



Occurrence of Life Cycle Dependent Monophasic and Biphasic Molting in a Parasitic Isopod, *Mothocya renardi*

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Abstract

This paper reports the occurrence of life cycle dependent monophasic and biphasic molting in *Mothocya renardi* (Bleeker, 1857), a protandrous hermaphroditic cymothoid parasitizing the banded needle fish, *Strongylura leiura*. Although the molting in manca I is monophasic, the infective manca II, juvenile and adult stages including male, transitional, and female opt biphasic molting in which the posterior half of the body molts first, followed by the anterior half. The molt cycle (monophasic and biphasic) in *M. renardi* is broadly divided into four sequential stages, premolt, molt, postmolt and intermolt. Five distinct premolt stages (D₀-D₄) were also identified through the microscopic observation of characteristic changes reflected in different appendages of manca stages and adult infective stages. Pleotelson, uropod rami and dactylus of the first pereopod and antennae were used for the identification of stages of monophasic molt cycle. By undergoing monophasic molting, the manca I was transformed into the manca II which then undergoes biphasic molt. The characteristic changes related to biphasic molting were well reflected in the maxillule. When the maxillule showed characters of the premolt stage D₂, the posterior half of the body had already exuviated. Molting of the anterior half ensued within 2–3 days after posterior half ecdysis. Occurrence of a series of biphasic molts resulted in the transformation of manca II into the successive stages in the order juvenile, male, transitional and female.

Keywords Cymothoid · *Mothocya renardi* · Molt cycle · Monophasic molt · Biphasic molt

Introduction

In crustaceans, molting, an important biological process which involves not only the removal of exoskeleton, but synthesis of new exoskeleton and tissue growth eventually replacing the old one (Drach 1939; Lawlor 1976; Anilkumar and Adiyodi 1985; Skinner 1985; Chang 1989 for review; Borowsky 1996; Sudha and Anilkumar 1996; Kuballa and Elizur 2008; Sudha et al. 2012; Supriya et al. 2017). Crustacean molt cycle has four major sequential stages such as premolt, ecdysis, postmolt and intermolt. The reflection of molt-related changes have been reported in certain appendages such as pleopod and maxilliped in several crustacean families (Carlisle and

Dohrn 1953; Peebles 1977; Mills and Lake 1975; Anilkumar 1980; Lyle and Macdonald 1983; Sudha 1992; Sudha and Anilkumar 1996, 2007; Supriya 2011; Sudha et al. 2012; Supriya et al. 2017).

The pattern of molting in isopods is different from other crustaceans that follow monophasic molting by which the whole exoskeleton is removed at a time (Sudha and Anilkumar 2007; Supriya et al., 2012, 2017). Isopods display a biphasic molt cycle in which the old cuticle of the posterior body part sheds prior to that of anterior (Gorvett 1947; George and Sheard 1954; Carlisle 1956; Vallabhan 1979; Suzuki et al., 2013; Amrutha et al., 2019). The phenomenon of biphasic molt was first reported in a terrestrial isopod, *Porcellio scaber* and then its confirmation was made in other terrestrial isopods such as *Ligia* sp. and *Oniscus* sp. (Schöbl, 1879; Tait 1917; Numanoi 1934; Wieser, 1964; Messner, 1965; Price and Holdich, 1980; Steel 1980, 1982; Štrus, 1990; Štrus and Compere, 1996). In a recent work in a marine isopod, *Norileca indica* biphasic molt cycle in the adult phases has been characterised based on the observation of uropod and maxillule (Amrutha et al., 2019).

