diplodus annularis* (L.) in the Black Sea, mounted in glycerine jelly and deposited in IBSS (Institute of the Southern Seas, Sevastopol) collection, were examined to clarify details of the morphology of the species from the 'ignoratus' group of *Lamellodiscus* spp. (Amine & Euzet, 2005).

Measurements and light micrographs were taken, using a Zeiss AxioScope A1 K fitted with an AxioCam Rc digital camera at magnifications of  $\times 100$ ,  $\times 200$ ,  $\times 400$  and  $\times 2,000$ , and an Olympus BX63 microscope fitted with DIC optics and a DP73 Olympus digital camera at magnifications of  $\times 1,000$ . The figures were made from a series of photos using the scalable vector graphics editor in the program Inkscape 0.48.2.-1 (<http://www.inkscape.org>).

The measurement scheme is presented in Fig. 1 and based on that suggested for the Dactylogyridea by Gusev (1985). We consider the male copulatory organ as including both the copulatory tube and the accessory piece, as has been used in most descriptions of *Lamellodiscus* spp. (e.g. Oliver, 1987; Justine & Briand, 2010). Abbreviations of the measurements are as follows: APD, length of small element of accessory piece (AP) of male copulatory organ (MCO) associated with distal part of copulatory tube; APDP, length of curved point of small element of AP; APP, length of largest element of AP associated with proximal part of copulatory tube; APPI, length of inner process of largest element of AP; APPS, length of sickle-shaped distal part of largest element of AP;



**Fig. 1** Diagrammatic representation of measurements of the haptor and male copulatory organ hard-parts of *Lamellogadus* spp. See “Materials and methods” section for abbreviations

CT, length of copulatory tube; DBL, length of dorsal bar; DBP, length of anterior process of dorsal bar; DBS, span between outer extremity and anterior process of dorsal bar; DBW, width of dorsal bar; DI, inner length of dorsal anchor; DO, outer length of dorsal anchor; LL, length of anterior lamella; LW, width of anterior lamella; VBL, length of ventral bar; VBW, width of ventral bar; VI, inner length of ventral anchor; VO, outer length of ventral anchor; VIR, length of ventral anchor inner root; VOR, length of ventral anchor outer root; VSR, span between ventral anchor roots. The length and width of organs and other measurements were measured along the longitudinal and transverse axes, respectively. All measurements are given in micrometres as the range followed by the mean and standard deviation in parentheses. Descriptive statistics were produced using the software package Statistica 6 for Windows. The authorities for the many species of *Lamellogadus* mentioned in the text are given in Table 2.

## Results

All examined fish were infected with monogeneans whose general internal morphology and haptor armaments conform to the diagnosis of *Lamellogadus* as amended by Justine & Briand (2010). A total of 352 specimens of *Lamellogadus* were found, all belonging to one and the same species, which is morphologically very close to *L. euzeti*. A different sparid host [*Cheimerius nufar* vs *Dentex canariensis* Steindachner and *D. gibbosus* (Rafinesque)] and

locality [Arabian Sea, off Oman, Indian Ocean vs off Senegal and the Ivory Coast, Atlantic Ocean and the Mediterranean Sea off Tunisia], in addition to some small morphological differences compared to the original description of *L. euzeti*, were motivation for the description of this material as *Lamellogadus* aff. *euzeti*.

### Diplectanidae Monticelli, 1903

#### *Lamellogadus* Johnston & Tieg, 1922

#### *Lamellogadus* aff. *euzeti* Diamanka, Boudaya, Toguebaye & Pariselle, 2011

*Host*: *Cheimerius nufar* (Valenciennes) (Sparidae).

*Locality*: Indian Ocean, Arabian Sea, off Oman.

*Site on host*: Gills.

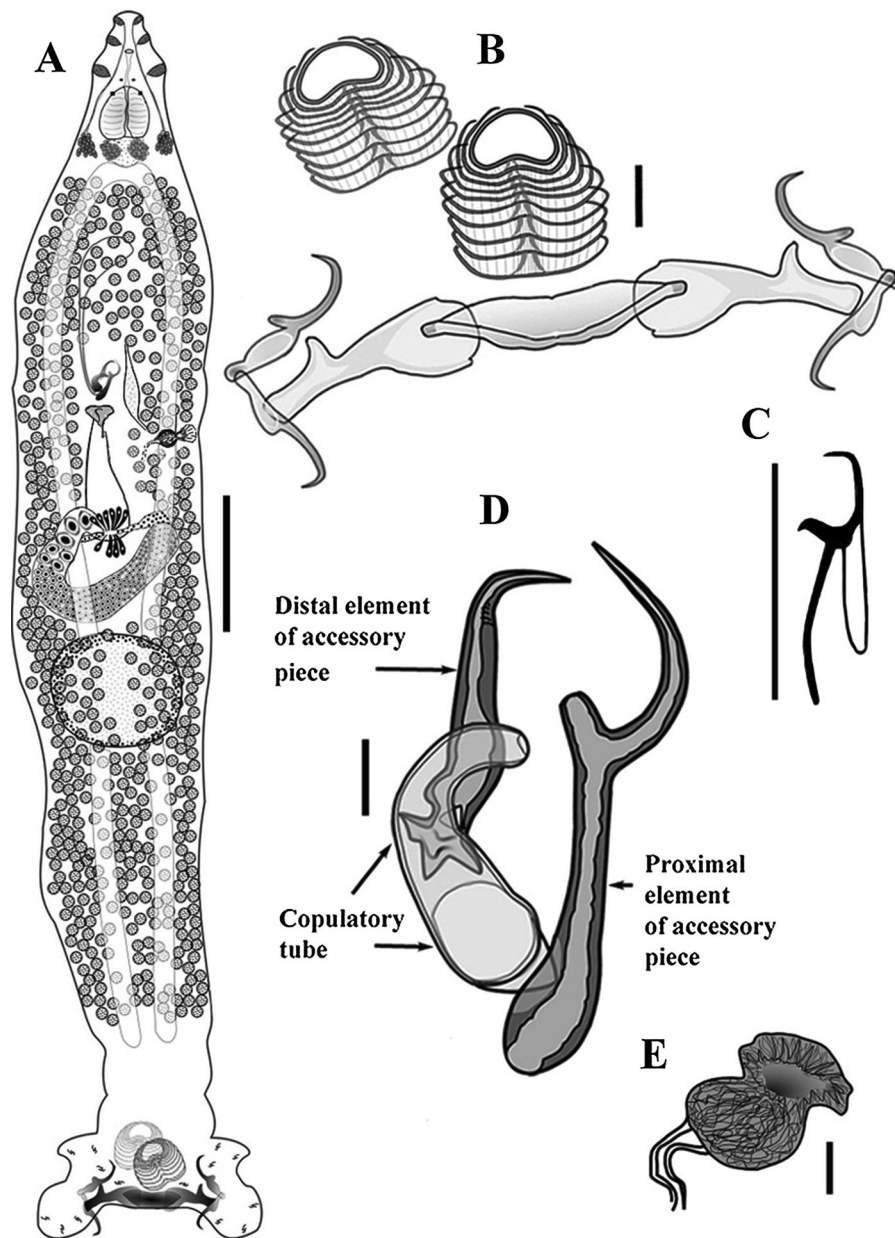
*Specimens studied*: 26 voucher specimens, collected from the gills of *C. nufar* in the Arabian Sea off Oman, were deposited in the BMNH collection (Reg. No. 2014.8.20.1-2) and in the IBSS collection (Reg. No. 525/1-16).

*Infection details*: Five fish caught off Shuweymiyah (November, 2012) were infected by 9–22 (mean  $\pm$  SD, 17  $\pm$  5) specimens per host, and eight fish taken off Sharbithat (December, 2012 and January, 2013) were parasitised by 5–125 (38  $\pm$  40) specimens per host.

*Description* (Figs. 2, 3A, 4A, 5)

[Based on 26 specimens; see Table 1 for metrical data.] Body elongate, slightly tapered anteriorly. Anterior region with 2 pairs of eye-spots; posterior pair larger and further apart. Body transforms smoothly into trapezoidal haptor, slightly wider than body itself (Fig. 2A).

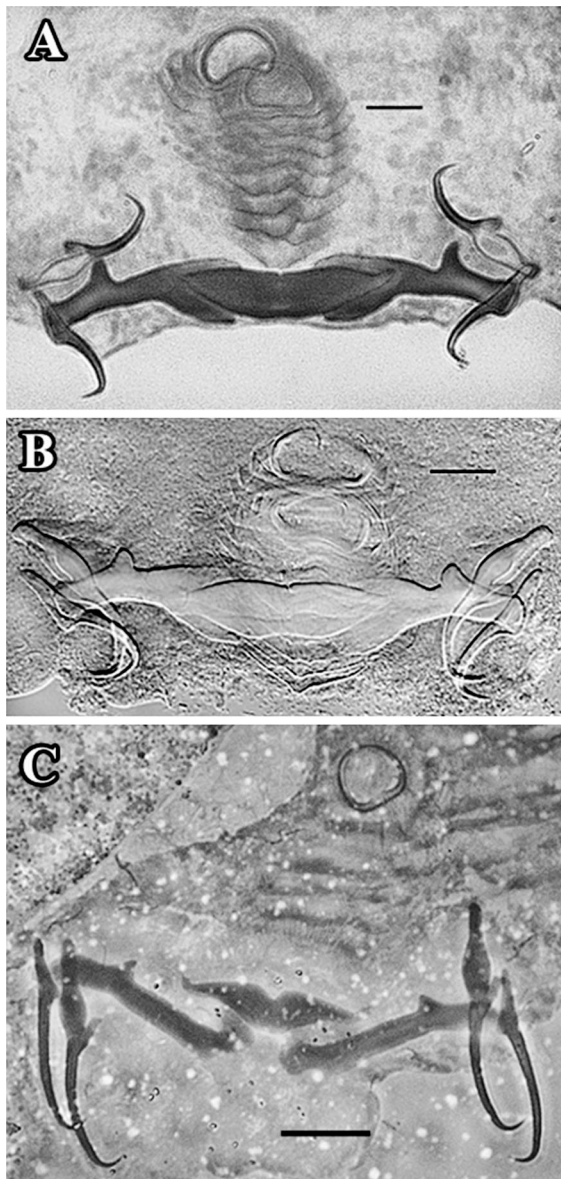
Ventral and dorsal lamellogadus (Figs. 2B, 3A) resemble those of ‘ignoratus’ group (Amine & Euzet, 2005), round, composed of 10 rows of concentric, reniform lamellae; anterior lamella completely closed, others crescentic. Both pairs of anchors elongate, with long outer root forming almost straight line with shaft; latter distinctly longer than point. Ventral anchors with short but well-differentiated inner root; outer root fusiform, bulbous, extended proximally. Dorsal anchors with indistinct inner root; outer root widened only on inside, rounded terminally. Marginal hooks 10–11 (10.5) long, unhinged, consist of sickle formed



**Fig. 2** *Lamellogadus* aff. *euzeti* ex *Cheimerius nufar* in the Arabian Sea. A, Whole-mount (composite, ventral view); B, Haptoral armament; C, Marginal hook; D, Male copulatory organ; E, Vaginal pore and chamber. Scale-bars: A, 200 µm; B, 20 µm; C–E, 10 µm

by short base with small upright thumb, slightly curved blade and straight shaft (Fig. 2C). One massive ventral bar, slightly narrowed in middle, enlarged submedially and tapered laterally, with extremities straight and blunt. Dorsal (lateral) bars sometimes slightly curved, with inner end distinctly wider than outer and prominent anterior process slightly curved towards lateral extremity of bar.

