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Mothocya renardi (Bleeker, 1857) (Crustacea: Isopoda: Cymothoidae) parasitising *Strongylura leiura* (Bleeker) (Belonidae) off the Malabar coast of India: Redescription, occurrence and life-cycle

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Abstract *Mothocya renardi* (Bleeker, 1857), a protandrically hermaphroditic cymothoid, parasitising the banded needle fish *Strongylura leiura* (Bleeker) from the Malabar Coast, India is redescribed and morphological data for different life-cycle stages [male, transitional and ovigerous female, larvae (pre-manca and manca) and juvenile] are provided. *Mothocya renardi* exhibited strict oligoxenous host specificity by infesting only *S. leiura* and showed high prevalence levels (reaching up to 92%). The life-cycle of *M. renardi* comprises three major phases (marsupial phase, free living phase and infestive phase). The marsupial phase comprised one zygotic, three embryonic and two larval stages, all of which remained in the marsupium until the final staged manca is released into the surrounding water. After having led a short free-swimming life, the manca infested the branchial cavity of the host fish, *S. leiura*. Subsequently it was transformed successively into juvenile, male, transitional and finally functional female through biphasic moult which occurs in between each stage. Based on the presence (or absence) of a brood pouch and/or marsupiumites, six successive stages of the female population were also identified. These data will help precise identification of the female *M. renardi* irrespective of their stage. The present paper also discusses the host-parasite interactions between *S. leiura* and *M. renardi*.

Introduction

The family Cymothoidae Leach, 1818 comprises exclusively ectoparasitic forms, infesting a diverse array of tropical and temperate marine and freshwater teleost fishes (Trilles, 1968, 1994; Brusca, 1981; Seng & Seng, 1990; Horton & Okamura, 2003; Trilles et al., 2011, 2012; Elshahawy & Desouky, 2012; Hadfield et al., 2013, 2015; Aneesh et al., 2013a, 2014, 2015b). *Mothocya* Hope, 1851, one of the major genera of this family comprises 31 named species associated with atheriniform and beloniform fishes (Bruce, 1986; Hadfield et al., 2015); almost all of them have attracted the attention of biologists worldwide as they cause deleterious impacts on their host fishes and thereby seriously limit aquaculture production and its economic viability. Despite the recent reports (Hadfield et al., 2013, 2014a, b; 2015; Aneesh et al., 2015a), many of the species of *Mothocya* still require revision not only to update the available information but also to

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understand the adaptation of their parasitic life-cycle stages on the host fishes. So far, three species, *Mothocya renardi*, *M. plagulophora* (Haller, 1880) and *M. collettei* Bruce, 1986 have been reported from the Indian Peninsula (Bruce, 1986; Gopalakrishnan et al., 2010; Trilles et al, 2011; Aneesh et al., 2013b, 2015a; Aneesh, 2014). During the present study, *Mothocya renardi* was frequently recovered from the branchial cavity of the belonid fish, *Strongylura leiura* from off the Malabar Coast. The other previously reported host species of *M. renardi* include *S. incisa* (Valenciennes) and *S. anastomella* (Valenciennes) (Bruce, 1986).

Surveying through the literature it is evident that most of the descriptions of cymothoids are based only on ovigerous females; other life-cycle stages have not received much attention (Richardson, 1905; Sartor & Pires, 1988; Thatcher et al., 2003, 2007; Trilles & Bariche, 2006; Hadfield et al., 2011; Aneesh et al., 2015b). Males and females and their larval stages (pre-manca and/or manca) have been described for five *Cymothoa* spp.: *C. liannae* Sartor & Pires, 1988; *C. catarinensis* Thatcher, de Loyola, Silva, Jost & Souza-Conceicao, 2003; *C. oestrum* (Linnaeus, 1758); *C. spinipalpa* Thatcher, de Araujo, de Lima & Chellappa, 2007; and *C. frontalis* H. Milne Edwards, 1840 (see Sartor & Pires, 1988; Thatcher et al., 2003, 2007; Aneesh et al., 2015b). Although there have been few detailed studies on *Mothocya* spp., the identity of this cymothoid, in most cases, is still uncertain (Bruce, 1986). Bleeker (1857) first described *M. renardi* as *Livoneca renardi* Bleeker, 1857 based only on the female body characters. Later the species description was revised by Bruce (1986) based on both ovigerous females and males, but without considering the male appendages. Since cymothoids exhibit an intense degree of protandric hermaphroditism, the life-cycle stage dependent taxonomical description would be helpful to understand the characteristic features pertaining to their hermaphroditic life-cycle stages.

Notwithstanding the following reports, the complete life-cycle of cymothoids has not received much attention. Adlard & Lester (1994, 1995) attempted to describe the biology and life-cycle of the parasitic isopod *Anilocra pomacentri* Bruce, 1987 using experimentally infected damselfish, *Chromis nitida* (Whitley), from the Great Barrier Reef (Australia). The development of *Glossobius hemiramphi* Williams & Williams, 1985 infecting *Hemiramphus brasiliensis* (L.) was partially described by Bakenhaster et al. (2006). Recently, Aneesh et al. (2015b) described the life-cycle of *Cymothoa frontalis* infecting *Strongylura strongylura* (van Hasselt). It is suggested that parasitic crustaceans complete their life-cycle through several moults (Maran et al., 2013; Aneesh et al., 2015b).

The present study was pursued to re-describe the male and female stages and describe all other life-cycle stages of *M. renardi* comprising transitional, juvenile, manca and pre-manca by using freshly-collected live samples from the banded needle fish, *Strongylura leiura* (Bleeker) (Beloniformes, Belonidae). Attempt was made to track the complete sequence of life-cycle stages as well as female stages of *M. renardi*. The results of detailed observations on the host-specificity, site-specificity, prevalence and intensity of *M. renardi* are also provided.

Materials and methods

Live fish, *Strongylura leiura,* were collected from the Ayyikkara fish landing centre (11°51′N, 75°22′E; off the Malabar Coast, India). Immediately after collection, fishes were subjected to examination for the presence of *M. renardi*. Parasites were subjected to morphological examination and then preserved in 75% ethanol according to Ramakrishna (1980) for further reference. The terminology and identification follow Bruce (1986). The survey was conducted twice a week, from November 2009 to November 2012. The total length of the live parasites was measured in millimetres. Mouthparts and other appendages of the parasite were carefully dissected out and observed under light microscopy (Leica DM-750); images were taken using image capturing software (LAS-EZ). Drawings of the mouthparts and appendages were performed using a camera lucida attached to the microscope. The moult stages and moult-related changes were determined according to Aneesh et al. (2015b). The assessment of the reproductive activity was carried out *via* microscopic observations of the ovary (dissected out) and marsupiumites (residents of marsupium) (Aneesh et al., 2015b). Classification of the marsupial stages follows Bakenhaster et al. (2006) and Aneesh et al. (2015b). Fish taxonomy and host nomenclature follow Fish Base (Froese & Pauly, 2015) and Eschmeyer (2015). Voucher specimens are deposited in the collections of the Parasitic Crustacean