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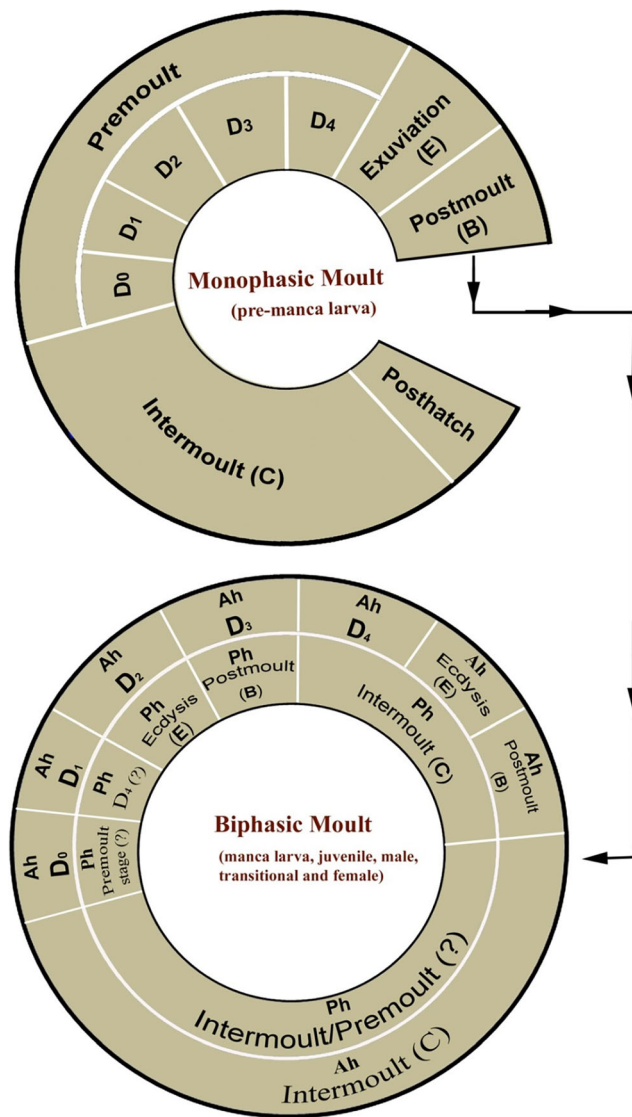


Fig. 1 Schematic representation of life cycle dependent monophasic and biphasic molt cycle in *M. renardi*. B - postmolt, C - intermolt, E - exuviation/ecdysis, (D₀ - D₄) - premolt, Ph - posterior half, Ah - anterior half

Except this, the stage wise characterization of biphasic molt cycle has not been evolved much from their morphological level. This paper reports the incidence of life cycle dependent monophasic and biphasic molt cycles of a parasitic isopod, *Mothocya renardi*.

Materials and Methods

Live specimens of *M. renardi* in different life cycle stages including manca stage (3.1–4.4 mm), juveniles (6.5–11.0 mm), males (10.0–19.0 mm), transitional (10.5–23.0) and ovigerous females (16.0–34.0 mm) with and without marsupium/ marsupiumites were collected from the branchial cavity of the host fish, *Strongylura leiura* which were obtained

from the Ayyikkara fish landing center (Lat. 11°51'N, Long. 75°22'E), Malabar coast, India. The ovigerous female and male of *M. renardi* were identified according to Bruce (1986). Other life cycle stages (such as transitional, juvenile, manca I and manca II larva) were identified on the bases of morphological characters described by Aneesh 2014 and Aneesh et al. (2015, 2016b, 2016a).

Molt (intermolt, premolt and postmolt) stages of the *M. renardi* were identified through microscopic observation of the characteristic changes in the appendages irrespective of the life cycle stages. In the manca I, antennae, dactylus of first three pereopods, uropod rami and pleotelson were considered for the accurate identification and characterization of molt cycle stages. In other life cycle stages (manca II, juvenile, male, transitional and female), the maxillule was used. The proper appendage was singled out using a fine forceps and mounted in filtered seawater on a clean glass slide and observed with a Leica research microscope - DM-750. Photomicrography was done using a Leica ICC50 camera with image capturing and processing software, LAS EZ (Leica Application Suit - Version 1.7.0).

Results

Monophasic Molt and its Characterization in Manca I

The manca of *M. renardi* exhibited monophasic molting. At the intermolt stage (C), no plumose setae were found in the pleotelson and uropod rami. The matrix appeared opaque and numerous hemocytes were also visible (Figs. 2A and 3A). The dactylus of first pereopod was toothless (Fig. 4A) and the antenna devoid of any setae and aesthetascs (Fig. 4D). By the onset of premolt, matrix of the appendages (pleotelson, uropod rami, dactylus of the first pereopod and antennae) of the manca I showed characteristic microscopical changes (Figs. 2B-E, 3B-E and 4B and E). The initial stage of premolt (D₀) was characterized by the retraction of epidermis from the cuticle which was more visible at the apex of the pleotelson and uropod rami. The tissue matrix was translucent and hemocytes were scanty. As premolt stage progressed towards the D₁ stage, the separation of epidermis from old cuticle was more visible along the entire length of the respective appendage and subsequent appearance of the setal grooves were clear (Figs. 2B and 3B). In the D₂ stage, development of the new epidermis was more prominent and the matrix exhibited the presence of setal grooves along with the marginally arranged hemocytes; the inner layer of old exoskeleton also showed signs of degradation (Figs. 2C and 3C). The D₃ stage was characterized by the protrusion of newly formed setae (juvenile