Single pair of cephalic glands posterolateral to pharynx, open into 3 pairs of head organs situated along anterolateral margin of body (Fig. 2A). Mouth anterior, ventrally subterminal. Prepharynx narrow. Pharynx oval. Oesophagus short, surrounded by digestive glands with which it forms round expansion posterior to pharynx. Intestine bifurcate; caeca simple, terminate blindly at level of posterior margin of vitelline field.



**Fig. 3** Photomicrographs of the haptor of *Lamellogadus* aff. *euzeti* ex *Cheimerius nufar* in the Arabian Sea off Oman (A); *L. euzeti* ex *Dentex canariensis* in the Atlantic Ocean off Senegal (B); and *L. fraternus* ex *Diplodus annularis* in the Black Sea off the Crimea (C). Scale-bars: 20  $\mu$ m

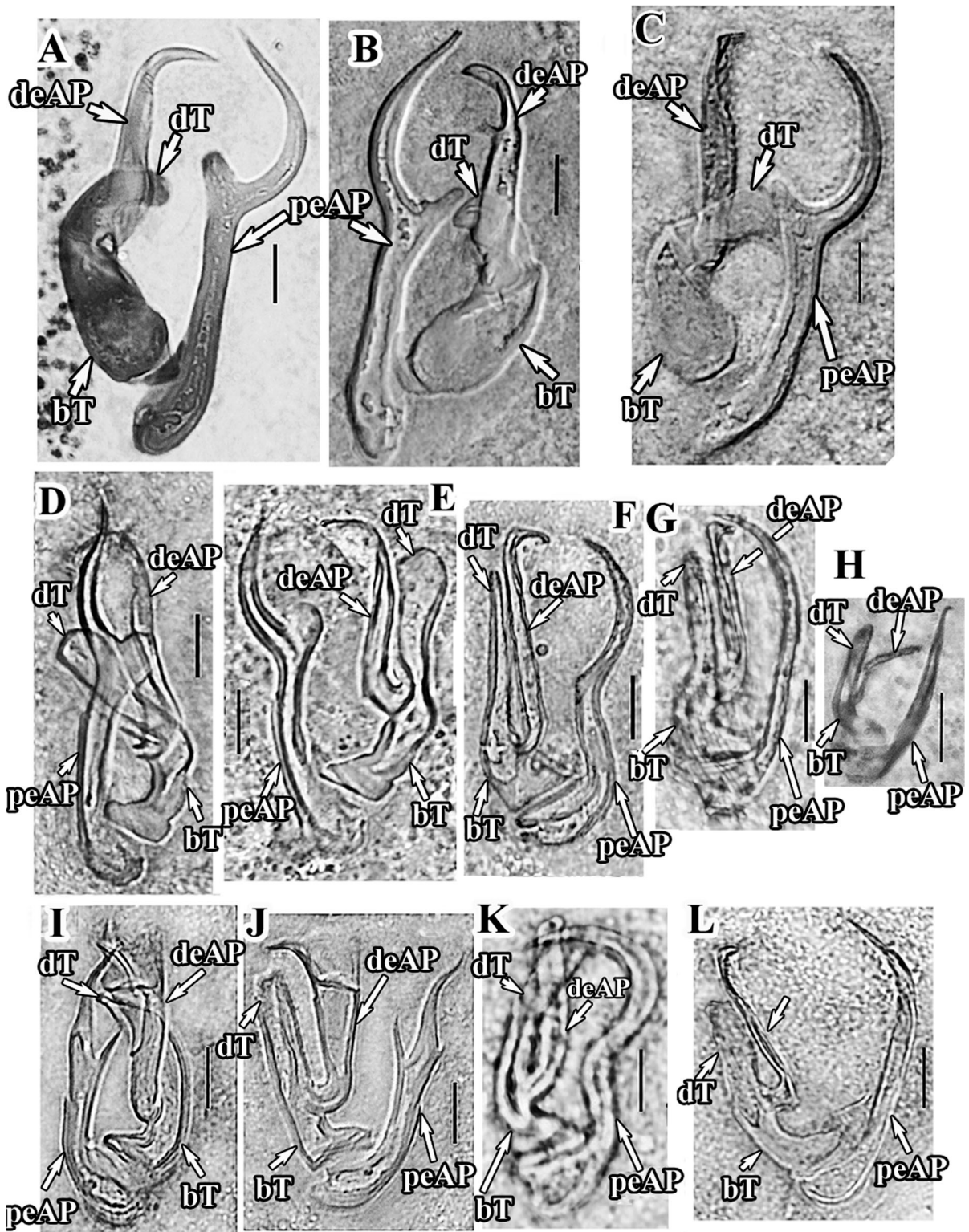
Testis suboval, intercaecal, in third quarter of body (Fig. 2A). Proximal and distal parts of vas deferens not observed, but fusiform seminal vesicle visible to left of cirrus. Prostatic glands not observed; prostatic reservoir anterior to male copulatory organ (MCO), opens posteriorly into distal part of copulatory tube. MCO comprised of 3 elements (Fig. 2D): thick,

saccular, curved copulatory tube with tapered base; and accessory piece (AP) composed of 2 unconnected elements (or it may be considered as 2 accessory pieces) which are articulated with copulatory tube in different positions. Structure of MCO resembles composition of this organ in *L. tubulicornis*. Largest element of AP (Fig. 4A: peAP) with sickle-shaped distal part situated facing copulatory tube and connected to it *via* its proximal end. Second element (Fig. 4A: deAP) small, associated with distal half of copulatory tube, with curved, pointed distal end, sometimes with slight folding of inner margin at base of bend in point; proximal part more extended and slightly reflexed, rounded proximally and abuts with small perpendicular plate around which copulatory tube curves.

Ovary situated anterior to testis (Fig. 2A), broad U-shaped, loops across body and around right intestinal caecum; germinal region posterior and dorsal. Oviduct and oötype indistinct; latter surrounded by clearly discernible Mehlis' gland. Proximal part of vaginal duct and seminal receptacle not observed. Vagina opens dorsally on lateral margin to left of uterus; vaginal opening funnel-shaped, enlarged proximally to form vaginal chamber 18–24 (22) in diameter (Figs. 2E, 5B). Uterus wide, extends anteriorly and medially, opens at posterior end of MCO. Vitellarium follicular, arranged in 2 lateral bands, coextensive with intestinal caeca, contiguous anterior to MCO and posterior to testis. One lateral vitelline collecting duct on each side of body opens into oötype. Single tetrahedral egg observed, 56 long, 62 wide, with single filament, 25.5 long (Fig. 5C).

#### Remarks

Specimens of *Lamellogadus* aff. *euzeti* have a close affinity to *L. euzeti* based on the morphological similarity of the haptor structures (Fig. 3A, B), male copulatory organ (MCO) (Fig. 4A–C) and the dimensions of most measurements (Table 1). In relation to *L. euzeti*, which was described from *Dentex canariensis* Steindachner and *D. gibbosus* (Rafinesque) in the Mediterranean Sea and in the Atlantic Ocean off Senegal and the Ivory coast (Diamanka et al., 2011a), specimens found in the Arabian Sea from *Cheimerius nufar* differ in some details of the MCO, namely in: (i) the longer inner process of the larger element of the accessory piece (AP) associated with the proximal part

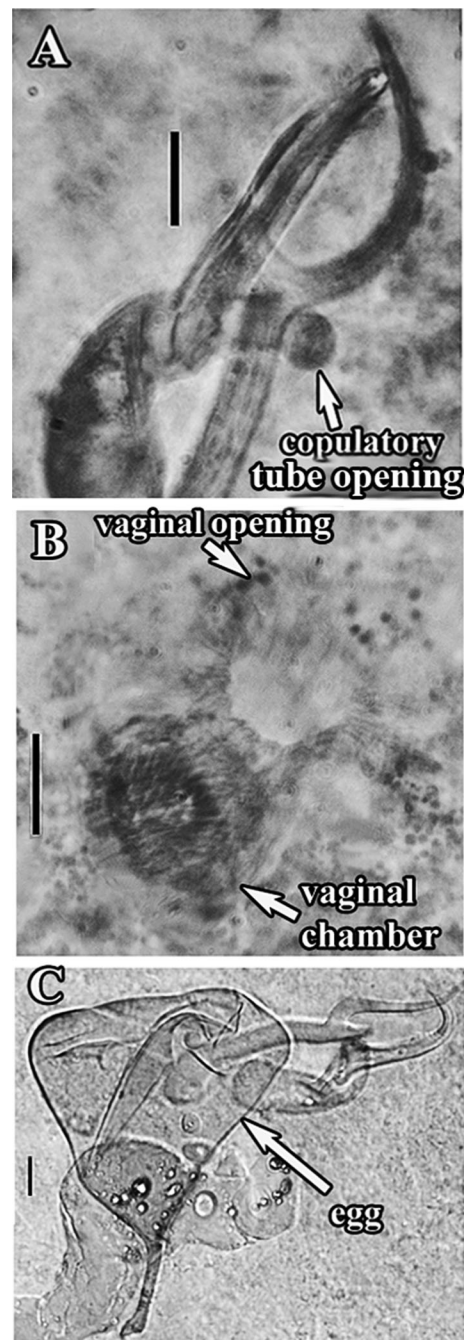




**Fig. 4** Photomicrographs of the male copulatory organ of *Lamellodiscus* aff. *euzeti* ex *Cheimerius nufar* in the Arabian Sea (A); *L. euzeti* ex *Dentex canariensis* (B, C) and *L. tougebyei* (D, E), *L. triacis* (I, J) and *L. vicinus* (L) ex *D. macrophthalmus* in the Atlantic Ocean off North Africa; *L. confusus* ex *Sarpa salpa* (F), *L. neifari* (G) and *L. falcus* (K) ex *Diplodus sargus* in the Mediterranean Sea; and *L. fraternus* ex *Diplodus annularis* in the Black Sea (H). Abbreviations: bT, basal part of copulatory tube; dT, distal part of copulatory tube; deAP, small distal element of accessory piece; peAP, large proximal element of accessory piece. Scale-bars: 10  $\mu$ m

of the copulatory tube; (ii) the longer point of the smaller element of the AP associated with the distal part of the copulatory tube (Table 1: APPI and APDP); and (iii) the smooth or slightly folded inner margin of the latter element (Fig. 4A) vs the presence of 5–6 spines in this position in the description of *L. euzeti* (figure 2G of Diamanka et al., 2011a) and 1–4 structures resembling spines visible in the two type-specimens of *L. euzeti* reinvestigated in the present study (Fig. 4B, C). Consequently, the present specimens infecting *C. nufar* in the Indo-Pacific possibly represent a taxon which is different from, but morphological very similar to, *L. euzeti*. However, in view of possibility that species differentiated by small morphological differences, mainly in the shape of the MCO, may be conspecific (Poisot et al., 2011), we are not completely certain that these small differences are not within the limits of intra-specific variation. We have, therefore, designated the present material as *Lamellodiscus* aff. *euzeti*. Since some of the species morphologically similar to *L. euzeti* have been described in insufficient detail, their type-material was re-examined; these species are differentiated below from specimens of *L. aff. euzeti* collected in the Arabian Sea.