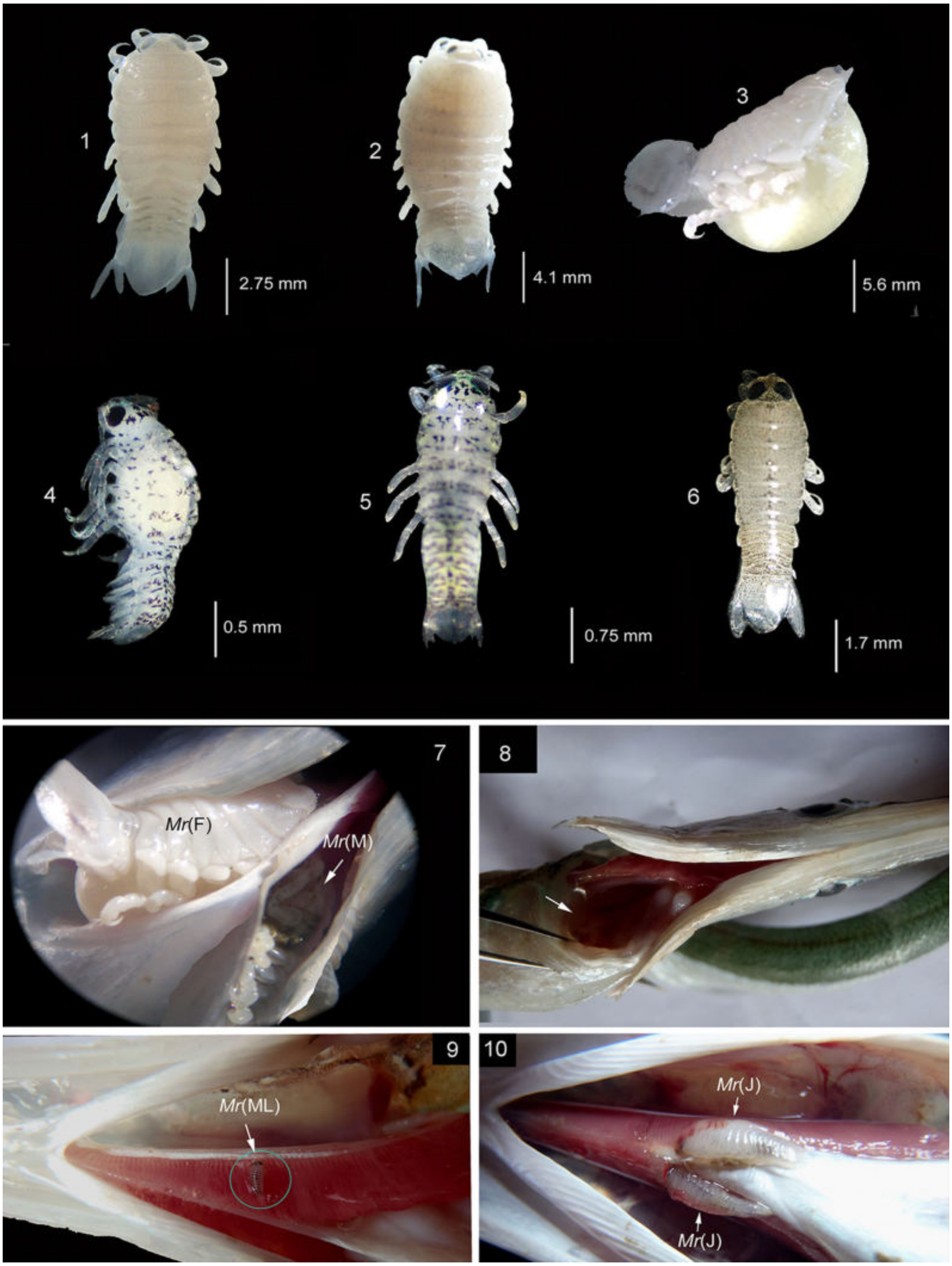

Fig. 1 *Mothocya renardi* (Bleeker, 1857) ex *Strongylura leiura* (Bleeker). 1, Male; 2, Transitional stage; 3, Ovigerous female; 4, Premanca larva; 5, Manca larva; 6, Juvenile; 7, Male and female *M. renardi* on *S. leiura*; 8, Large pitted scar (*arrow*) formed in the branchial cavity of the host due to *M. renardi*; 9, Manca on *S. leiura*; 10, Juveniles on *S. leiura*. *Scale-bars*: 1, 2.75 mm; 2, 4.10 mm; 3, 5.60 mm; 4, 0.50 mm; 5, 0.75 mm; 6, 1.70 mm

Museum (PCM), Crustacean Biology Research Laboratory, Sree Narayana College, Kannur, Kerala, India.

Family Cymothoidae Leach, 1818
Genus *Mothocya* Hope, 1851

Mothocya renardi (Bleeker, 1857)

Syns *Livoneca renardi* Bleeker, 1857; *Irona renardi* Schioedte & Meinert, 1884; *Irona melanosticta* Barnard, 1914; *Irona renardi* Nierstrasz, 1915; *Irona robusta* Nair, 1950

Hosts: *Strongylura leiura* (Bleeker) (present material). According to Bruce (1986), this is the most common host; other host species include *S. incisa* (Valenciennes) and *S. anastomella* (Valenciennes). The records from *Tylosurus crocodilus crocodilus* (Péron & Lesueur) and *Strongylura strongylura* (van Hasselt) are still unconfirmed.

Distribution: Indo-West Pacific, Mozambique, Kuwait, Western and Eastern coasts of Australia, the Philippines and Japan (Bruce, 1986); off Malabar Coast, Kerala, India (present study).

Material examined: 185 ♀♀, 112 ♂♂, 39 transitional stages, 9 juveniles, 74 manca larvae and 68 pre-manca larvae.

Voucher specimens: 1♀ (PCM MR–01); 1♂ (PCM MR–02); 1♀ (PCM MR–03); 1♀ (PCM MR–04); 1♀ (PCM MR–05); 1♀ (PCM MR–06); 30 pre-manca larvae (PCM MR–07); 1♀ (PCM MR–08); 1♀ (PCM MR–09); 1 juvenile (PCM MR–10); 1♀ (PCM MR–11); 1 transitional stage (PCM MR–12); 1♀ (PCM MR–13); 1♀ with 2–5 manca-staged marsupiumites (PCM MR–14; 15 manca larva (PCM MR–15); 1 transitional stage (PCM MR–16); 1♀ (PCM MR–17); 1 ♂ (PCM MR–18); 1♂ (PCM MR–19); 1♂ (PCM MR–20); 1♀ (PCM MR–24), all from *S. leiura* (Bleeker) and deposited in the collections of the Parasitic Crustacean Museum (PCM), Crustacean Biology Research Laboratory, Sree Narayana College, Kannur, Kerala, India.

Description (Figs. 1–6)

Ovigerous female (Figs. 1.3, 2). Body creamy-white, 16–34 mm long, about 2.2–2.4 times as long as wide, widest at pereonite 3. Cephalon (Fig. 2.1, 2.2) wider than long, accommodated in deeply recessed pereonite 1. Eyes small, distinct, width 0.35–0.45 width of cephalon. Coxae 2–7 (Fig. 2.1, 2.2) narrow, visible in dorsal view; 2–4 shorter than segment; 5–7 longer than segment. Pereonite 1 (Fig. 2.1, 2.2) longest, pereonites increase in width from 1 to 3; pereonites 4–7 decreasing in width progressively, pereonite 7 widely recessed. Pleonite 1 (Fig. 2.1, 2.2) and most of pleonite 2 concealed by pereonite 7; one side of pleonite 3 and most of pleonite 4 overlapped by coxal plates of pereonite of its side. Pleon wider than pereonite 7. Pleotelson (Fig. 2.1, 2.2) about 1.1–1.2× as wide as long, posterior margin rounded.

Antennule (Fig. 2.5) stouter than antenna, composed of 8 articles; article 3 longest; articles 1–3 slightly wider than others; apex of article 8 curved with many terminal aesthetascs. Antenna (Fig. 2.6) 9-articled, decreasing gradually in width, article 9 with few terminal aesthetascs. Mandible (Fig. 2.7) palp 3 segmented, without setae, extending beyond incisor. Maxillule (Fig. 2.8) with 4 slightly recurved apical spines. Maxilla (Fig. 2.9) bi-lobed, with 2 spines on inner median lobe and 3 spines on outer lateral lobe. Maxilliped (Fig. 2.10) article 3 with 3 large terminal recurved spines and small spine on proximomedial surface.

Pereopods 1–7 (Fig. 2.11–2.17) without spines. Pereopod 1 short, robust; pereopods 2–6 subequal; pereopod 7 longer than others. Exopodite of pleopods 1–5 without seta. Pleopod 2 (Fig. 2.19) without appendix masculina. Pleopod 1 (Fig. 2.18) with narrow peduncle and undeveloped lateral lobes; pleopod 2–5 (Fig. 2.19–2.22), peduncles with well-developed lateral lobe; endopods of pleopod 3 and 4 with well-developed proximomedial lobe. Endopod of pleopod 5 (Fig. 2.22) with large proximomedial lobe. Uropod rami (Fig. 2.25) long; exopod and endopod extending beyond distal margin of pleotelson; rami taper gradually; apex narrowly rounded. Exopod (Fig. 2.24) about 1.8–1.9× longer than endopod.

Brood pouch (Fig. 2.23) made up of 4 pairs of overlapping oostegites arising from bases of pereopods 2, 3, 4 and 6. Number of eggs or larvae per brood pouch (marsupium) 420–1,280 depending on female size.