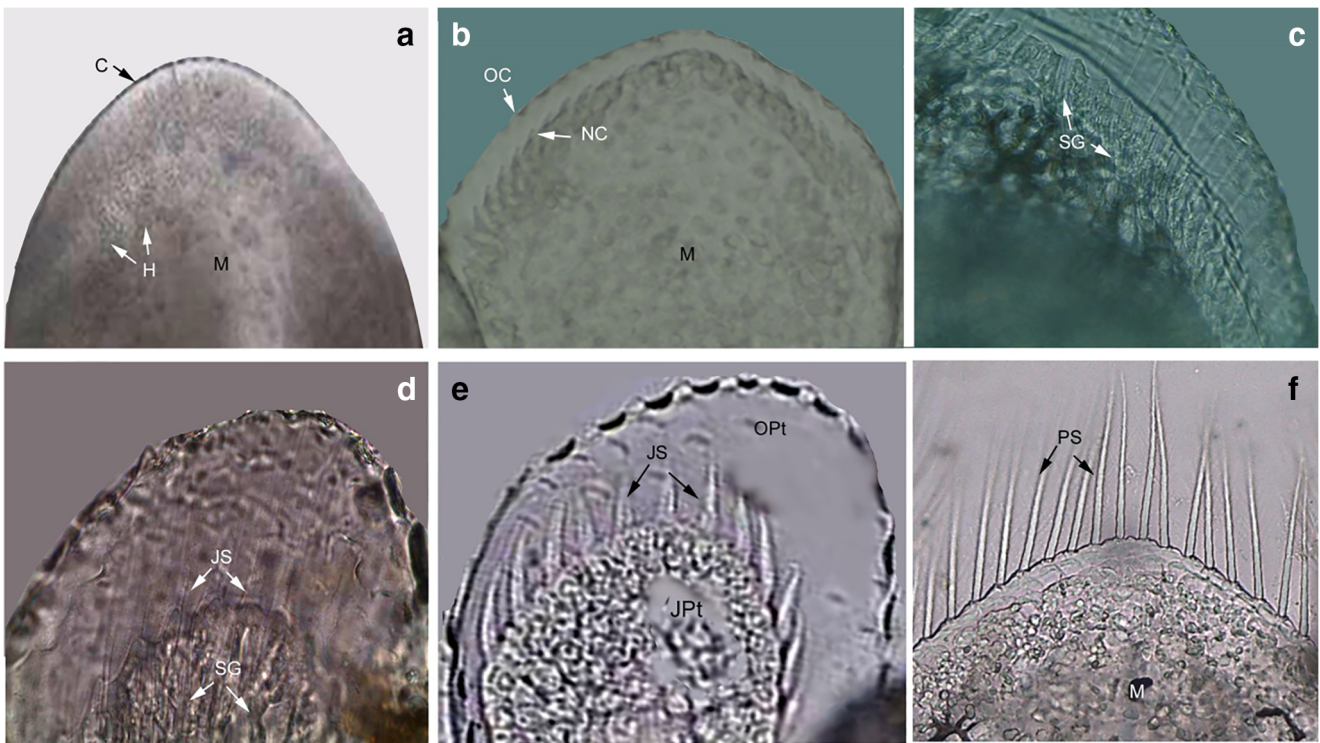


Fig. 2 Pleotelson of manca I: Monophasic molt cycle related changes (40X). a- intermolt; b- D₁; c- D₂; d- D₃; e- D₄; f- postmolt. H - haemocytes, C - cuticle, M - matrix; NC - new cuticle, SG - setal groove, JS - juvenile setae, OC - old cuticle, OPt - old pleotelson, JPt - juvenile pleotelson, PS - plumose setae

setae) (Figs. 2D and 3D) and at D₄, the juvenile setae were more prominent (Figs. 2E and 3E). D₄ stage of

manca I is also characterized by the toothed juvenile dactylus in the first pereopod (Fig. 4 B) and the juvenile