*Lamellodiscus* aff. *euzeti* closely resembles, in the general shape of the MCO and haptoral structures, *L. sarculus*, described from *Pagrus coeruleostoticus* (Val.) in the Mediterranean Sea and in the Atlantic Ocean off Senegal (Neifar et al., 2004). However, it differs in: (i) the shape of the small distal element of the MCO AP, which has a distinctly longer curved point (a quarter of the subunit's total length), compared with the poorly defined point of this structure in *L. sarculus* (compare Fig. 4A with figure 2F of Neifar et al., 2004); (ii) a longer large element of the AP connected to the proximal end of the copulatory tube (APP: 70–82 vs 84–100  $\mu$ m); (iii) a well-differentiated inner



**Fig. 5** Photomicrographs of the male copulatory organ (A), vagina (B) and egg (C) of *Lamellodiscus* aff. *euzeti* ex *Cheimerius nufar* in the Arabian Sea off Oman. Scale-bars: A, B, 10  $\mu$ m; C, 20  $\mu$ m

process of this element, which is indistinct in *L. sarculus*; and (iv) a well-pronounced and rather long anterior processes of the dorsal bar vs a small swelling

**Table 1** Metrical comparison of *Lamellodiscus* aff. *euzeti* parasitising *Cheimertius nufar* in the Arabian Sea with morphologically closely related species

Species	<i>L. aff. euzeti</i>		<i>L. euzeti</i>		<i>L. triacies</i>		<i>L. toquebayei</i>		<i>L. victus</i>		<i>L. nufari</i>		<i>L. falcus</i>		<i>L. confusus</i>		<i>L. fratermus</i>
	Arabian Sea	O	P	O	P	O	P	O	P	O	P	O	P	O	P	O	Black Sea
Locality	Atlantic Ocean off northern coast of Africa																
Host	<i>Cheimertius nufar</i>																
	<i>Dentex macrocephalus</i>																
Source of data	Mediterranean Sea																
	<i>Diplodus sargus, D. vulgaris</i>																
N	<i>Sarpa salpa</i>																
	O	P	O	P	O	P	O	P	O	P	O	P	O	P	O	P	O
BL <sup>b</sup>	838–2,000 (1,155±332)	1,092	802–1,622 (1,142±74)	685–795 (614)	564–900 (630)	533–687 (620)	504–694 (589)	523–902 (630)	544	500–850 (652)	740	500–850 (652)	430	300–500 (394)	876–1,228 (988)	550–800 (700±93)	200–400 (280)
BW	156–330 (214±51)	201	135–280 (211±33)	134–181 (157)	92–161 (135)	109–132 (122)	121–179 (146)	111–168 (143)	96	90–145 (102)	95	90–145 (102)	74	75–90 (825)	121–165 (150)	130–180 (160±15)	55–110 (80)
HL	78–188 (113±27)	89	–	121–132 (124)	–	79–127 (100)	–	66	66	–	78	–	67	133–150 (142)	–	55–70 (60)	–
HW	102–333 (223±62)	226	134–314 (251±34)	151–195 (177)	118–183 (148)	105–186 (141)	135–165 (153)	140	115–222 (160)	140	95–135 (115)	130	–	207–282 (239)	140–200 (166±18)	80–120 (96.5)	–
PhL	65–91 (78±8)	62	–	58–69 (63)	–	37–54 (46)	–	52	–	46	–	29	–	44–60 (51)	40–55 (43±4)	18–27 (22)	–
PhW	60–94 (79±9)	74	78–95 (86)	41–77 (61)	49–58 (52)	32–53 (40)	39–54 (47)	31	40–49 (45)	41	–	26	–	39–53 (45)	30–45 (35±4)	20–30 (23.5)	–
CT	45–52 (48±2)	44	–	31–39 (36)	–	39–42 (40)	–	33	–	33	–	38	–	36–39 (38)	–	17–23 (19)	–
APP	70–82 (74±3)	69	71–79 (75±2)	45–49 (47)	41–49 (46)	56–60 (58)	49–59 (54)	47	47–57 (50)	47	33–47 (41)	40	39–42 (40.5)	47–51 (49)	45–50 (47±2)	27–32 (29)	–
APPS	30–35 (32±1)	31	–	19–24 (21)	–	24–29 (26)	–	–	–	–	–	20	–	23–26 (24)	–	–	–
APPI	9–12 (10±1)	14	–	9–11 (10)	–	7–9 (7.5)	–	–	–	–	–	–	–	–	–	–	–
APD	32–40 (36±2)	37	34–46 (41±2)	20–23 (21)	25–30 (27)	32–35 (34)	24–30 (28)	29	25–31 (28)	28	–	29	–	30–35 (33)	–	15–19 (17)	–
APDP	8–10 (8.5±1)	4	–	5–7 (6)	–	–	–	3	–	4	–	2	–	5–6 (6)	–	–	–
VO	52–58 (55±1)	54	49–61 (55±3)	50–53 (52)	46–53 (49)	59–64 (62)	53–64 (59)	39	37–45 (41)	34	23–32 (29)	32	30–32 (31)	32–36 (34.5)	32–36 (34±1)	45–56 (50.5)	–
VI	28–33 (31±1)	23	–	27–29 (28)	–	37–41 (40)	–	26	–	18	–	17	–	17–20 (18)	–	34–36 (35)	–
VOR	26–30 (28±1)	29	28–34 (31±1)	27–30 (29)	23–29 (27)	31–33 (32)	24–34 (30)	17	17–22 (19)	16	13–15 (14.5)	16	13–15 (14)	16–19 (17)	14–18 (15±1)	19–23 (20)	–
VIR	9–11 (10±1)	10	9–14 (12±1)	8–10 (9)	8–12 (9)	12–14 (13)	9–16 (13)	7	6–10 (8.5)	5	5–6 (5)	5	5–6 (5.5)	4–6 (5)	4–6 (5±1)	6–7 (7)	–

**Table 1** continued

Species	<i>L. aff. euzeti</i>		<i>L. euzeti</i>		<i>L. triacis</i>		<i>L. tognebayei</i>		<i>L. vicinus</i>		<i>L. neifari</i>		<i>L. falcus</i>		<i>L. confusus</i>		<i>L. fratermus</i>		
	Locality	Arabian Sea	Atlantic Ocean off northern coast of Africa		Dentex macrophthalmus		Dentex canariensis		Mediterranean Sea		Diploodus sargus, D. vulgaris		Sarpa salpa		Black Sea		<i>Diploodus annularis</i>		
Host	<i>Cheimereus nufar</i>	O	P	O	P	O	P	O	P	O	P	O	P	O	P	O	P	O	
Source of data	O <sup>a</sup>	2	31	2	31	2	31	2	31	2	31	2	31	2	31	2	31	2	31
N	26	21	23	9	10	45	47	24	26	16.5	17	14	16	15	12	15	15	15	17
VSR <sup>b</sup>	23–26 (24±1)	21–29 (25±2)	24–25 (24.5)	7–8 (8)	40–42 (41)	20–23 (22)	7–8 (7.5)	64–70 (68)	15–20 (17.5)	13–17 (14)	62–68 (64)	18–22 (20)	1	8	15–19 (17±1)	17–24 (20±2)	20–29 (24±1)	7–11 (8.5±1)	17–24 (20±2)
VP	9–10 (10±0.4)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
DO	45–50 (47±1)	44–51 (48±1.5)	40–42 (41)	35–43 (40)	49–53 (50.5)	30–34 (31.5)	7–8 (7.5)	64–70 (68)	15–20 (17.5)	13–17 (14)	62–68 (64)	18–22 (20)	1	8	15–19 (17±1)	17–24 (20±2)	20–29 (24±1)	7–11 (8.5±1)	17–24 (20±2)
DI	23–27 (25±1)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
DP	9–10 (9.5±0.5)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
VBW	77–98 (85±4.5)	74–82 (77±2)	64–70 (68)	61–68 (64)	56–65 (59)	52–63 (57)	7–8 (7.5)	64–70 (68)	15–20 (17.5)	13–17 (14)	62–68 (64)	18–22 (20)	1	8	15–19 (17±1)	17–24 (20±2)	20–29 (24±1)	7–11 (8.5±1)	17–24 (20±2)
VBL	15–20 (17±1)	16–23 (20±2)	13–17 (14)	8–10 (9)	66–69 (67)	60–72 (66)	7–8 (7.5)	64–70 (68)	15–20 (17.5)	13–17 (14)	62–68 (64)	18–22 (20)	1	8	15–19 (17±1)	17–24 (20±2)	20–29 (24±1)	7–11 (8.5±1)	17–24 (20±2)
DBW	66–80 (72±4)	60–68 (64±2)	62–68 (64)	57–65 (61)	66–69 (67)	60–72 (66)	7–8 (7.5)	64–70 (68)	15–20 (17.5)	13–17 (14)	62–68 (64)	18–22 (20)	1	8	15–19 (17±1)	17–24 (20±2)	20–29 (24±1)	7–11 (8.5±1)	17–24 (20±2)
DBL	21–25 (23±1.5)	22–24 (23±1)	18–22 (20)	13–15 (14)	13–15 (14)	13–15 (14)	1	15–19 (16)	22–26 (24)	22–27 (25)	20–26 (23)	18–20 (19)	15–22 (19)	15–22 (19)	15–22 (19)	15–22 (19)	15–22 (19)	15–22 (19)	15–22 (19)
DBP	7–11 (8.5±1)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
DBS	17–24 (20±2)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
LL	15–19 (17±1)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
LW	25–29 (27±1.5)	24–36 (29±2)	22–27 (25)	20–26 (23)	18–20 (19)	15–22 (19)	22–27 (25)	20–26 (23)	18–20 (19)	15–22 (19)	22–27 (25)	20–26 (23)	18–20 (19)	15–22 (19)	22–27 (25)	20–26 (23)	18–20 (19)	15–22 (19)	22–27 (25)

<sup>a</sup> O, own data; P, data published in Diamanka et al. (2011a, b) and Amine et al. (2006, 2007a); <sup>b</sup>For character abbreviations, see 'Materials and methods'

in *L. sarculus* (compare Fig. 3A with figure 2B of Neifar et al., 2004).

Of the two species of the ‘ignoratus sensu stricto’ subgroup, which are also found in the Indian Ocean region, i.e. *L. corallinus* described from *Dascyllus marginatus* Rüppell and *Centropyge bispinosus* (Günther) in the Red Sea (Paperna, 1965) and *L. pagrosomi* from *Chrysophrys auratus* (Forster) off South Australia (Roubal, 1996), the former differs distinctly from *L. aff. euzeti* in the absence of an MCO AP, whereas in the latter the MCO appears to be similar in shape. However, *L. aff. euzeti* differs from *L. pagrosomi* in: (i) the presence of an anterior process on the dorsal bar (absent in *L. pagrosomi*); (ii) the greater length of the proximal element of the MCO AP (70–82 vs 33–53 µm); and (iii) the sickle-shaped distal part of this element of the AP with a well-differentiated inner process, as opposed to this structure being slightly bent and lacking any process (compare Fig. 2D with figures 12–19.2 of Zhang et al., 2001) (data for *L. pagrosomi* from the latter authors).