Transitional stage (Figs. 1.2, 3). Body (Fig. 3.1, 3.3) creamy-white, 10.5–23.0 mm long, 2.25–2.45× as long as wide. Eyes small, distinct, width 0.35–0.40× times width of cephalon. Pereonites, pleonites, antennule and antenna similar to those in the ovigerous

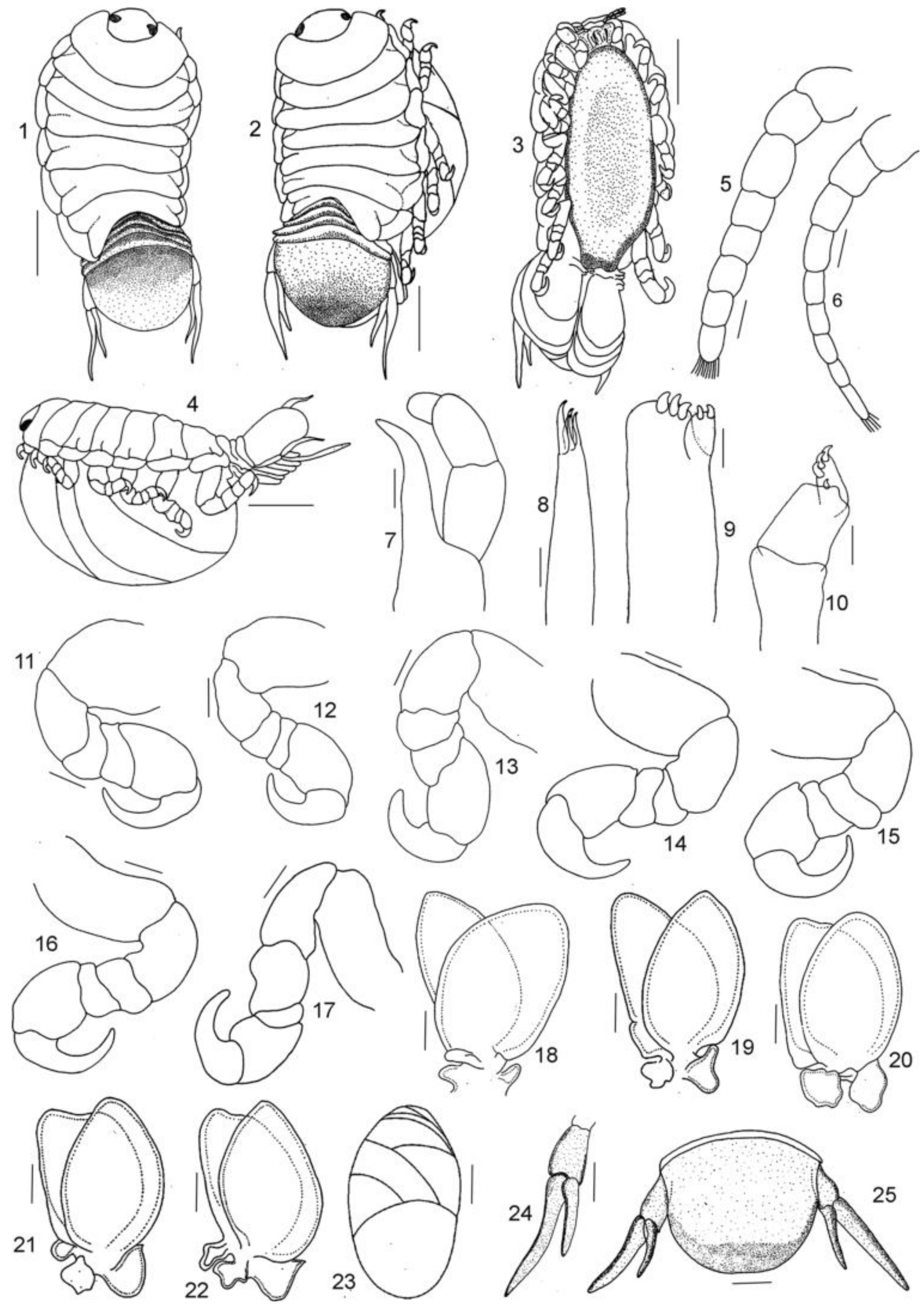

Fig. 2 *Mothocya renardi* (Bleeker, 1857), ovigerous female ex *Strongylura leiura* (Bleeker). 1–2, Dorsal view; 3, Ventral view; 4, Lateral view; 5, Antennule; 6, Antenna; 7, Mandible; 8, Maxillule; 9, Maxilla; 10, Maxilliped; 11–17, Pereopods 1–7; 18–22, Pleopods 1–5; 23, Brood pouch; 24, Uropod with rami; 25, Uropod and pleotelson. *Scale-bars*: 1–4, 6.20 mm; 5, 6, 0.40 mm; 7, 0.50 mm; 8, 9, 0.21 mm; 10, 0.45 mm; 11–14, 22, 0.80 mm; 15-17, 0.95 mm; 18, 0.65 mm, 19, 20, 0.70 mm; 21, 0.75; 23, 4.50 mm; 24, 2.30 mm; 25, 2.50 mm

female. Mandible palp (Fig. 3.4) and maxilla (Fig. 3.5), similar to those in the male. Rudimentary penis (Fig. 3.2, 3.7) visible on sternite 7. Pleopod 2 (Fig. 3.6) with appendix masculina as in male. Pleotelson and uropods similar to those in ovigerous female. Pereopods also similar to those in adults. Pleopods not distinctly visible in dorsal view, similar to those in the male.

Male (Figs. 1.1, 4). Relatively smaller than transitional stage and female. Body creamy-white, 10.0–19.0 mm long, with light pigmentation on lateral and posterior margins of pereonites and pleonites . Body 2.75–2.87× as long as wide (Fig. 4.1). Cephalon wider than long. Eyes small, distinct, about 0.36–0.40× width of cephalon. Pereonites decreasing in width from 4–7; pereonite 1 longest, pereonites 2–6 subequal, pereonite 7 shortest. Coxae not much clear in dorsal view (Fig. 4.1). Pleon slightly wider than pereonite 7. Pleonite 1 largely concealed by pereonite 7. Pleonites 1–5 subequal in length. Pleotelson (Fig. 4.1) as long as wide, posterior margin more or less rounded.

Antennule (Fig. 4.3) stouter than antenna, 8-articled; article 3 longest; first 3 articles slightly wider than others; distal margin of articles 4–7 with 2–5 setae; apex of article 8 curved with many terminal aesthetascs. Antenna (Fig. 4.4) longer than antennule, composed of 9 articles, decreasing gradually in width, articles 5 and 6 with 1 plumose seta; article 9 with few terminal aesthetascs. Mandible palp (Fig. 4.5) 3-segmented, slender, without setae and extending beyond incisor. Maxillule (Fig. 4.6) with 4 apical slightly recurved spines. Maxilla bi-lobed (Fig. 4.7), with 2 spines on inner median and outer lateral lobes. Maxilliped (Fig. 4.8) article 3 with 3 large terminal recurved spines and small spine on proximomedial surface.

Pereopods 1–7 (Fig. 4.9–4.15) without spines. Basis little narrower than in female. Pereopod 1 short and robust, pereopods 2–6 subequal, pereopod 7 longer than others. Penes (Fig. 4.2, 4.16) visible on sternite 7. Pleopods (Fig. 4.1) not distinctly visible in dorsal view. Pleopod 2 (Fig. 4.18) with appendix masculina. Exopodite of pleopods 1–5 (Fig. 4.17–4.21) without seta. Peduncle longer than in female, lateral lobes not developed in pleopod 1 and 2; pleopods 3–5, peduncles with well-developed lateral and proximomedial lobe. Uropod (Fig. 4.23) long, rami extending beyond distal margin of pleotelson, taper gradually; apex narrowly rounded. Exopod (Fig. 4.22) about 1.8× length of endopod.

Juvenile (Figs. 1.6, 5). Body transparent 6.5–11.0 mm long, relatively narrower and smaller than in other post-larval stages (male, transitional stage and female). Body approximately 3.4× as long as wide. Eyes (Fig. 5.1) prominent, ovate, conspicuous in dorsal view, width *c.*0.4× width of cephalon. Cephalon (Fig. 5.1) 1.6× as wide as long, anterior margin rounded. Pereonite 1 not recessed. Pereonite 1 (Fig. 5.1) longest, pereonites 2–4 subequal, pereonite 5–7 gradually decreasing in length. Pereonite 3 widest, pereonites 4–7 decreasing in width. Penes poorly developed (Fig. 5.2) on sternite 7. All pleonites (Fig. 5.1) visible in dorsal view. Pleonites 1 and 2, subequal to pereonite 7 in length. Pleonites 1 and 2 widest; pleonites 3–5 gradually decreasing in width. Pleotelson (Fig. 5.21) 1.1× as long as wide; apical margin more or less rounded with many setae.