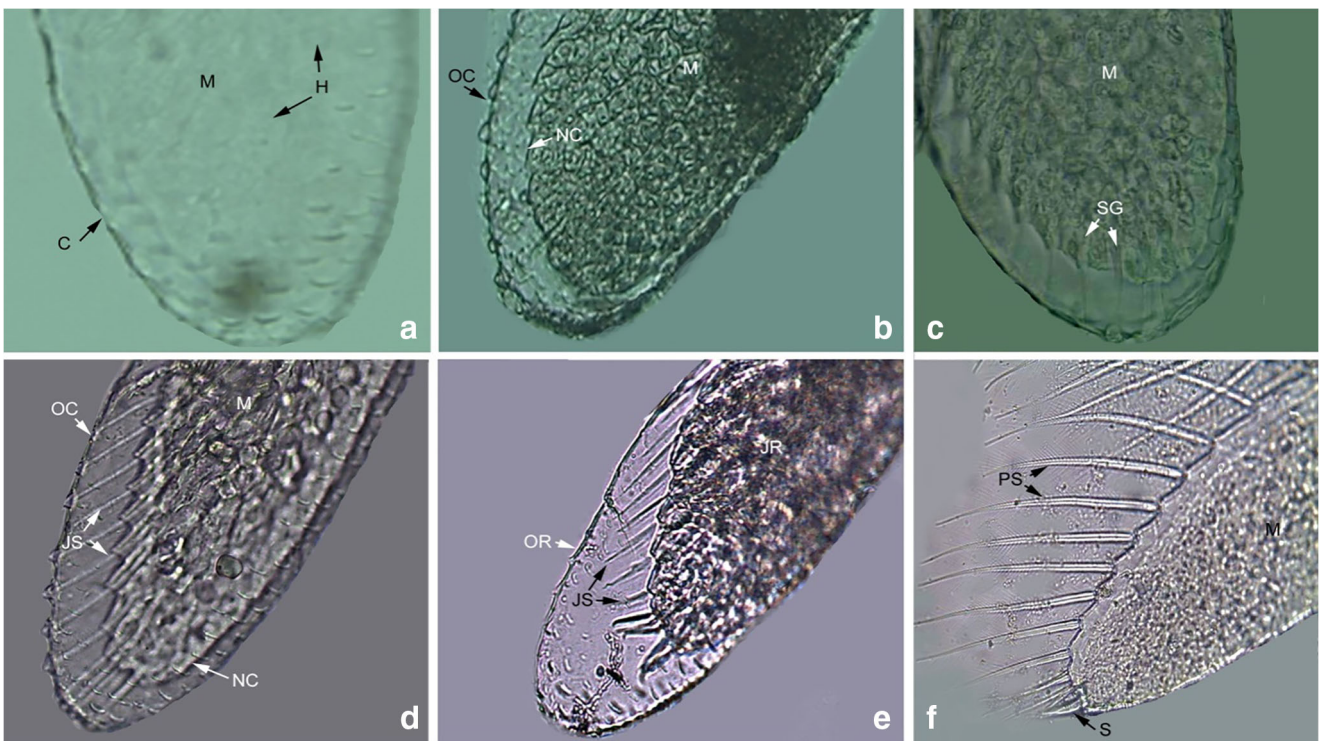


Fig. 3 Uropod rami of manca I: Monophasic molt cycle related changes (40X). a- intermolt; b- D₁; c- D₂; d- D₃; e- D₄; F- postmolt. M- matrix, H - haemocytes, C- cuticle; OC- old cuticle, NC- new cuticle; SG- setal groove, JS- juvenile setae, S- spine, PS- plumose setae, JR- juvenile rami, OR - old rami