*Lamellodiscus* aff. *euzeti* can be easily distinguished from *L. fraternus*, which infects *Diplodus* spp. in the Mediterranean, Adriatic and Black Seas (Bychowsky, 1957; Oliver, 1987; Radujkovic & Euzet, 1989), and also belongs to the ‘ignoratus s. str.’ subgroup, by: (i) its larger ventral bar (Table 1: VBW, VBL); (ii) the shape of the dorsal bars with distinctly widened inner ends, whereas they are equal in width along their entire length in *L. fraternus* (cf. Figs. 3A vs 2H); (iii) greater measurements of the MCO (Table 1: CT, APP, APD); and (iv) the shape of largest element of the AP of the MCO, which has a well-pronounced inner process which is lacking in *L. fraternus* (cf. Figs. 4A vs 4H). Note that measurements and figures of the haptoral hard-parts and MCO of *L. fraternus*, from its type-host and locality, are presented here for the first time.

Of those species of *Lamellodiscus* from this same subgroup which are found in the other regions, *L. toguebayei*, reported from *Dentex macrophthalmus* (Bloch) off the Atlantic coast of North Africa (Diamanka et al., 2011b), has an MCO resembling that of *L. aff. euzeti* (Fig. 4A, D, E). However, *L. aff. euzeti* differs in: (i) the greater total length of the largest proximal element of the AP (Table 1: APP); (ii) the larger sizes of the ventral bar (Table 1: VBW, VBL); and (iii) the distinctly longer anterior processes of the dorsal bar (Table 1: DBP).

*Lamellodiscus confusus*, *L. crampus*, *L. erythrini*, *L. ignoratus*, *L. falcus*, *L. knoepffleri*, *L. neifari*, *L. sigillatus* and *L. vicinus*, all parasites of sparids in the Eastern Atlantic and the Mediterranean and Adriatic Seas (Oliver, 1969; Radujkovic & Euzet, 1989; Neifar et al., 2004; Amine et al., 2006a, 2007a; Neifar, 2008; Diamanka et al. 2011b), are similar to *L. aff. euzeti* in the curved, pointed tip of the smallest distal element of the MCO AP. However, the latter differs from them all in: (i) the shape of the largest element of the AP possessing a well-pronounced inner process (absent in the above-mentioned species) (cf. Fig. 4A vs 4F, G, K, L); and (ii) the shape of the dorsal bar with a well-pronounced anterior process (absent, or virtually so, in the other species) (Table 1: DBP). The remaining known species of the ‘ignoratus s. str.’ subgroup, i.e. *L. rastelus* from *Pagrus auriga* Valenciennes and *L. triacies* from *Dentex macrophthalmus*, differ greatly from *L. aff. euzeti* in the shape of both attachment and copulatory structures (Neifar et al., 2004; Diamanka et al., 2011b).

Amended species composition and morphology of the male copulatory organ of the ‘ignoratus s. str.’ subgroup of *Lamellodiscus* spp.

Three morphological groups of *Lamellodiscus* spp., i.e. the ‘ignoratus’, ‘elegans’ and ‘tubulicornis’ groups, are distinguished according to the structure of the lamellodiscs and the male copulatory organ (Oliver, 1987; Neifar et al., 2004; Amine et al., 2006a; Justine & Briand, 2010). In addition, two subgroups of the ‘ignoratus’ species group are defined by the shape of the dorsal bar (Amine & Euzet, 2005). The ‘ignoratus s. str.’ subgroup of Amine & Euzet (2005) currently comprises, according to Diamanka et al. (2011a), 16 species. It should be noted that according to Diamanka et al. (2011a), *L. acanthopagri* Roubal, 1981 was erroneously listed as a member of the ‘ignoratus’ group, because of the structure of the lamellodiscs in this species, i.e. 2–9 rows composed of paired elements (Roubal, 1981), which is characteristic of the ‘elegans’ group sensu Oliver (1987). On the other hand, it is apparent that *L. corallinus* Paperna, 1965 should be included in the ‘ignoratus’ group sensu Oliver (1987), because, in the original description of this species, the lamellae of the dorsal lamellodisc were described as “shaped as closed rings” and those of the ventral lamellodisc as “bow shaped units, each plate constricted in its middle” (Paperna, 1965: p. 7),

**Table 2** Occurrence of *Lamellodiscus* spp. in different hosts and regions, with remarks on their membership of species groups in relation to the morphology of the haptor structures and the MCO

Species of <i>Lamellodiscus</i> <sup>a</sup>	Host <sup>b</sup>	Region <sup>c</sup>	Species groups/type of the haptor structures	Species groups/type according to the morphology of the MCO	Source of data
<i>L. dentexi</i> Aleshkina, 1984	<i>Dentex macrophthalmus</i>	EA	'elegans' group	'polymorphous' type; 'elongatus' type	Oliver (1987); Diamanka et al. (2011b)
<i>L. toguebayei</i> Diamanka, Neifar, Pariselle & Euzet, 2011	<i>Dentex macrophthalmus</i>	EA	'ignoratus' group; 'ignoratus s. str.' subgroup	'lyre' type	Diamanka et al. (2011b)
<i>L. triacies</i> Diamanka, Neifar, Pariselle & Euzet, 2011	<i>Dentex macrophthalmus</i>	EA	'ignoratus' group; 'ignoratus s. str.' subgroup	'lyre' type	Diamanka et al. (2011b)
<i>L. victinus</i> Diamanka, Neifar, Pariselle & Euzet, 2011	<i>Dentex macrophthalmus</i>	EA	'ignoratus' group; 'ignoratus s. str.' subgroup	'lyre' type	Diamanka et al. (2011b)
<i>L. coronatus</i> Euzet & Oliver, 1966 <sup>a</sup>	<i>Diplodus cervinus</i> ; <i>D. annularis</i> ; <i>D. sargus</i>	EA; MS	'elegans' group	'furca' type	Oliver (1987); Desdevises et al. (2002b)
<i>L. drummondi</i> Euzet & Oliver, 1967	<i>Pagellus acarne</i>	EA; MS	'elegans' group	'polymorphous' type	Oliver (1987)
<i>L. furcosus</i> Euzet & Oliver, 1966	<i>Diplodus sargus</i> ; <i>D. annularis</i>	EA; MS	'elegans' group	'furca' type	Oliver (1987)
<i>L. gracilis</i> Euzet & Oliver, 1966	<i>Diplodus sargus</i> ; <i>D. annularis</i> ; <i>Oblada melanura</i> ; <i>Spondyliosoma cantharus</i>	EA; MS	'elegans' group	'furca' type	Oliver (1987)
<i>L. knoeffleri</i> Oliver, 1969	<i>Spondyliosoma cantharus</i> ; <i>Spicara maena</i> ; <i>S. smaris</i> (Centranchidae)	EA; MS	'ignoratus' group; 'ignoratus s. str.' subgroup	'lyre' type	Oliver (1987); Amine & Euzet (2005)
<i>L. mirandus</i> Euzet & Oliver, 1966	<i>Diplodus sargus</i>	EA; MS	'elegans' group	'furca' type	Oliver (1987)
<i>L. obeltae</i> Oliver, 1973 <sup>d</sup>	<i>Pagellus bogaraveo</i> ; <i>P. acarne</i>	EA; MS	'elegans' group	'furca' type; 'elongatus' type	Oliver (1987); Diamanka et al. (2011b)
<i>L. parisi</i> Oliver, 1969	<i>Sarpa salpa</i>	EA; MS	'elegans' group	'furca' type	Oliver (1987)
<i>L. rastellus</i> Neifar, Euzet & Oliver, 2004	<i>Pagrus auriga</i>	EA; MS	'ignoratus' group; 'ignoratus s. str.' subgroup	'lyre' type	Neifar et al. (2004)
<i>L. sarculus</i> Neifar, Euzet & Oliver, 2004	<i>Pagrus caeruleostictus</i>	EA; MS	'ignoratus' group; 'ignoratus s. str.' subgroup	'lyre' type	Neifar et al. (2004)

Table 2 continued

Species of <i>Lamellodiscus</i> <sup>a</sup>	Host <sup>b</sup>	Region <sup>c</sup>	Species groups/type according to the morphology:		Source of data
			of the haptoral structures	of the MCO	
<i>L. sigillatus</i> Neifar, Euzet & Oliver, 2004	<i>Pagrus caeruleostictus</i>	EA; MS	'ignoratus' group; 'ignoratus s. str.' subgroup	'lyre' type	Neifar et al. (2004)
<i>L. virgula</i> Euzet & Oliver, 1967	<i>Pagellus bogaraveo</i> ; <i>P. acarne</i>	EA; MS	'elegans' group	'furca' type; 'elongatus' type	Oliver (1987); Diamanka et al. (2011b)
<i>L. echenis</i> (Wagener, 1857)	<i>Sparus aurata</i>	EA; MS; AS	'elegans' group	'furca' type	Oliver (1987); Radujkovic & Euzet (1989) (as <i>Furnestinia echenis</i> ); Desdevises (2001)
<i>L. ergensi</i> Euzet & Oliver, 1966	<i>Diplodus sargus</i> ; <i>D. vulgaris</i> ; <i>D. annularis</i>	EA; MS; AS	'ignoratus' group, 'ergensi' subgroup	'lyre' type	Oliver (1987); Radujkovic & Euzet (1989); Amine & Euzet (2005)
<i>L. erythrinus</i> Euzet & Oliver, 1966	<i>Pagellus erythrinus</i>	EA; MS; AS	'ignoratus' group, 'ignoratus s. str.' subgroup	'lyre' type	Oliver (1987); Radujkovic & Euzet (1989); Amine & Euzet (2005)
<i>L. ignoratus</i> Palombi, 1943	<i>Diplodus sargus</i> ; <i>D. vulgaris</i> ; <i>D. annularis</i> ; <i>D. puntazzo</i> ; <i>Lithognathus mormyrus</i> ; <i>Eynniss ehrenbergii</i> ; <i>Sarpa salpa</i>	EA; MS; AS	'ignoratus' group; 'ignoratus s. str.' subgroup	'lyre' type	Oliver (1987); Radujkovic & Euzet (1989); Desdevises et al. (2002b); Amine et al. (2006a, b); Poisot et al. (2011)
<i>L. mormyrus</i> Euzet & Oliver, 1967	<i>Lithognathus mormyrus</i>	EA; MS; AS	'elegans' group	'furca' type	Oliver (1987); Radujkovic & Euzet (1989); Boudaya et al. (2009)
<i>L. verberis</i> Euzet & Oliver, 1967	<i>Lithognathus mormyrus</i>	EA; MS; AS	'elegans' group	'furca' type	Oliver (1987); Radujkovic & Euzet (1989); Boudaya et al. (2009)
<i>L. elegans</i> Bychowsky, 1957	<i>Diplodus sargus</i> ; <i>D. vulgaris</i> ; <i>D. annularis</i> ; <i>Oblada melanura</i> ; <i>Boops boops</i> ; <i>Spondyliosoma cantharus</i> ; <i>Acanthopagrus sivicolus</i>	EA; MS; AS; Black Sea; WP; off Japan, East China and Yellow Seas	'elegans' group	'furca' type	Bychowsky (1957); Oliver (1987); Gaevskaya & Aleshkina (1988); Radujkovic & Euzet (1989); Gibson et al. (2005)
<i>L. euzeti</i> Diamanka, Boudaya, Toguebaye & Pariselle, 2011	<i>Dentex canariensis</i> ; <i>D. gibbosus</i>	EA; MS	'ignoratus' group, 'ignoratus s. str.' subgroup	'lyre' type	Diamanka et al. (2011a)