Antennule (Fig. 5.3) stouter than antenna, 8-articled; distal margin of articles 3–7 with 4–8 setae; apex of article 8 curved, with many terminal aesthetascs. Antenna (Fig. 5.4) longer than antennule, composed of 9 articles, decreasing gradually in width, article 2 with 4, article 3 with 4 and article 4 with 6 plumose setae; article 9 with few terminal aesthetascs. Mandible palp (Fig. 5.5) article 3 with 6–9 similar setae arising from disto-lateral margin; apical setae recurved and longer than others. Article 2 with 3 setae on disto-lateral and 1 seta on mediolateral margin. Article 1 without setae. Maxillule (Fig. 5.6), maxilla (Fig. 5.7) and maxilliped (Fig. 5.8) similar to those in the male.

Pereopods 1, 2, 3 and 7 (Fig. 5.9–5.15) with 1 spine on posterior margin of merus; posterior margin of propodus of pereopods 1–3 with 1 and that of pereopod 7 with 3 spines; carpus of pereopod 7 with 1 spine. Dactylus of pereopods 1–3 (Fig. 5.9–5.15) with reduced teeth; pereopods 4–7 without teeth. Dactylus of pereopod 7 blunt. All pereopods with scattered chromatophores.

Inner margin of exopodite of pleopods 1–5 with few setae. Median margin of protopod of pleopods 1 and 2 (Fig. 5.16, 5.17) with 6–8 plumose setae and 4–6 setae. Pleopod 2 (Fig. 5.17) with thick and vestigial appendix masculina, shorter than endopodite. Pleopod 1–3 (Fig. 5.16–5.20) with long peduncle, lateral lobes not developed; peduncle of pleopods 4–5 with

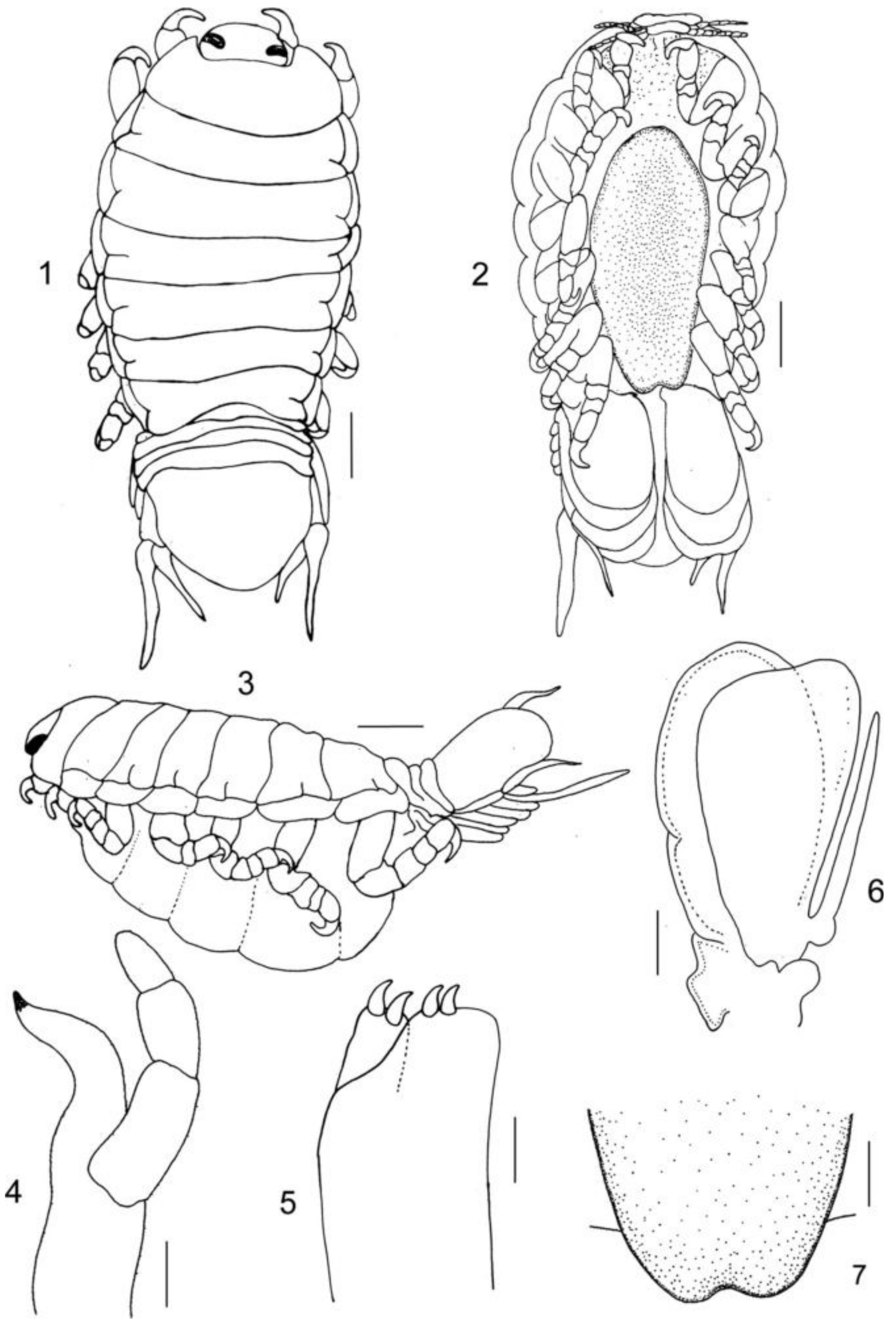

Fig. 3 *Mothocya renardi* (Bleeker, 1857), transitional stage ex *Strongylura leiura* (Bleeker). 1, Dorsal view; 2, Ventral view; 3, Lateral view; 4, Mandible; 5, Maxilla; 6, Pleopod 2; 7, Penes. *Scale-bars*: 1, 2, 2.30 mm; 3, 2.50 mm; 4, 0.35 mm; 5, 0.25 mm; 6, 7, 0.70 mm

well-developed lateral and proximomedial lobes. Uropod rami (Fig. 5.21) extending beyond distal margin of pleotelson, subequal in length but endopodite slightly short, curved, rounded apically; exopodite with 30–40 setae, endopodite with 40–45 setae.

Manca (Figs 5.5, 6.1–6.18). The manca developed from the pre-manca through moulting shows distinct morphological characters. Body elongate, transparent, with scattered chromatophores particularly on uropods and pleotelson, 3.1–4.4 mm long, *c*.3.9× as long as