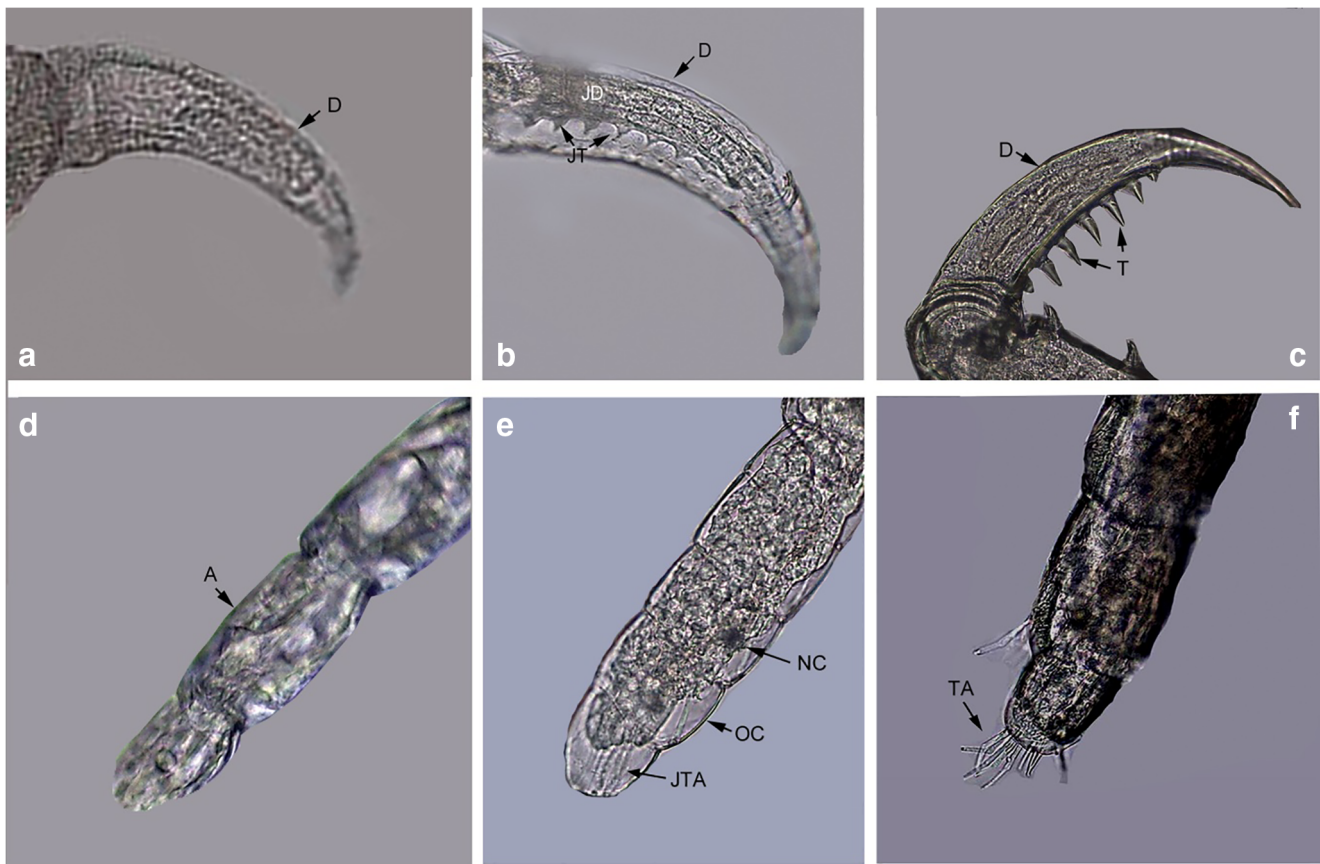


Fig. 4 Dactylus and Antenna of manca I: Monophasic molt cycle related changes (40X). a-c: Dactylus of pereopod 1 of manca I: a- intermolt; b- premolt showing toothed juvenile dactylus; c- postmolt with teeth. d-f:

Antenna of manca I: d- intermolt; e- premolt; f- postmolt. D- dactylus, JD- juvenile dactylus, JT- juvenile teeth, T- teeth, A- antenna, OC- old cuticle, NC- new cuticle, JTA- juvenile terminal aesthetascs, TA- terminal aesthetascs

aesthetascs in antennae (Fig. 4 E). Molting was completed within 10–20 min. Monophasic molting in the manca I resulted in its metamorphosis into the manca II with following features: (i) presence of plumose setae on pleotelson and uropod rami (Figs. 2F and 3F), (ii) presence of a spine on the exopodite of uropod rami (Fig. 3F), (iii) terminal aesthetascs on the antennae (Fig. 4F) and (iv) toothed dactylus on the first pereopod (Fig. 4C).