**Table 2** continued

Species of <i>Lamellodiscus</i> <sup>a</sup>	Host <sup>b</sup>	Region <sup>c</sup>	Species groups/type according to the morphology:		Source of data
			of the haptor structures	of the MCO	
<i>L. aff. euzeti</i>	<i>Cheimereius nufar</i>	Arabian Sea	'ignoratus' group, 'ignoratus s. str.' subgroup	'lyre' type	Present study
<i>L. baeri</i> Oliver, 1974	<i>Pagrus pagrus</i>	MS	'ignoratus' group; 'ergensi' subgroup	'lyre' type	Oliver (1987); Amine & Euzet (2005)
<i>L. confusus</i> Amine, Euzet & Kechemir-Issad, 2007 <sup>d</sup>	<i>Sarpa salpa</i>	MS	'ignoratus' group; 'ignoratus s. str.' subgroup	'lyre' type	Amine et al. (2007a)
<i>L. crampus</i> Neifar, 2008	<i>Dentex maroccanus</i>	MS	'ignoratus' group; 'ignoratus s. str.' subgroup	'lyre' type	Neifar (2008)
<i>L. falcus</i> Amine, Euzet & Kechemir-Issad, 2006 <sup>d</sup>	<i>Diplodus sargus</i> ; <i>D. vulgaris</i>	MS	'ignoratus' group; 'ergensi' subgroup	'lyre' type	Amine et al. (2006a)
<i>L. flagellatus</i> Boudaya, Neifar & Euzet, 2009	<i>Lithognathus mormyrus</i>	MS	'elegans' group	'furca' type	Boudaya et al. (2009)
<i>L. impervius</i> Euzet, 1984	<i>Diplodus puntazzo</i>	MS	'elegans' group	'polymorphous' type	Oliver (1987)
<i>L. kechemirae</i> Amine & Euzet, 2005	<i>Diplodus sargus</i> ; <i>D. vulgaris</i>	MS	'ignoratus' group, 'ergensi' subgroup	'lyre' type	Amine & Euzet (2005)
<i>L. neifari</i> Amine, Euzet & Kechemir-Issad, 2006	<i>Diplodus sargus</i> ; <i>D. vulgaris</i>	MS	'ignoratus' group, 'ignoratus s. str.' subgroup	'lyre' type	Amine et al. (2006a)
<i>L. sanfilippoi</i> Amine, Neifar & Euzet, 2006	<i>Diplodus sargus</i>	MS	'ignoratus' group, 'ergensi' subgroup	'lyre' type	Amine et al. (2006b)
<i>L. theroni</i> Amine, Euzet & Kechemir-Issad, 2007	<i>Diplodus puntazzo</i>	MS	'ignoratus' group, 'ergensi' subgroup	'lyre' type	Amine et al. (2007b)
<i>L. tomentosus</i> Amine & Euzet, 2005	<i>Diplodus sargus</i> ; <i>D. vulgaris</i>	MS	'ignoratus' group, 'ergensi' subgroup	'lyre' type	Amine & Euzet (2005)
<i>L. bidens</i> Euzet, 1984	<i>Diplodus puntazzo</i>	MS; AS	'elegans' group	'furca' type	Euzet (1984); Oliver (1987); Radujkovic & Euzet (1989)
<i>L. hiliti</i> Euzet, 1984	<i>Diplodus puntazzo</i>	MS; AS	'elegans' group	'polymorphous' type	Euzet (1984); Oliver (1987); Radujkovic & Euzet (1989)

Table 2 continued

Species of <i>Lamellodiscus</i> <sup>a</sup>	Host <sup>b</sup>	Region <sup>c</sup>	Species groups/type according to the morphology:		Source of data
			of the haptoral structures	of the MCO	
<i>L. fraternus</i> Bychowsky, 1957 <sup>d</sup>	<i>Diplodus vulgaris</i> ; <i>D. annularis</i>	MS; AS; BS	'ignoratus' group; 'ignoratus s. str.' subgroup	'lyre' type	Bychowsky (1957); Oliver (1987); Radujkovic & Euzet (1989)
<i>L. coralinus</i> Paperna, 1965	<i>Dascyllus marginatus</i> (Pomacentridae); <i>Centropyge bispinosus</i> (Pomacanthidae)	Red Sea	'ignoratus' group; 'ignoratus s. str.' subgroup	without accessory piece	Paperna (1965)
<i>L. donatellae</i> Aquaro, Riva & Galli, 2009	<i>Acanthopagrus bifasciatus</i>	Red Sea	'ignoratus' group; 'ergensi' subgroup	'lyre' type	Aquaro et al. (2009)
<i>L. furcillatus</i> Kritsky, Jimenez-Ruiz & Sey, 2000	<i>Diplodus noct</i>	Arabian Gulf	'ignoratus' group; 'ergensi' subgroup	'lyre' type	Kritsky et al. (2000)
<i>L. acanthopagri</i> Roubal, 1981	<i>Acanthopagrus australis</i> ; <i>A. berda</i> ; <i>A. latus</i>	IO; Arabian Gulf; WPO: off Australia	'elegans' group	'furca' type	Roubal (1981); Byrnes (1986); Oliver (1987); Al-Marzouk & Al-Qarabaliy (2001)
<i>L. caballeroi</i> Venkatanarsaiah & Kullkarni, 1980	<i>Crenidens crenidens</i>	IO: Bay of Bengal	'elegans' group	'polymorphous' type	Oliver (1987)
<i>L. indicus</i> Tripathi, 1959	<i>Rhabdosargus sarba</i>	IO: off eastern India	'elegans' group	'polymorphous' type	Oliver (1987)
<i>L. butcheri</i> Byrnes, 1987	<i>Acanthopagrus australis</i> ; <i>A. butcheri</i>	IO and WP: off Australia	'elegans' group	'composed of two elements'; 'polymorphous' type	Byrnes (1986); Oliver (1987)
<i>L. cirrusspiralis</i> Byrnes, 1987	<i>Acanthopagrus berda</i> ; <i>A. latus</i>	IO and WP: off Australia	'elegans' group	'composed of two elements'; 'polymorphous' type	Byrnes & Rohde (1992); Oliver (1987)
<i>L. major</i> Murray, 1931	<i>Acanthopagrus australis</i> ; <i>A. berda</i> ; <i>A. latus</i> ; <i>A. butcheri</i>	IO and WP: off Australia	'elegans' group	'composed of two elements'; 'polymorphous' type	Roubal (1981); Byrnes (1986); Oliver (1987)
<i>L. squamosus</i> Roubal, 1981	<i>Acanthopagrus australis</i> ; <i>A. berda</i> ; <i>A. latus</i>	IO and WP: off Australia	'elegans' group	'composed of two elements'; 'polymorphous' type	Roubal (1981); Byrnes (1986); Oliver (1987)
<i>L. vaginalis</i> Byrnes, 1987	<i>Acanthopagrus australis</i> ; <i>A. butcheri</i>	IO and WP: off Australia	'elegans' group	'composed of two elements'; 'polymorphous' type	Byrnes (1986); Oliver (1987)



**Table 2** continued

Species of <i>Lamellodiscus</i> <sup>a</sup>	Host <sup>b</sup>	Region <sup>c</sup>	Species groups/type of the haptor structures	Species groups/type according to the morphology of the MCO	Source of data
<i>L. pagrosomi</i> Murray, 1931	<i>Chrysophrys major</i> ; <i>C. auratus</i> ; <i>Parargyros edita</i> ; <i>Acanthopagrus latus</i> ; <i>Evyunis tumifrons</i> ; <i>Epinephelus awoara</i> ; <i>E. akaara</i> (Serranidae)	IO: Gulf St. Vincent; WP: off Australia, New Zealand, China, Japan	'ignoratus' group; 'ignoratus s. str.' subgroup	'lyre' type	Oliver (1987); Roubal (1996); Zhang et al. (2001); Amine & Euzet (2005)
<i>L. typicus</i> Johnston & Tiegs, 1922	<i>Acanthopagrus australis</i>	WP: off Australia	'elegans' group	two simple elements; 'polymorphous' type	Oliver (1987); Roubal (1990)
<i>L. niedashui</i> Li, Zhang & Yang, 1995	<i>Acanthopagrus latus</i>	WP: South China Sea	'elegans' group	two simple elements	Zhang et al. (2001)
<i>L. japonicus</i> Ogawa & Egusa, 1978	<i>Acanthopagrus schlegelii</i> ; <i>A. latus</i>	WP: South China Sea and off Japan	'elegans' group	accessory piece distally diverged; 'furca' type	Ogawa & Egusa (1978); Oliver (1987); Zhang et al. (2001)
<i>L. spari</i> Zukov, 1970	<i>Acanthopagrus schlegelii</i>	WP: East China and Yellow Seas and off Japan	'elegans' group	two simple elements; 'polymorphous' type	Ogawa & Egusa (1978); Oliver (1987)
<i>L. takitai</i> Ogawa & Egusa, 1978	<i>Acanthopagrus schlegelii</i>	WP: off Japan	'elegans' group	two simple elements; 'polymorphous' type	Ogawa & Egusa (1978); Oliver (1987)
<i>L. parvicornis</i> Justine & Briand, 2010	<i>Gymnocranius euanus</i> ; <i>G. grandoculis</i> ; <i>Gymnocranius</i> sp. (Lethrinidae)	WP: off New Caledonia	'tubulicornis' group	MCO made up of 3 elements	Justine & Briand (2010)
<i>L. magnicornis</i> Justine & Briand, 2010	<i>Gymnocranius grandoculis</i> ; <i>G. euanus</i> ; <i>Gymnocranius</i> spp. (Lethrinidae)	WP: off New Caledonia	'tubulicornis' group	MCO made up of 3 elements	Justine & Briand (2010)
<i>L. tubulicornis</i> Justine & Briand, 2010	<i>Gymnocranius grandoculis</i> ; <i>Gymnocranius</i> sp. (Lethrinidae)	WP: off New Caledonia	'tubulicornis' group	MCO made up of 4 elements	Justine & Briand (2010)
<i>L. epsilon</i> Yamaguti, 1968	<i>Monotaxis grandoculis</i> (Lethrinidae)	CPO: off Hawaii	'elegans' group; 'tubulicornis' group	'polymorphous' type; MCO made up of 3 elements	Oliver (1987); Justine & Briand (2010)

<sup>a</sup> Species are ordered in accordance with their occurrence from the Eastern Atlantic to the Central Pacific Ocean; <sup>b</sup>All Sparidae, except where indicated; <sup>c</sup>Regional abbreviations: AS, Adriatic Sea; CP, Central Pacific Ocean; EA, Eastern Atlantic Ocean; IO, Indian Ocean; MS, Mediterranean Sea; WP, Western Pacific Ocean; <sup>d</sup>According to some molecular studies, these species may be synonyms of other species, namely *L. obeliae* is a junior synonym of *L. virgule sensu* Desdèvises et al. (2000), and, according to Poisot et al. (2011), *L. coronatus* is a synonym of *L. furcosus*, *L. fraternus* of *L. ergensi*, and both *L. falcus* and *L. confusus* of *L. ignoratus*

and, furthermore, because of the simple shape of the dorsal bars (Paperna, 1965: plate 2G), within the 'ignoratus s. str.' subgroup *sensu* Amine & Euzet (2005). Thus, this subgroup comprises 17 species (Table 2), namely the 17, less *L. acanthopagri*, listed by Diamanka et al. (2011a) and including *L. corallinus*.