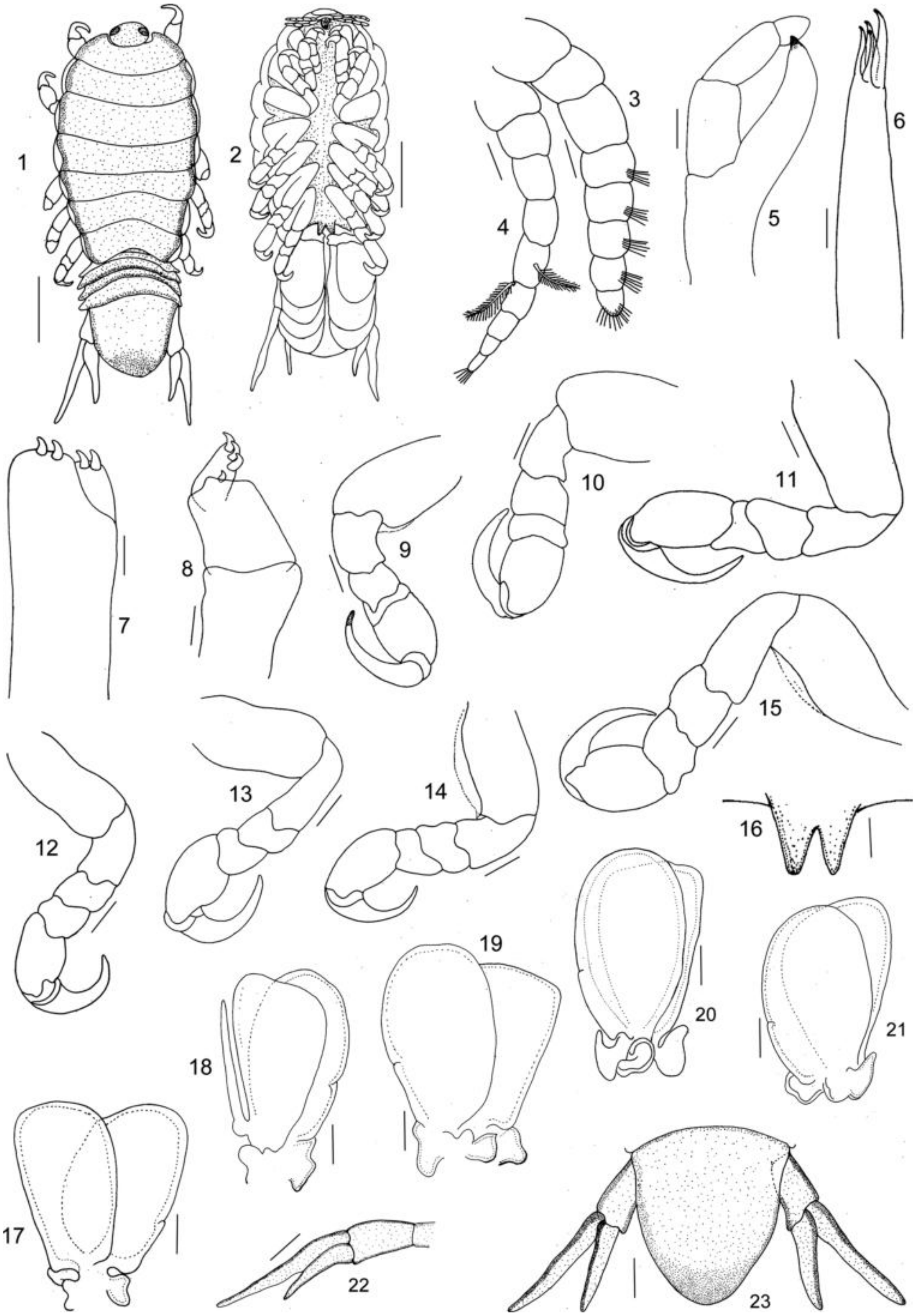

Fig. 4 *Mothocya renardi* (Bleeker, 1857), male ex *Strongylura leiura* (Bleeker). 1, Dorsal view; 2, Ventral view; 3, Antennule; 4, Antenna; 5, Mandible; 6, Maxillule; 7, Maxilla; 8, Maxilliped; 9–15, Pereopods 1–7; 16, Penes; 17–21, Pleopods 1–5; 22, Uropod with rami; 23, Uropod and pleotelson. *Scale-bars*: 1, 2, 2.70 mm; 3, 4, 5, 0.40 mm; 6, 0.15 mm; 7, 0.18 mm; 8, 0.35 mm; 9, 10, 0.80 mm; 11–13, 0.85 mm; 14, 15, 0.90 mm; 16, 0.75 mm; 17–21, 0.70 mm, 22, 2.4 mm; 23, 2.50 mm

wide. Eyes (Fig. 6.1) black, prominent, ovate, conspicuous in dorsal view. Cephalon 1.6× as wide as long, golden yellow in colour. Pereonite 3 widest; pereonite 1 longest; pereonites 4–7 gradually decreasing in width; pereonite 7 (Fig. 6.1) shortest and narrowest. All pleonites visible and subequal in width and length; 4× as wide as long. Pleotelson (Fig. 6.1, 6.2, 6.18) 1.1× as long as wide, with 16–18 plumose setae on apical margin.

Antennule (Fig. 6.3) 8-articled, article 3 longest; distal margin of articles 1 and 2 with 2–4 almost equal spinules; articles 5 and 6 with 1 and article 7 with 2 elongate setae; article 8 with 4 elongate setae and 4 terminal aesthetascs. Antenna (Fig. 6.4) longer than antennule, 9-articled, extending to anterior margin of pereonite 1; all articles with spinules; article 9 with 6–8 terminal aesthetascs. Mandible palp (Fig. 6.5) article 2 with 1 seta arising from distal margin; article 3 with three marginal setae and 1 apical recurved seta. Maxillule (Fig. 6.6), maxilla (Fig. 6.7) and maxilliped (Fig. 6.8) as in the male.

Dactylus of pereopods 1–3 (Fig. 6.9–6.15) toothed, pereopods 4–6 without teeth. Pereopods 1, 2, 3 and 6 (Fig. 6.9–6.11, 6.15) with 1 spine on posterior margin of merus; posterior margin of propodus of pereopods 1–3 with 3 spines; pereopod 6 with 4–5 spines; carpus of pereopods 1, 2, 3 and 6 with 1 spine. Pereopods 4 and 5 (Fig. 6.13, 6.14) without spines. Dactylus of pereopod 1 (Fig. 6.12) with 5–8 teeth; pereopods 2 and 3 with 8–10 teeth. Pleopods (Fig. 6.1, 6.2) not distinctly visible in dorsal view. Pleopod 1 (Fig. 6.16) with 14–18 plumose setae on endopodite and 24–26 plumose setae on exopodite. Pleopods 2–5 (Fig. 6.17), apical margin of exopodite with 24–26 plumose setae. Pleopods 1–5, median margin of protopod with 4/5 retinaculae and retinaculae 1 with few aesthetascs. Uropod rami (Fig. 6.18) extending beyond distal margin of pleotelson; rami, curved, rounded apically; exopod about 1.3× longer than endopod. Exopodite with 8–12 plumose setae and apical border with a slightly recurved spine; endopodite with 16–20 plumose setae (Fig. 6.18).

Pre-manca (Figs. 1.4, 6.19–6.29). Body (Fig. 6.19, 6.20) elongate, slightly curved and transparent, *c*.4 times as long as wide, with scattered chromatophores particularly on uropods and pleotelson, 2.0–2.5 mm long. Eyes (Fig. 6.19) black, prominent, ovate, conspicuous in dorsal view. Cephalon 1.3× as wide as long, not immersed in pereonite 1. Centrally arranged yolk globules (Fig. 6.19, 6.20) visible in pereon, between pereonites 2 and 6. All appendages (Fig. 6.20) devoid of setae and spines. Mouthparts (Fig. 6.23–6.26) not well developed. Uropod rami extending beyond distal margin of pleotelson; rami, curved, rounded apically; exopod slightly longer than endopod. Apical border of rami devoid of plumose setae. Pereonite 1 relatively long, pereonite 7 short and thin than remaining, pereonites 4 and 5 widest. All pleonites visible and subequal in width and length; 3.4× as wide as long. Pleotelson (Fig. 6.19) as wide as long, without plumose setae.

Antennule 8-articled (Fig. 6.21), extends to anterior margin of pereonite 2; antenna (Fig. 6.22) longer than antennule, 9-articled, extending to anterior margin of pereonite 3; all articles without setae and spinules. Mouthparts not well developed; mandible palp (Fig. 6.23) articles without setae and spines; maxillule (Fig. 6.24), maxilla (Fig. 6.25) and maxilliped (Fig. 6.26) not recurved, with poorly developed apical spines.

Pereopods 1–6 (Fig. 6.27) without spines. Distal margin of dactylus of pereopods 1–6 (Fig. 6.28) slightly indented, forming narrow terminal part. Dactylus of pereopods not toothed. Pleopods (Fig. 6.29) not distinctly visible in dorsal view. Pleopods 1–5 without plumose setae. Uropods and pleotelson with dark chromatophores. Uropod rami (Fig. 6.19) extending beyond the distal margin of pleotelson; rami subequal in length but endopodite slightly short, curved, rounded apically, without plumose setae.

Occurrence of *Mothocya renardi*

Of a total of 408 *S. leiura* examined, 376 were found to be infected with *M. renardi* (Fig. 1), the prevalence reached up to 92.15%. A total of 684 parasites (*M. renardi*) including brooded ovigerous females (carrying marsupiumites), non-brooded ovigerous females, males, transitionals and juveniles were recovered; the overall mean intensity was 1.81. Interestingly, the prevalence of *M. renardi* on *S. leiura* was found to be more or less uniform (more than 85%) without showing any sign of fluctuation, throughout the study period (from November 2009 to November 2012).