Biphasic Molting and its Characterization

Microscopic Characteristics of Maxillule at Different Stages of Biphasic Molt Cycle

From the manca II stage, *M. renardi* followed biphasic molting during which the following sequential events were observed: (i) exuviation of the posterior half of the body including 5th–7th pereonite, pleon, pleotelson and their respective appendages, and then exuviation of the anterior half of the body including the cephalon, first four pereonites, and their respective appendages. The maxillule (Fig. 5A–G) appeared to be an appropriate appendage to identify all molt stages during the biphasic molting in

M. renardi during its manca II, juvenile, male, transitional, and female stages. During C stage, the epidermal layer of maxillule was found adhered to the cuticle and opaque matrix was with abundant hemocytes (Fig. 5A). At D_0 , epidermis retracted from the cuticle at the apex of the maxillule and also from the base of its apical recurved spines; the matrix of the maxillule became translucent with the substantial decrease in the number of hemocytes (Fig. 5B). At the D_1 stage, the epidermis from the old cuticle was separated and the four juvenile apical recurved spines were also appeared in the underlying tissue (Fig. 5C). The D_2 stage was marked with the following changes in the maxillule: (i) juvenile apical recurved spines were more visible, (ii) presence of a narrow ecdysial gap between the tip of juvenile apical spine and the base of old apical spine and (iii) the newly developed epidermal layer beneath the old cuticle became more visible (Fig. 5D). At this time, the posterior half of the body undergoes exuviation (E) partial shedding of the exoskeleton up to the 5th pereonite. When the exuviated posterior half attained postmolt (B) stage, the maxillule were at the D_3 stage, during which all four juvenile apical recurved spines were clearly visible (Fig. 5E). The texture of the exoskeleton of