For all of these species, except for *L. corallinus*, a 'lyre' type of MCO composed of two parts, a simple piece and a bifurcate piece with axial and lateral branches, are described (Oliver, 1987; Neifar et al., 2004; Diamanka et al., 2011b). However, in descriptions of the MCO of most species mentioned above, the copulatory tube has not been recognised (Oliver, 1969; Euzet & Oliver, 1967; Neifar et al., 2004; Amine et al., 2006a, 2007a, b; Neifar, 2008; Diamanka et al., 2011a, b). The general shape of the MCO in *L. aff. euzeti* strongly resembles that found in other representatives of this subgroup, but it has a well-defined copulatory tube (Fig. 4A–C) and, in most of the specimens examined, the circular opening at the distal end of the tube is clearly visible (Fig. 5A).

Our examination of the type-specimens of seven species of the 'ignoratus s. str.' subgroup, plus new specimens of *L. fraternus* which were freshly collected from its type-host and locality, revealed that all of them have an MCO resembling that of *L. aff. euzeti* (Fig. 4). It is worth noting that, in general, the copulatory tube in representatives of the Dactylogyridea varies in terms of the degree of sclerotisation, width and twisting, but it is always a simple tube without processes and a distal bifurcation (Gusev, 1985). Therefore, it is most probable that the copulatory tube in *Lamellodiscus* spp. has the same simple form. It is also doubtful that the copulatory tube in different species with a similar 'lyre'-type of MCO is likely to be homologous with different parts of the latter. In fact, one of the parts of the 'bifurcate piece' in all of the species studied resembles a simple tube with strongly sclerotised walls, an expanded base and an undivided distal end (Fig. 4: dT, bT), which is obviously the actual copulatory tube. The other two parts (which, in the original descriptions, are referred to as the 'simple piece' and the 'axial branch of the bifurcate piece', e.g. Diamanka et al., 2011b) have a greater variety of shapes (Fig. 4: peAP and deAP), with a different degree of curvature and sometimes a branched distal end (Fig. 4 I, J), and are obviously elements of the AP. These are located opposite each

other, with their points turned-in, and in contact when the copulatory tube is curved (Fig. 4D, I, K).

Thus, the 'lyre'-type of MCO in the 'ignoratus s. str.' subgroup consists of the copulatory tube itself (Fig. 4: 'dT' and 'bT'), which is partly homologous with the 'lateral branch' of the 'bifurcate piece' of the MCO in previous descriptions of species of this subgroup, and a complex AP. The latter includes the largest element of the AP, which is connected only to the proximal end of the copulatory tube (Fig. 4: peAP), and a second, smaller element associated with the distal part of the copulatory tube (Fig. 4: deAP). These parts of the AP are considered homologous with, respectively, the 'axial branch' of the 'bifurcate piece' and the 'simple piece' of the MCO, which have been described in other species of the 'ignoratus s. str.' subgroup.

A similar structure for the MCO, consisting of the copulatory tube and a few elements of the AP, has recently been described for species of the 'tubulicornis' group (Justine & Briand, 2010). In addition, two elements of the AP, one of which is associated with the proximal end of the copulatory tube and the other with the distal end, have been observed in some species of the 'elegans' group, e.g. *L. virgula* and *L. dentexi* (see Oliver, 1987; Diamanka et al., 2011b).

In general, among the forms of the MCO of the known species of *Lamellodiscus*, an AP can be distinguished consisting of: a single element (e.g. *L. bidens*, *L. butcheri*, *L. cirrusspiralis*, *L. drummondi*, *L. elegans*, *L. flagellatus*, *L. gracilis*, *L. impervius*, *L. major*, *L. squamosus*, *L. spari*, *L. takitai* and *L. typicus*); two elements (most of the species of the 'ignoratus' group, plus *L. dentexi*, *L. coronatus*, *L. mirandus*, *L. virgula*, *L. hili* and *L. vaginalis*); and three elements (species of the 'tubulicornis' group); and in one species, *L. corallinus*, an AP is absent. However, the determination of the number of the MCO parts for some species requires reinvestigation, because their descriptions and figures are difficult to interpret in relation to the nature of the copulatory tube.

## Discussion

*Lamellodiscus* spp. mainly parasitise sparid teleosts in the Eastern Atlantic and Indo-Pacific regions (Table 2). Only one species of this genus is found in the Central Pacific and in a fish from another family, and no records of these monogeneans are known from

the Western Atlantic or Eastern Pacific, despite the fact that the Sparidae is one of the most diverse families of coastal fishes [115 nominal species belonging to 33 genera, which are broadly distributed in tropical and temperate waters of all oceans, according to Nelson (2006)].

In a recent study of the molecular phylogeny of sparid fishes, Chiba et al. (2009) have suggested that the ancestors of present-day sparids probably originated during the Mesozoic era in the Tethys Sea and migrated to the coastal region off the Americas during the Upper Cretaceous. Their data indicated that the common ancestors of the genera then inhabiting coastal waters off the North and South American continents diverged from other sparids and migrated to the Eastern Pacific and Western Atlantic early in their evolutionary history. These hypotheses may explain the absence of species of the diverse monogenean genus *Lamellodiscus* in the coastal waters of the New World. Thus, although representatives of other monogenean taxa (six genera of the Polyopisthocotylea and one of the Gyrodactylidea) have been found in sparids off South America, not a single representative of *Lamellodiscus* has been reported from there (Cohen et al., 2013). Consequently, the origin of *Lamellodiscus* spp. is associated with the more recent evolutionary history of sparids inhabiting the Western Atlantic and Indo-Pacific, and occurred after the divergence between the common ancestors of 'New World' and 'Old World' sparid species.

The greatest number of *Lamellodiscus* spp. (i.e. 34) has been found in the Mediterranean Sea (Table 2) and the neighbouring region of the Eastern Atlantic (24). This can be partly explained by the fact that the greatest number of studies on the diplectanid fauna have been carried out in these areas. However, it should be noted that the diversity of both *Lamellodiscus* spp. and their hosts are negatively correlated with salinity. Thus, five species of *Diplodus*, parasitised by 17 species of *Lamellodiscus*, occur in the Mediterranean Sea, but only *D. annularis* extends its range into the Black Sea, and only two of six species of *Lamellodiscus* infecting this fish in the Mediterranean also occur in the Black Sea.

The above hypothesis regarding the ancestral origin of present-day sparid species in the Tethys Sea (Chiba et al., 2009) tends to coincide with the numerical occurrence of species in different regions. Thus, the Eastern Atlantic, Western Pacific and Arabian Gulf are

considered as regions associated with the Tethys Sea in ancient times, whereas the Indian Ocean and Red Sea formed later (Wegener, 1966; Encyclopædia Britannica, 2013). Even when data from the Eastern Atlantic, where number of species may be overestimated according to Poisot et al. (2011), are excluded, it appears that the known *Lamellodiscus* fauna in the western and central parts of the Indian Ocean is the least diverse, comprising only five species (Table 2), whereas 15 species are found off Australia and in the Western Pacific.

Half of the species of *Lamellodiscus* parasitise only a single host species and c.90% infect closely related host species of the same genus (Table 3) and/or of the same terminal clade on the phylogenetic tree of Chiba et al. (2009) (Table 4). Comparison of the level of specificity of the species of this genus with other narrowly specific genera of the Dactylogyridea reveals that these estimations are comparable with and even higher than in *Dactylogyrus* Diesing, 1850 which is considered to be a highly host-specific monogenean genus (88 vs 63% of the specialist species; see Table 5) (Šimková & Morand, 2008). Strict host-specificity is not necessarily the outcome of strict co-speciation between parasites and their hosts, but can also be the result of host-switching followed by speciation on the new host. In fact, Desdevises et al. (2002b) have suggested that *Lamellodiscus* spp. from the Mediterranean Sea have evolved by host-switching rather than by co-speciation and concluded that the co-evolutionary processes were only minimally involved in the formation of *Lamellodiscus*/sparid host-parasite associations in this region. Nevertheless, over the last decade, 12 new species of this genus have been described from this region, including some which have been differentiated from existing 'species' with a wide host range which have proved to represent species complexes (Neifar et al., 2004; Amine & Euzet, 2005; Amine et al., 2006a, b; 2007a, b; Neifar, 2008; Bounday et al., 2009). However, based on molecular data, Poisot et al. (2011) have proposed that two of these species (*L. falculus* and *L. confusus*) are truly synonyms of the species from which had previously been differentiated based on morphological data. Indeed, some *Lamellodiscus* spp. from the Mediterranean Sea, especially of the 'ignoratus sensu lato' group are distinguished from each other by small morphological differences, mainly in the shape of the MCO, and may really be conspecific. On the other

**Table 3** Host ranges of *Lamellogadiscus* spp. based on the current classification of the Sparoidea according to Froese & Pauly (2011) and Eschmeyer (2014)

Hosts belonging to	one species	two species	> two species	≥ two genera of one family	≥ two genera of different families
one genus					
one species		<p><i>L. baeri</i>; <i>L. bidens</i>; <i>L. caballeri</i>; (<i>L. confusus</i>); <i>L. crampus</i>; <i>L. denexi</i>; <i>L. donatellae</i>; <i>L. drummondi</i>; <i>L. echenetsi</i>; <i>L. epsilon</i>; <i>L. erythrimi</i>; <i>L. flagellatus</i>; <i>L. furcillatus</i>; <i>L. hilti</i>; <i>L. impervius</i>; <i>L. indicus</i>; <i>L. mirandus</i>; <i>L. mormyri</i>; <i>L. niedashui</i>; <i>L. parisi</i>; <i>L. rastellus</i>; <i>L. sanfilippoi</i>; <i>L. sarculus</i>; <i>L. siglatus</i>; <i>L. spari</i>; <i>L. takitai</i>; <i>L. theroni</i>; <i>L. toguebayei</i>; <i>L. triacies</i>; <i>L. typicus</i>; <i>L. verberis</i>; <i>L. vicinus</i></p>	<p><i>L. butcheri</i>; <i>L. cirrusspiralis</i>; (<i>L. falcus</i>); (<i>L. fraternus</i>); <i>L. furcosus</i>; <i>L. virgula</i>; <i>L. japonicus</i>; <i>L. kechemirae</i>; <i>L. nefjari</i>; (<i>L. obelidae</i>); <i>L. tomentosus</i>; <i>L. tubulicornis</i>; <i>L. vaginalis</i></p>	<p><i>L. acanthopagri</i>; (<i>L. coronatus</i>); <i>L. ergensi</i>; <i>L. gracilis</i>; <i>L. ignoratus</i></p>	<p><i>L. elegans</i>; <i>L. euzeti</i>; <i>L. gracilis</i>; <i>L. ignoratus</i>; <i>L. pagrosomi</i></p>
	32 spp.	13 spp.	7 spp.	4 spp.	3 spp.