In several instances (81.9%; 308 out of 376), *M. renardi* was found in pairs but with diverse

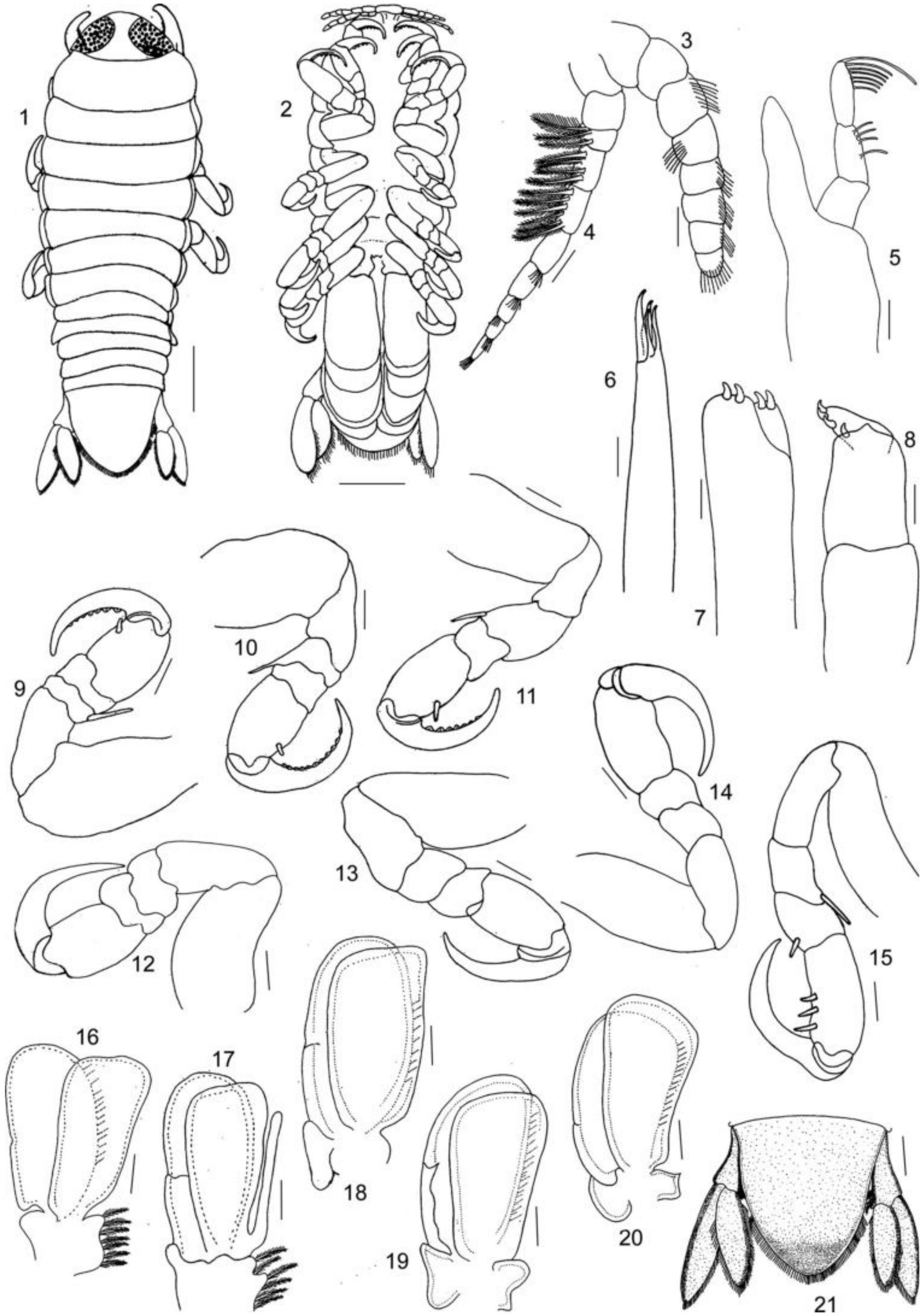

Fig. 5 *Mothocya renardi* (Bleeker, 1857), juvenile ex *Strongylura leiura* (Bleeker). 1, Dorsal view; 2, Ventral view; 3, Antennule; 4, Antenna; 5, Mandible with palp; 6, Maxillule; 7, Maxilla; 8, Maxilliped; 9–15, Pereopods 1–7; 16, Pleopod 1; 17, Pleopod 2 with vestigial appendix masculina; 18–20, Pleopods 3–5; 21, Pleotelson and uropods. *Scale-bars*: 1, 2, 1.35 mm; 3, 4, 8, 0.25 mm; 5, 0.40 mm; 6, 7, 0.20 mm; 9, 0.30 mm; 10, 11, 13–15, 0.35 mm; 12, 0.40 mm; 16–18, 20, 0.60 mm; 19, 0.65 mm; 21, 0.55 mm

combinations, such as male-female (88.31%; 272 out of 308) (Fig. 1.7), male-transitional (9.42%; 29 out of 308), female-juvenile (1 out of 308), juvenile-transitional (1.3%; 4 out of 308) and juvenile-juvenile (0.65%; 2 out of 308) (Fig. 1.10). In the remaining cases (18.1%; 68 out of 376), parasites were found unpaired (62 females and six transitionals). The floor of the branchial cavity of the host represents the main site of infection irrespective of the stages (male, female, transitional and juvenile) and pair combinations (male-female/male-transitional/female-juvenile/juvenile-transitional). It is interesting to note that the body of female *M. renardi* exhibited a bend (either towards right or left) depending on the branchial side: if the parasite is located in the right branchial cavity, its body bends towards the left and *vice versa*. In more than 80% of cases, the females were recovered from the floor of the right branchial chamber where they were attached. Contrary to the common pattern, in two cases, male-ovigerous female pairs were found occupying the same branchial cavity. In all cases, the gill cavity showed the presence of a pit-like depression with significant damage in the tissue lining and appressed gill filaments (Fig. 1.8).

Life-cycle of *Mothocya renardi*

The present study revealed that the life cycle of *M. renardi* encompasses three major phases: marsupial, free living and infective (see Table 1 and Figs. 1, 7.1 for details). During the marsupial phase, marsupiumites appear in six sequential, morphologically distinct, developmental stages (zygotic stage, ES-I, ES-II, ES-III, pre-manca and manca; Fig. 7.1.–7.5). Embryonic development culminates into the formation of a pre-manca which transforms to a manca through moulting. After having spent a short period in the marsupium, the mancae are released into the surrounding sea water to lead a free-swimming life for up to six days (borne out from experiments conducted in our laboratory).

Paired mancae infect and settle in the branchial cavity of its specific host (*S. leiura*) where they undergo series of moults to transform to juveniles and subsequently to adult males (Fig. 7.1). One of the males becomes ‘transitional’ (Fig. 3.4–3.6) while the other remains in the male phase. The ‘transitional’ male further undergoes two sequential moults (the second being referred to as “oostegition moult”) and transforms into an ovigerous female with marsupium. During its parasitic life, the female exhibits breeding and parental care several times, coupled with de-oostegition and oostegition moults, when the old marsupium is replaced with a new one (oostegition moult precedes spawning, followed by marsupial life and then larval release, after which de-oostegition moult ensues).

Based on the presence or absence of marsupium and/or marsupiumites, six successive stages of ovigerous female (Fs-1 through Fs-6) were identified (Fig. 7.1 and Table 1). Fs-1 stage females, develop from the transitionals through first oostegition moult. This stage is characterised by the presence of growing/mature oocytes in the ovary (first ovarian cycle) and the newly-formed (first) marsupium. The Fs-2 and Fs-3 stages appear with marsupiumites and old empty marsupium, respectively. Through de-oostegition moult, Fs-3 transforms to Fs-4 which then undergoes oostegition moult and transforms into Fs-5 possessing newly-formed (second) marsupium; its ovary undergoes the second ovarian cycle. Following oviposition, Fs-5 transforms to Fs-6 possessing the second batch of marsupiumites. All female stages (Fs-1 to Fs-6) were profusely seen throughout the study period indicating the high reproductive potential of the parasite.