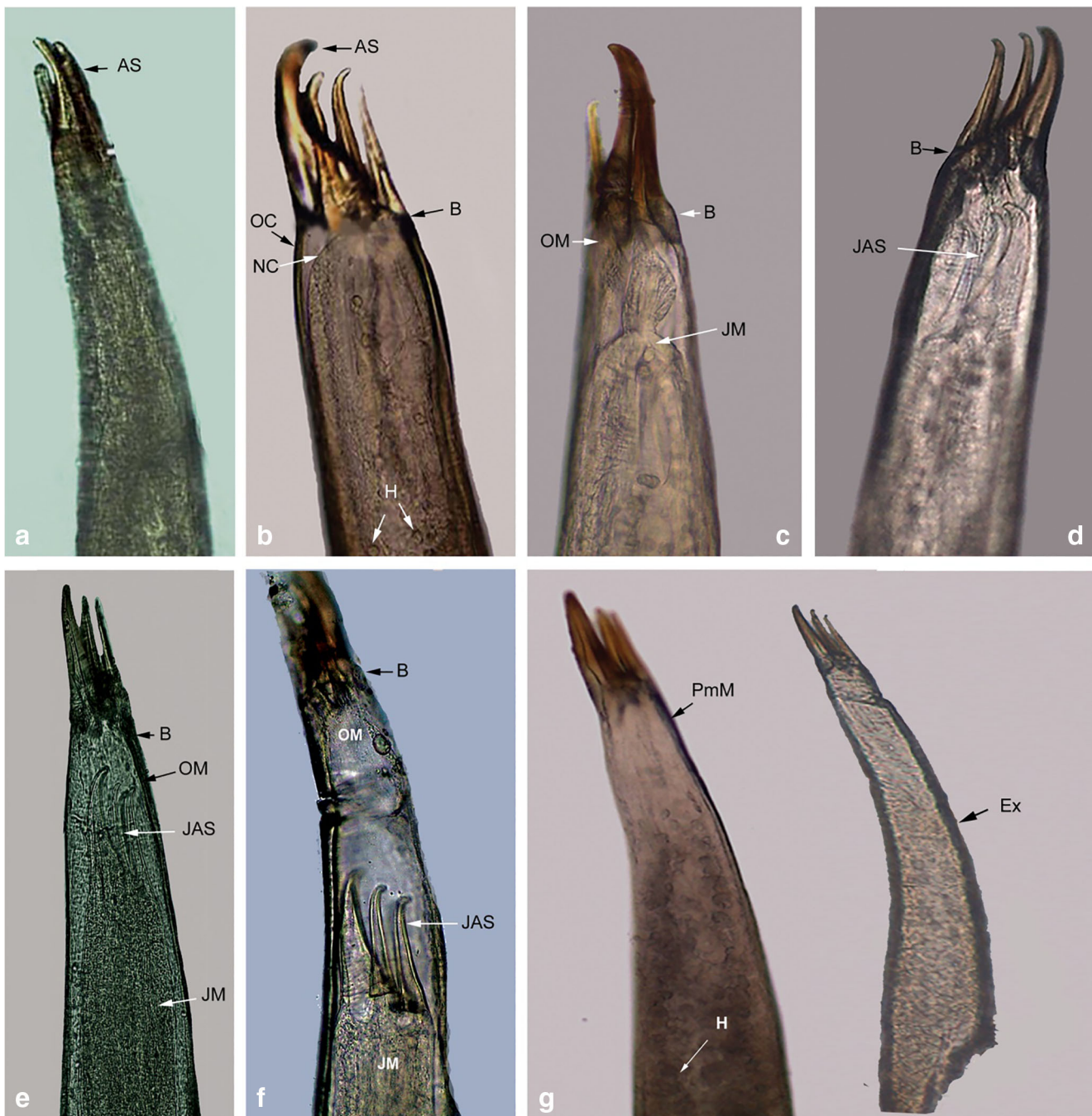
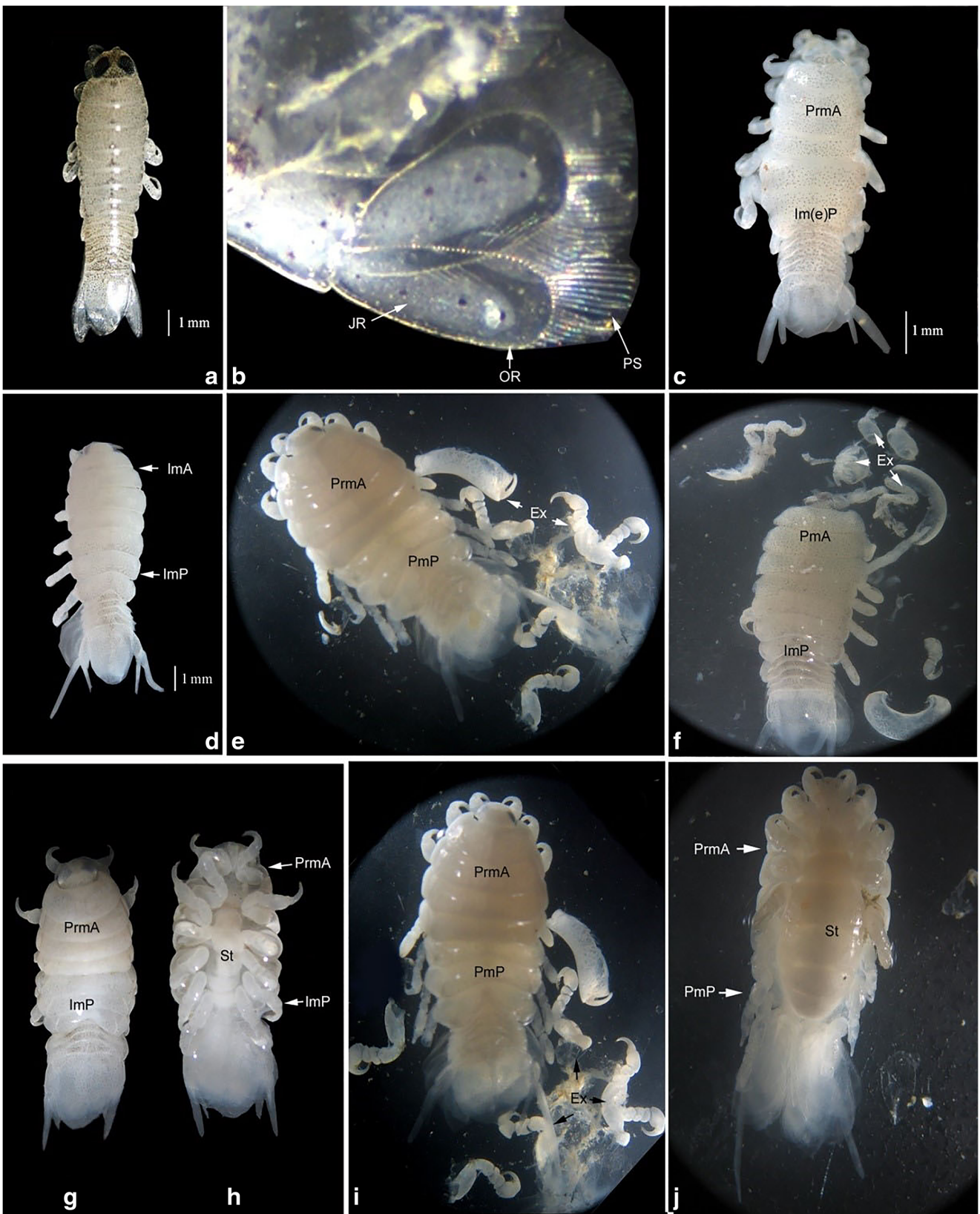