Species in parentheses may be synonyms of other species (Desdevises et al., 2000; Poisot et al., 2011)

**Table 4** Characteristics of the host ranges of *Lamellogadiscus* spp., parasitising more than one host species, based on the molecular phylogeny of the Sparidae and the centracanthid genus *Spicara* according to Chiba et al. (2009)

Occurrence on hosts belonging to	two species	three species	≥ two species unrelated species from different monophyletic groups
closely related species forming one monophyletic group			
	<p><i>L. butcheri</i>; <i>L. cirrusspiralis</i>; (<i>L. falcus</i>); (<i>L. fraternus</i>); <i>L. japonicus</i>; <i>L. kechemirae</i>; <i>L. nefjari</i>; (<i>L. obelidae</i>); <i>L. tomentosus</i>; <i>L. tubulicornis</i>; <i>L. vaginalis</i>; <i>L. virgula</i></p>	<p><i>L. acanthopagri</i>; (<i>L. coronatus</i>); <i>L. ergensi</i>; <i>L. euzeti</i>; <i>L. furcosus</i>; <i>L. knoeffleri</i>; <i>L. magnicornis</i>; <i>L. major</i>; <i>L. parvicornis</i>; <i>L. squamosus</i></p>	<p><i>L. coronatus</i>; <i>L. elegans</i>; <i>L. gracilis</i>; <i>L. ignoratus</i>; <i>L. pagrosomi</i></p>
	12 spp.	10 spp.	5 spp.

hand, although, in the article of Poisot et al. (2011), specimens from *Sarpa salpa* identified as *L. confusus* have been synonymised with *L. ignoratus*, the monophyly of the latter species was not supported. In fact, specimens of *L. ignoratus* from different species of *Diplodus* (e.g. *D. sargus* vs *D. vulgaris*) were found in different clusters in the phylogenetic tree of *Lamellodiscus* spp. reconstructed from partial sequences of 18S rDNA. Similarly, three of the five species parasitising *D. puntazzo* have been included in the same clade, and two, *L. ignoratus* and *L. ergensi*, which have a wide host range, as members of different clades (Desdevises et al., 2002b). However, the rDNA sequences for *L. ergensi* were only from material collected from *D. annularis*, and the monogeneans from *D. puntazzo* previously identified as *L. ergensi* (no sequence data available) have since been described as a new species, *L. theroni*, by Amine et al. (2007b). It is also worth noting that four species of *Lamellodiscus* are presently known to occur on *Pagrus* spp. in the Mediterranean Sea, all of which have very similar haptor structures and the same type of MCO (Table 2). Likewise, four species of *Lamellodiscus* have recently been described from *D. sargus* in this region, and they are also morphologically closely related to each other and to *L. ergensi*, a species previously described from this host (Amine & Euzet, 2005). Thus, the inclusion of data from these recently described species has increased the number of closely related species parasitising the same host or hosts of the same genus in the Mediterranean. Similarly, in the Eastern Atlantic, three (*L. toguebayei*, *L. triacies* and *L. vicinus*) of the four known species from *Dentex macrophthalmus* have the same morphological type of the attachment and MCO structures, and are also morphologically closely similar to *L.*

*euzeti* and *L. crampus*, which parasitise other species of *Dentex* in the same region (Table 2). The above-mentioned examples coincide with a greater involvement of intra-host speciation in the evolutionary scenario of *Lamellodiscus* spp. Intra-host speciation has been also observed as an important process involved in the evolution of *Dactylogyrus* spp. infecting sympatric cyprinids (Šimková & Morand, 2008). Intra-host divergence can be considered as a special case of the co-evolution of parasite and host, along with co-speciation, when a newly diverged host species is parasitised by one or several new congeneric species of monogeneans.

Moreover, the variability for 18S rDNA within the genus *Lamellodiscus* is estimated to be almost twice as great as within *Dactylogyrus* (see Poisot et al., 2011), by far the largest helminth genus, with more than 900 nominal species (Gibson et al., 1996). Such genetic diversity within *Lamellodiscus* and the morphological variability of its members may reflect an ongoing process of species divergence.

It should be noted that Desdevises et al. (2002b) have suggested that co-speciation may be a by-product of host geographical isolation and that co-evolutionary events are more often associated with allopatric speciation. In reality, the co-evolutionary model of speciation within *Lamellodiscus* is more discernible if it includes a consideration of the occurrence of morphologically similar species from different regions and host taxa. Accordingly, species of the ‘tubulicornis’ group are strongly specific to monotaxine lethrinids in the Indo-Pacific (Justine & Briand, 2010). Nine of the 12 species parasitising *Acanthopagrus* spp. off Australia also have the same type of lamellodiscs and a common type of MCO composed of two simple elements (Table 2). *Lamellodiscus corallinus*,

**Table 5** Comparison of the host specificity of species of *Lamellodiscus* and other dactylogyridean genera according to the classification suggested by Šimková et al. (2006)

	<i>Lamellodiscus</i> spp.	<i>Euryhaliotrema</i> spp. <sup>a</sup>	<i>Ligophorus</i> spp. <sup>b</sup>	<i>Dactylogyrus</i> spp. <sup>c</sup>
Number (%) of strict specialists	32 (54)	35 (54)	42 (71)	25 (49)
Number (%) of intermediate specialists	20 (34)	24 (37)	7 (12)	7 (14)
Number (%) of intermediate generalists	2 (3.5)	4 (6)	4 (7)	7 (14)
Number (%) of generalists and wide range generalists	5 (8.5)	2 (3)	6 (10)	12 (23)

<sup>a</sup> Data for 65 species (Kritsky, 2012; Kritsky & Diggles, 2014); <sup>b</sup>Data for 59 species (Dmitrieva et al., 2012; Kritsky et al. 2013; Sarabev et al., 2013; Soo & Lim, 2013); <sup>c</sup>Data for 51 species (Šimková et al., 2006)

described by Paperna (1965) from pomacanthids and pomacentrids in the Red Sea, has a unique MCO without an AP. Moreover, most (21) of the representatives of the 'ignoratus' group are found in the Eastern Atlantic and Mediterranean region, four in the Red Sea, Arabian Sea and Arabian Gulf, and only one species in the Indo-Pacific (Table 2). In retrospect, the occurrence of morphologically similar species in different host taxa and regions more likely reflects the phylogeography of the host and is more apt to involve co-evolution events.

More information on the occurrence of *Lamellodiscus* spp., especially from the insufficiently studied eastern and central regions of the Indian Ocean and particularly genetic data, is needed to supplement our knowledge of the distribution, specificity and evolution of the members of this genus.

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## References

- Al-Abdessalaam, T. Z. S. (1995). Marine species of the Sultanate of Oman. *Ministry of Agriculture and Fisheries Wealth, Publication No. 46/95*, pp. 283–285.
- Al-Marzouk, A., & Al-Qarabaliy, H. (2001). Monogeneans of cultured marine fishes in Kuwait. *Abstracts of Papers: Fourth International Symposium on the Monogenea (ISM 4)*. University of Queensland, Brisbane, Queensland, Australia, July 9–13, 2001, p. 101.
- Amine, F., & Euzet, L. (2005). Deux nouvelles espèces du genre *Lamellodiscus* Johnston & Tiegs, 1922 (Monogenea: Diplectanidae) parasites de Sparidae (Teleostei) des côtes de l'Algérie. *Systematic Parasitology*, *60*, 187–196.
- Amine, F., Euzet, L., & Kechemir-Issad, N. (2006a). Description de deux nouvelles espèces de *Lamellodiscus* Johnston & Tiegs, 1922 (Monogenea: Diplectanidae) du groupe morphologique "ignoratus", parasites de *Diplodus sargus* et *D. vulgaris* (Teleostei: Sparidae). *Systematic Parasitology*, *64*, 37–45.
- Amine, F., Euzet, L., & Kechemir-Issad, N. (2007a). Description de *Lamellodiscus confusus* n. sp. (Monogenea: Diplectanidae) parasite de *Sarpa salpa* (Teleostei: Sparidae). *Parasite*, *14*, 281–285.
- Amine, F., Euzet, L., & Kechemir-Issad, N. (2007b). *Lamellodiscus theroni* sp. nov. (Monogenea: Diplectanidae) a gill parasite from *Diplodus puntazzo* (Teleostei: Sparidae). *Acta Parasitologica*, *52*, 305–309.
- Amine, F., Neifar, L., & Euzet, L. (2006b). *Lamellodiscus sanfilippoi* n. sp. (Monogenea: Diplectanidae) parasite branchial de *Diplodus sargus* (Teleostei, Sparidae) en Méditerranée. *Parasite*, *13*, 45–49.
- Aquaro, G., Riva, C., & Galli, P. (2009). Monogenoids from the gills of *Acanthopagrus bifasciatus* (Forsskål, 1775) (Perciformes: Sparidae) of the Red Sea, Egypt, with the description of *Lamellodiscus donatellae* sp. n. (Diplectanidae). *Comparative Parasitology*, *76*, 51–57.
- Boudaya, L., Neifar, L., & Euzet, L. (2009). Diplectanid parasites of *Lithognathus mormyrus* (L.) (Teleostei: Sparidae) from the Mediterranean Sea, with the description of *Lamellodiscus flagellatus* n. sp. (Monogenea: Diplectanidae). *Systematic Parasitology*, *74*, 149–159.
- Bray, R. A. (1986). Some helminth parasites of marine fishes of Southern Africa: *Santeria rubalo* gen. et sp. nov. (Digenea: Cryptogonimidae). *Journal of Natural History*, *20*, 817–823.
- Bychowksy, B. E. (1957). [*Monogenetic trematodes, their systematic and phylogeny.*] Moscow-Leningrad: Nauka, 509 pp (In Russian).
- Byrnes, T. (1986). Six species of *Lamellodiscus* (Monogenea: Diplectanidae) collected from Australian bream (*Acanthopagrus* spp.). *Publications of the Seto Marine Biological Laboratory*, *31*, 169–190.
- Byrnes, T., & Rohde, K. (1992). Geographical distribution and host specificity of ectoparasites of Australian bream, *Acanthopagrus* spp. (Sparidae). *Folia Parasitologica*, *39*, 249–264.
- Chiba, S. N., Iwatsuki, Y., Yoshino, T., & Hanzawa, N. (2009). Comprehensive phylogeny of the family Sparidae (Perciformes: Teleostei) inferred from mitochondrial gene analyses. *Genes & Genetic Systems*, *84*, 153–170.
- Cohen, S. C., Justo, M. C. N., & Kohn A. (2013). *South American Monogenoidea parasites of fishes, amphibians and reptiles*. Rio de Janeiro: Published by the authors, 662 pp.
- Desdevises, Y. (2001). The phylogenetic position of *Furnestinia echeneis* (Monogenea, Diplectanidae) based on molecular data: a case of morphological adaptation? *International Journal for Parasitology*, *31*, 205–208.
- Desdevises, Y. (2006). Determinants of parasite species richness on small taxonomical and geographical scales: *Lamellodiscus* monogeneans of northwestern Mediterranean sparid fish. *Journal of Helminthology*, *80*, 235–241.
- Desdevises, Y., Jovelín, R., Jousson, O., & Morand, S. (2000). Comparison of ribosomal DNA sequences of *Lamellodiscus* spp. (Monogenea, Diplectanidae) parasitising *Pagellus* (Sparidae, Teleostei) in the North Mediterranean Sea: species divergence and coevolutionary interactions. *International Journal for Parasitology*, *30*, 741–746.
- Desdevises, Y., Morand, S., Jousson, O., & Legendre, P. (2002a). Coevolution between *Lamellodiscus* (Monogenea: Diplectanidae) and Sparidae (Teleostei): The study of a complex host–parasite system. *Evolution*, *56*, 2459–2471.
- Desdevises, Y., Morand, S., & Legendre, P. (2002b). Evolution and determinants of host specificity in the genus *Lamellodiscus* (Monogenea). *Biological Journal of the Linnean Society*, *77*, 431–443.
- Desdevises, Y., Morand, S., & Oliver, G. (2001). Linking specialisation to diversification in the Diplectanidae Bychowksy 1957 (Monogenea, Platyhelminthes). *Parasitology Research*, *87*, 223–230.
- Diamanka, A., Boudaya, I., Toguebaye, B. S., & Pariselle, A. (2011a). *Lamellodiscus euzeti* n. sp. (Monogenea: Diplectanidae), a parasite from *Dentex canariensis* and *D.*