Discussion

To the best of our knowledge, the present study is the first report describing the transitional, juvenile, manca and pre-manca stages of a *Mothocya* spp., *M. renardi*, which in turn facilitates its precise identification irrespective of the stage of development. Adult males and females of *M. renardi* can now be easily differentiated from other species (of the genus *Mothocya*) by their large size, very narrow pleon and exceptionally long uropodal rami extending well beyond the distal margin of the pleotelson. This study also allowed us to compare the morphological features of *M. renardi* with those of closely allied groups of parasitic crustaceans. The uropodal rami in *M. renardi*, for instance, showed only meager extension beyond the distal margin of pleotelson, whereas in *C. frontalis,* these are extremely extended (Aneesh et al., 2015b). The toothed dactyli of the first three pairs of pereopods and spines present in the manca of *C.*

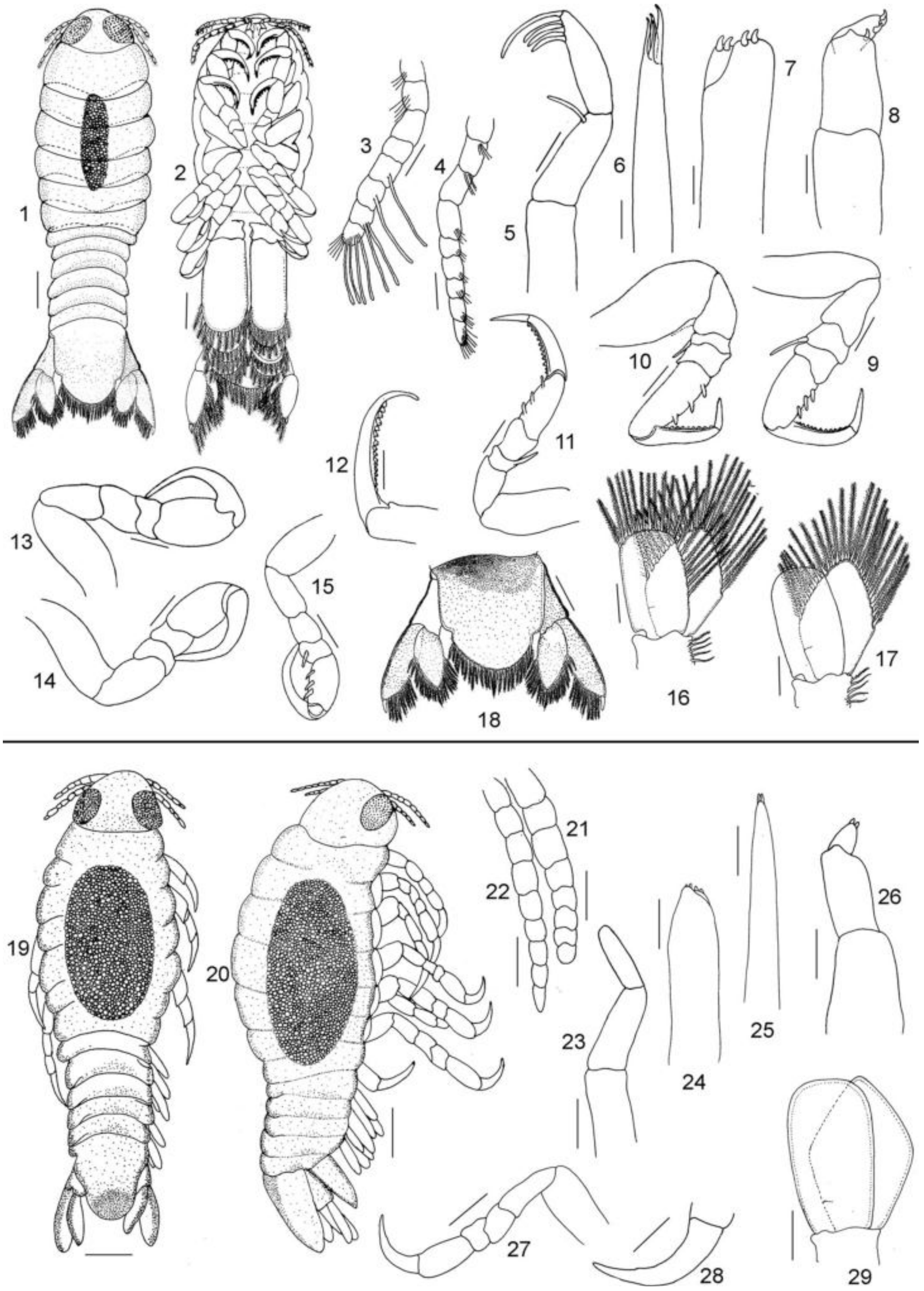

Fig. 6 *Mothocya renardi* (Bleeker, 1857), manca (1–18) and pre-manca larva (19–29) from the brood of female ex *Strongylura leiura,* (Bleeker). 1, Dorsal view; 2, Ventral view; 3, Antennule; 4, Antenna; 5, Mandible palp; 6, Maxillule; 7, Maxilla; 8, Maxilliped; 9–11, Pereopods 1–3; 12, Dactylus of pereopod 3; 13–15, Pereopods 4–6; 16, Pleopod 1; 17, Pleopod 4; 18, Pleotelson and uropod; 19, Dorsal view; 20, Lateral view; 21, Antennule; 22, Antenna; 23, Mandible palp; 24, Maxillule; 25, Maxilla; 26, Maxilliped; 27, Pereopod 2; 28, Dactylus of pereopod 2; 29, Pleopod 2. *Scale-bars*: 1, 2, 0.36 mm; 3, 4, 0.10 mm; 5, 9–11, 15, 0.30 mm; 6, 7, 0.20 mm; 8, 18, 27, 0.25 mm; 12, 21, 22, 0.15 mm; 13, 0.35 mm; 14, 0.32 mm; 16, 17, 0.40 mm; 19, 20, 0.24 mm; 23, 0.05 mm; 24–26, 0.06 mm; 28, 0.12 mm; 29, 0.07 mm

frontalis and *M. renardi* help the parasites to cling on to the host fish during their infective stages. Contrary to this, in the mancae of *Agarna malayi* Tiwari, 1953 and *Norileca indica* (Milne Edwards, 1840), dactyli are present only on the propodus of first three pereopods (Aneesh et al., unpublished data). The transitional stage in *M. renardi* depicts an ensemble of male and female characters, quite reminiscent of several protandrous cymothoids (such as *G. hemiramphi, A. malayi, Joryma brachysoma* Pilli, 1964 and *C. frontalis*) (Williams & Williams, 1985; Aneesh, 2014; Aneesh et al., 2015b).

Although 80 different species of fishes distributed along the Malabar coast were examined for three consecutive years between November 2009 to November 2012 (see Supplementary Table S1), only the belonid *Strongylura leiura* was infected with *M. renardi*, indicating its oligoxenous host specificity. According to our previous studies (Aneesh et al., 2013a, 2015b; Aneesh, 2014) oligoxenous host specificity was also evident in four cymothoid species, such as *C. frontalis, N. indica, M. collettei* and *Nerocila longispina* Miers, 1800 parasitising *S. strongylura, Rastrelliger kanagurta* (Cuvier), *T. crocodilus crocodilus* and *Ambassis ambassis* (Lacépède), respectively, distributed along the Malabar coast. The factors determining host specificity of the most fish parasites in the marine system are assumed to be ecological, host habitat and diet (Sukhdeo & Sukhdeo, 1994; Marcogliese, 2002).

Table 1 Life-cycle stages of *Mothocya renardi* (Bleeker, 1857) and their characteristic features

Life-cycle stages		Characteristic features
Marsupial stages	Zygotic stage	Round or oval, light florescent-yellow (1.25–1.3 mm)
	Embryonic stages (ES)	Sub-spherical to ovoid, structural differentiation not evident, light florescent-yellow. Size: 1.35–1.45 × 1.25–1.30 mm
	ES-I	
	ES-II	Elongate/ oblong, with a cephalic end and early limb bud developed: early pigmentation of the eye-spot present. Size: 1.6–1.7 × 1.3–1.35 mm
	ES-III	Curved, segmented, with pigmented eye-spots and thoracic and abdominal limb buds; dorsal surface with chromatophores. Size: 1.9–2 × 1.3–1.4 mm
	Larval stages	The first hatch out larva remains in the marsupium and undergoes moulting to transform to manca larva
	Pre-manca	
	Manca	Final marsupial stage released into the water
Free-living stage	Manca larva	Free-swimming stage; swims and searches for the specific host (*S. leiura*)
Infective stages	Manca larva (infective stage)	Infests the host; undergoes moulting (sequential?) to transform into juvenile
	Juvenile	Undergoes moulting (sequential?) to transform into male
	Male	Undergoes sequential moulting; if two males, one enters into the transitional stage and other remains male
	Transitional stage	Undergoes first oostegition moult to form the female stage I (Fs I)
	Female	Ovigerous female with fully grown ovary and newly formed brood plates, but with no marsupiumites: undergoes oviposition to form Fs-2
	Fs-1	
	Fs-2	Ovigerous female with growing ovary and carrying first set of brood; marsupiumites show synchrony in their development
	Fs-3	Ovigerous female with growing ovary and carrying empty old brood pouch, after releasing manca larva; undergoes first de-oostegition moult to form Fs-4
	Fs-4	Ovigerous female with growing ovary and no brood pouch/brood plates; undergoes 2nd oostegition moult to form Fs-5
	Fs-5	Ovigerous female after 2nd oostegition moult, with newly formed brood plates but no marsupiumites; .undergoes oviposition to form Fs-6
	Fs-6	Ovigerous female carrying second set of brood; marsupiumites show synchrony in their development