- gibbosus* (Teleostei: Sparidae) in the Atlantic Ocean and Mediterranean Sea. *Parasite*, 18, 145–150.
- Diamanka, A., Neifar, L., Pariselle, A., & Euzet, L. (2011b). Diplectanid parasites of *Dentex macrophthalmus* (Bloch) (Teleostei: Sparidae) from north east coast of Africa, with redescription of *Lamellodiscus dentexi* Aljoshkina, 1984, and description of three new species of *Lamellodiscus* Johnston & Tiegs, 1922 (Monogenea: Diplectanidae). *Folia Parasitologica*, 58, 17–26.
- Dmitrieva, E. V., Gerasev, P. I., Gibson, D. I., Pron'kina, N. V., & Galli, P. (2012). Descriptions of eight new species of *Ligophorus* Euzet and Suriano, 1977 (Monogenea: Ancyrocephalidae) from Red Sea mullets. *Systematic Parasitology*, 81, 203–237.
- Domingues, M. V., & Boeger, W. A. (2008). Phylogeny and revision of Diplectanidae Monticelli, 1903 (Platyhelminthes: Monogeneoidea). *Zootaxa*, 1698, 1–40.
- Encyclopædia Britannica (2013). Tethys Sea. Retrieved September, 2013 from <http://www.britannica.com/EBchecked/topic/588887/Tethys-Sea>.
- Eschmeyer, W. N. (Ed). (2014) *Catalog of fishes: genera, species, references*. (<http://research.calacademy.org/research/ichthyology/catalog/fishcatmain.asp>).
- Euzet, L. (1984). Diplectanidae (Monogenea) parasites de poissons des Îles Kerkennah (Tunisie). *Archives de l'Institut Pasteur de Tunis*, 61, 463–474.
- Euzet, L., & Oliver, G. (1967). Diplectanidae (Monogenea) de téléostéens de la Méditerranée occidentale. IV. Quelques *Lamellodiscus* Johnston et Tiegs, 1922 parasites de poissons du genre *Diplodus* (Sparidae). *Annales de Parasitologie Humaine et Comparée*, 41, 573–598.
- Froese, R., & Pauly, D. (Eds) (2011). *FishBase*. World Wide Web electronic publication. <http://www.fishbase.org>, version (06/2011).
- Gaevskaya, A. V., & Aleshkina, L. D. (1988). Fauna of Monogenea of the South-East Atlantic, its ecological and geographical analysis. *Zoologicheskii Zhurnal*, 67, 325–330. (In Russian).
- Gibson, D. I., Bray, R. A., & Harris, E. A. (Compilers) (2005). *Host-Parasite Database of the Natural History Museum, London*. URL <http://www.nhm.ac.uk/research-curation/scientific-resources/taxonomy-systematics/host-parasites/database/index.jsp>.
- Gibson, D. I., Harris, P. D., & Bray, R. A. (2013). *Lamellodiscus* Johnston & Tiegs, 1922. Accessed through: World Register of Marine Species at <http://www.marinespecies.org/aphia.php?p=taxdetails&id=119293> on 2013-09-16.
- Gibson, D. I., Timofeeva, T. A., & Gerasev, P. I. (1996). A catalogue of the nominal species of the monogenean genus *Dactylogyrus* Diesing, 1850 and their host genera. *Systematic Parasitology*, 35, 3–48.
- Gusev, A. V. (1985). [Order Dactylogyridea.] In: O. N. Bauer (Ed.) [Key to parasites of freshwater fish of the fauna of the USSR. Vol. 2. Parasitic metazoans.] Leningrad: Nauka, pp. 15–251 (In Russian).
- Justine, J.-L., & Briand, M. J. (2010). Three new species, *Lamellodiscus tubulicornis* n. sp., *L. magnicornis* n. sp. and *L. parvicornis* n. sp. (Monogenea: Diplectanidae) from *Gymnocranius* spp. (Lethrinidae: Monotaxinae) off New Caledonia, with the proposal of the new morphological group “tubulicornis” within *Lamellodiscus* Johnston & Tiegs, 1922. *Systematic Parasitology*, 75, 159–179.
- Kritsky, D. C. (2012). Dactylogyrids (Monogeneoidea: Polyonchoinea) parasitizing the gills of snappers (Perciformes: Lutjanidae): Revision of *Euryhaliotrema* with new and previously described species from the Red Sea, Persian Gulf, the eastern and Indo-west Pacific Ocean, and the Gulf of Mexico. *Zoologia*, 29, 227–276.
- Kritsky, D. C., & Diggles, B. K. (2014). Dactylogyrids (Monogeneoidea: Polyonchoinea) parasitizing the gills of snappers (Perciformes: Lutjanidae): Species of *Euryhaliotrema* Kritsky & Boeger, 2002 from the golden snapper *Lutjanus johnii* (Bloch) off northern Australia, with a redescription of *Euryhaliotrema johni* (Tripathi, 1959) and descriptions of two new species. *Systematic Parasitology*, 87, 73–82.
- Kritsky, D. C., Jimenez-Ruiz, F. A., & Sey, O. (2000). Diplectanids (Monogeneoidea: Dactylogyridea) from the gills of marine fishes of the Persian Gulf off Kuwait. *Comparative Parasitology*, 67, 145–164.
- Kritsky, D. C., Khamees, N. R., & Ali, A. H. (2013). *Ligophorus* spp. (Monogeneoidea: Dactylogyridae) parasitizing mullets (Teleostei: Mugiliformes: Mugilidae) occurring in the fresh and brackish waters of the Shatt Al-Arab River and Estuary in southern Iraq, with the description of *Ligophorus sagmarius* sp. n. from the greenback mullet *Chelon subviridis* (Valenciennes). *Parasitology Research*, 112, 4029–4041.
- Machkewskyi, V. K., Dmitrieva, E. V., Al-Jufaili, S., & Al-Mazrooei, N. A. M. (2013). *Microcotyle omanae* n. sp. (Monogenea: Microcotylidae), a parasite of *Cheimerius nufar* (Valenciennes) (Sparidae) from the Arabian Sea. *Systematic Parasitology*, 86, 153–163.
- Neifar, L. (2008). *Lamellodiscus crampus* sp. nov. (Monogenea, Diplectanidae), a parasite of *Dentex maroccanus* (Teleostei, Sparidae) from off Tunisia. *Acta Parasitologica*, 53, 258–262.
- Neifar, L., Euzet, L., & Oliver, G. (2004). *Lamellodiscus* (Platyhelminthes, Monogenea, Diplectanidae) nouveaux parasites branchiaux des poissons marins du genre *Pagrus* (Teleostei, Sparidae). *Zoosystema*, 26, 365–376.
- Nelson, J. S. (2006). *Fishes of the world*. New York: John Wiley & Sons Inc., 601 pp.
- Ogawa, K., & Egusa, S. (1978). Three species of *Lamellodiscus* (Monogenea: Diplectanidae) from the gills of the Japanese black sea bream, *Acanthopagrus schlegelii* (Bleeker). *Bulletin of the Japanese Society of Scientific Fisheries*, 44, 607–612.
- Oliver, G. (1969). Recherches sur les *Diplectanidae* (Monogenea) parasites de Téléostéens du golfe du Lion. II. *Lamellodiscinae* nov. sub-fam. *Vie et Milieu*, Sér. A, 10, 43–72.
- Oliver, G. (1987). *Les Diplectanidae* Bychowsky, 1957 (Monogenea, Monopisthocotylea, Dactylogyridea). *Systématique. Biologie. Ontogénie. Écologie. Essai de phylogénèse*. Thèse d'État mention Sciences, Université des Sciences et Techniques du Languedoc, Montpellier, France, 433 pp.
- Paperna, I. (1965). Contribution to the knowledge of the Red Sea. No. 32. Monogenetic trematodes from the gills of Red Sea fishes. *Bulletin. Sea Fishes Researches Station, Haifa*, 39, 17–26.

- Poisot, T., & Desdevises, Y. (2010). Putative speciation events in *Lamellodiscus* (Monogenea: Diplectanidae) assessed by a morphometric approach. *Biological Journal of the Linnean Society*, 99, 559–569.
- Poisot, T., Verneau, O., & Desdevises, Y. (2011). Morphological and molecular evolution are not linked in *Lamellodiscus* (Plathyhelminthes, Monogenea). *PLOS ONE*, 6(10), e26252. doi:10.1371/journal.pone.0026252.
- Radujkovic, B. M., & Euzet, L. (1989). Parasite des poissons marins du Monténégro: Monogènes. *Acta Adriatica*, 30, 51–135.
- Randall, J. E. (1995). *Coastal fishes of Oman*. Bathurst, Australia: Crawford House Publishing Pty Ltd, 439 pp.
- Roubal, F. R. (1981). The taxonomy and site specificity of the metazoan ectoparasite of the black bream *Acanthopagrus australis* (Gunter), in northern New South Wales. *Australian Journal of Zoology, Suppl.* 84, 100 pp.
- Roubal, F. R. (1990). The parasites of the sparid *Acanthopagrus australis* in Australia. *Bulletin of the European Association of Fish Pathologists*, 10, 110–111.
- Roubal, F. R. (1996). A comparison of the ectoparasite assemblage on snapper, *Pagrus auratus*, from different regions in Australia and from New Zealand. *International Journal for Parasitology*, 26, 661–665.
- Sarabeev, V. L., Rubtsova, N. Yu., Yang, T., & Balbuena, J. A. (2013). Taxonomic revision of the Atlantic and Pacific species of *Ligophorus* Euzet and Suriano, 1977 (Monogenea: Dactylogyridae) from mullets (Teleostei: Mugilidae) with proposal of a new genus and description of four new species. *Vestnik Zoologii, Supplement* 28, 112 pp.
- Šimková, A., & Morand, S. (2008). Co-evolutionary patterns in congeneric monogeneans: a review of *Dactylogyrus* species and their cyprinid hosts. *Journal of Fish Biology*, 73, 2210–2227.
- Šimková, A., Verneau, O., Gelnar, M., & Morand, S. (2006). Specificity and specialisation of congeneric monogeneans parasitizing cyprinid fish. *Evolution*, 60, 1023–1037.
- Soo, O. Y. M., & Lim, L. H. S. (2013). A description of two new species of *Ligophorus* Euzet & Suriano, 1977 (Monogenea: Ancyrocephalidae) from Malaysian mugilid fish using principal component analysis and numerical taxonomy. *Journal of Helminthology*. doi:10.1017/S0022149X13000655.
- Wegener, A. (1966). *The origin of continents and oceans*. New York: Dover Publications, 246 pp.
- Zhang J.-Y., Yang T.-B., & Liu L. (Eds) (2001). *Monogeneans of Chinese marine fishes*. Beijing: Agriculture Press, 400 pp (In Chinese).