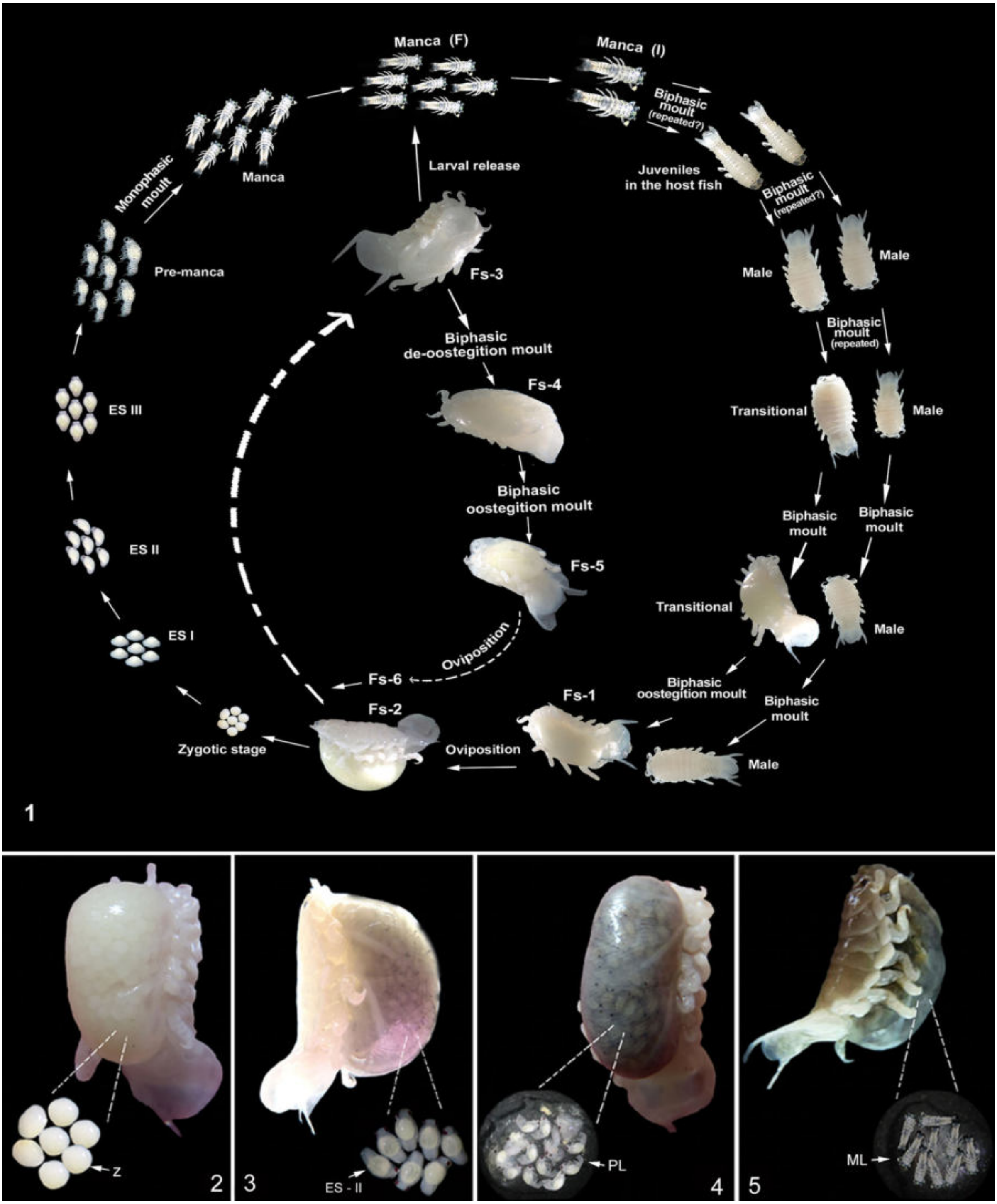

Fig. 7 1, Schematic representation of the life-cycle of *Mothocya renardi* (Bleeker, 1857) ex *Strongylura leiura,* (Bleeker); 2–5, *Mothocya renardi* (Bleeker, 1857) ex *Strongylura leiura,* (Bleeker) carrying marsupiumites which show synchronised pattern of development; 2, Marsupiumites at zygotic stage; 3, Marsupiumites at embryonic stage ii; 4, Marsupiumites at pre-manca stage; 5, Marsupiumites at manca stage. *Abbreviations*: Manca (F), manca at free living stage; Manca (I), manca at infestive stage; ES, embryonic stage; Fs, female stage; Z, zygote; ES II, embryonic stage II; PL, pre-manca larvae; ML, manca larvae

According to Bruce (1986), the confirmed fish hosts of *M. renardi* include *S. leiura*, *S. incise* and *S. anastomella*. Although *T. crocodilus crocodilus* and *S. strongylura* have been reported to host *M. renardi* (see Bruce, 1986), the present study could not recover this parasite from these hosts even once; but they were usually found infected with *Mothocya collettei* and *Cymothoa frontalis*, respectively (Aneesh, 2014; Aneesh et al., 2015b). Although on several instances, parasites have been shown to infect several host species of a particular genus or family, arguably it could be that the parasite in question may have an inclination to stick onto a specific host species (Cressey et al., 1983).

The prevalence of *M. renardi* on *S. leiura* has been more or less uniform throughout the study period, with no signs of fluctuations. Contrary to this, four species of *Nerocila* infecting the body surface of the host fishes have been reported to show significant seasonal fluctuations in their prevalence, reaching a peak during October–April; the infection was minimal or absent during May–September (Aneesh et al., 2013a). The prevalence of *Nerocila serra* Schioedte & Meinert, 1881 infecting the sea snake, *Enhydrina schistose* (Daudin) was found to reach a maximum during the monsoon period (Saravanakumar et al., 2012).

The negative impacts of cymothoid parasites on the host could vary with the species and its location on the host. Atrophied gills and large pit-like depressions occurring in the branchial cavity of the host are seen as the aftermath of an infection with *M. renardi*. Branchial cymothoids have been suggested to cause reduced respiratory metabolism (Trilles, 1994), while, the buccal parasites are known to cause tongue degeneration and skull deformations (Romestand & Trilles, 1979; Brusca & Gilligan, 1983). Isopods infecting fish body surface degenerate the fins and damage the scales and epidermis, and can cause pronounced epithelial hyperplasia (Brusca, 1978; Rand, 1986). *Anilocra nemipteri* Bruce, 1987 that attaches to the fish host *Scolopsis bilineata* (Bloch), grows to almost one third of fish length, jeopardising host growth (Adlard & Lester, 1994; Williams & Williams, 1998; Roche et al., 2013).

In *M. renardi*, the manca is released into the ambient water within two days of their appearance in the marsupium and leads a free-swimming life until it infects a specific host; this is reminiscent of the reports from *Anilocra apogonae* Bruce, 1987 and *C. frontalis* (see Fogelman & Grutter, 2008; Aneesh et al., 2015b). Interestingly, the manca of *G. hemiramphi,* has been shown to infect other host species temporarily, before settling on its specific host (Bakenhaster et al., 2006). The exact mechanism that leads the manca to its specific host is yet to be explored. According to Bakenhaster et al. (2006), the physical characteristics of the manca facilitate the attachment to the specific host. The environmental cues or host-derived factors are likely to facilitate site-specific attachment (Adlard & Lester, 1995). Further, there is no evidence available to gauge the number of successful larval attachments out of the total number of larvae produced.

In summary, the present redescription of *M. renardi*, and the description of its life-cycle stages provide key information on its parasitic and protandric hermaphroditic life, as well as important cues for the precise identification of other cymothoids as well. Further, very importantly, the features such as strict host- and site-specificity with amazing rate of prevalence throughout the year, characteristic life-cycle stages, the occurrence of different classes of fecund females all the way through different moult stages, make this protandric hermaphroditic cymothoid species an ideal organism to study the physiological and molecular basis of parasitism and hermaphroditism which in turn could pave the way to propose measures to optimise aquaculture practices.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable institutional, national and international guidelines for the care and use of animals were followed.

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