Fig. 5 Maxillule of *M. renardi*: Biphasic molt cycle related changes (100X). a- intermolt; b- D₀; c- D₁; d- D₂; e- D₃; f- D₄; g- postmolt and its exuvium. AS- apical spine, OC - old cuticle, B- base, NC- new cuticle,

OM- old maxillule, JM- juvenile maxillule, JAS - juvenile apical spine, H- haemocytes, PmM - postmolt maxillule, Ex - exuvium

pre-molt staged (D₃) anterior half was more or less hard and brittle and that of posterior half was gelatinous and pliable (Fig. 6E and I). At the D₄ stage, the ecdysial gap between the tip of the juvenile apical spine and the base of old apical spine was substantially increased (Fig. 5F). By the time, the posterior half of the body attained the intermolt stage, judged by the presence of hard exoskeleton. The molting of the anterior half (including cephalon

and first four pereonites) along with their respective appendages (cephalic appendages and pereopods) ensued. This usually occurred within 2–3 days after the posterior half ecdysis. The post-ecdysis matrix of maxillule was highly translucent with moderate number of hemocytes (Fig. 5G); the exoskeleton of the postmolt was soft and gelatinous whereas that of posterior half at intermolt, was hard and white in color.



◀ **Fig. 6** Life cycle stages of (juvenile to transitional) *M. renardi* showing biphasic premolt changes and ecdysis. a-d: Juvenile: a-premolt stage; b-caudal rami of the juvenile showing D₁ stage; c- posterior half molted; d- anterior half molted become male; e- male posterior half molted; f- male anterior half molted; g-male - transitional molt dorsal view; h- male - transitional molt ventral view; i and (j) posterior half molted transitional dorsal view; j- posterior half molted transitional ventral view. JR - juvenile rami, OR- old rami, PS- plumose setae, St- sternite, PrmA- premolt anterior half, Im(e)P - intermolt(early) posterior half, PmP - postmolt posterior half, ImA - intermolt anterior half, ImP- intermolt posterior half, PmA - post molt anterior half, Ex- exuvium

Morphological Observation of the Different Life Cycle Stages Undergoing the Biphasic Molt Cycle

Molting in the Manca II: It remained at intermolt stage while they were in the marsupium of female. The biphasic premolt changes (D₀-D₄) took place when the Manca II permanently settled in the branchial cavity of the host fish (*S. leiura*). Exuviation of the posterior half of the manca II resulted in the formation of a rudimentary pereopod at 7th pereonite. By the completion of anterior half molt, the manca II I was transformed into a juvenile (Fig. 6A) which was characterized by the presence of seven pereopods.

Molting in Juvenile and Adult: Through the biphasic molting, juvenile of *M. renardi* transformed into male, which possessed seven spineless and toothless functional pereopods and a functional penis. The plumose setae present in the uropod rami and pleotelson of the juvenile stage had completely disappeared by the completion of the molt (Fig. 6A-D). The male members of *M. renardi* underwent repeated biphasic molting until they transform into the transitional stage with the secondary sexual characteristics of both male and female (Figs. 6 D-F).

The transitional stage of *M. renardi* at intermolt stage possessed the following male characters: (i) maxilla with two recurved spines on lateral and median lobes, (ii) 2nd pleopod with appendix masculina and the reduced penis, (iii) relatively less convexity of the pereonite sternites. However, the pereopods of the transitional stage appeared quite similar to those of the female. Through repeated biphasic molting (Fig. 6 G-J), the transitional stage attained its female stage characterized by the presence of convex abdomen resembling to that of typical females (Fig. 7A). Subsequently it underwent biphasic molting for the development of oostegites (Fig. 7B-F). When the posterior half molted, a pair of juvenile oostegites developed from the endopodite of the 6th pereopod; the juvenile oostegites showed the presence of venation (Fig. 7E). By the time, the anterior half attained D₄ and is ready for molting; the exuviation of anterior half resulted in the formation of the remaining three pairs of anterior oostegites from the endopodites of the 2nd, 3rd and 4th pereopods. At the completion of the biphasic molting, the transitional was transformed into a functional female possessing four pairs of functional brood

plates (oostegites) which form the ventral marsupium for receiving the eggs during oviposition.

Biphasic Molt in Female

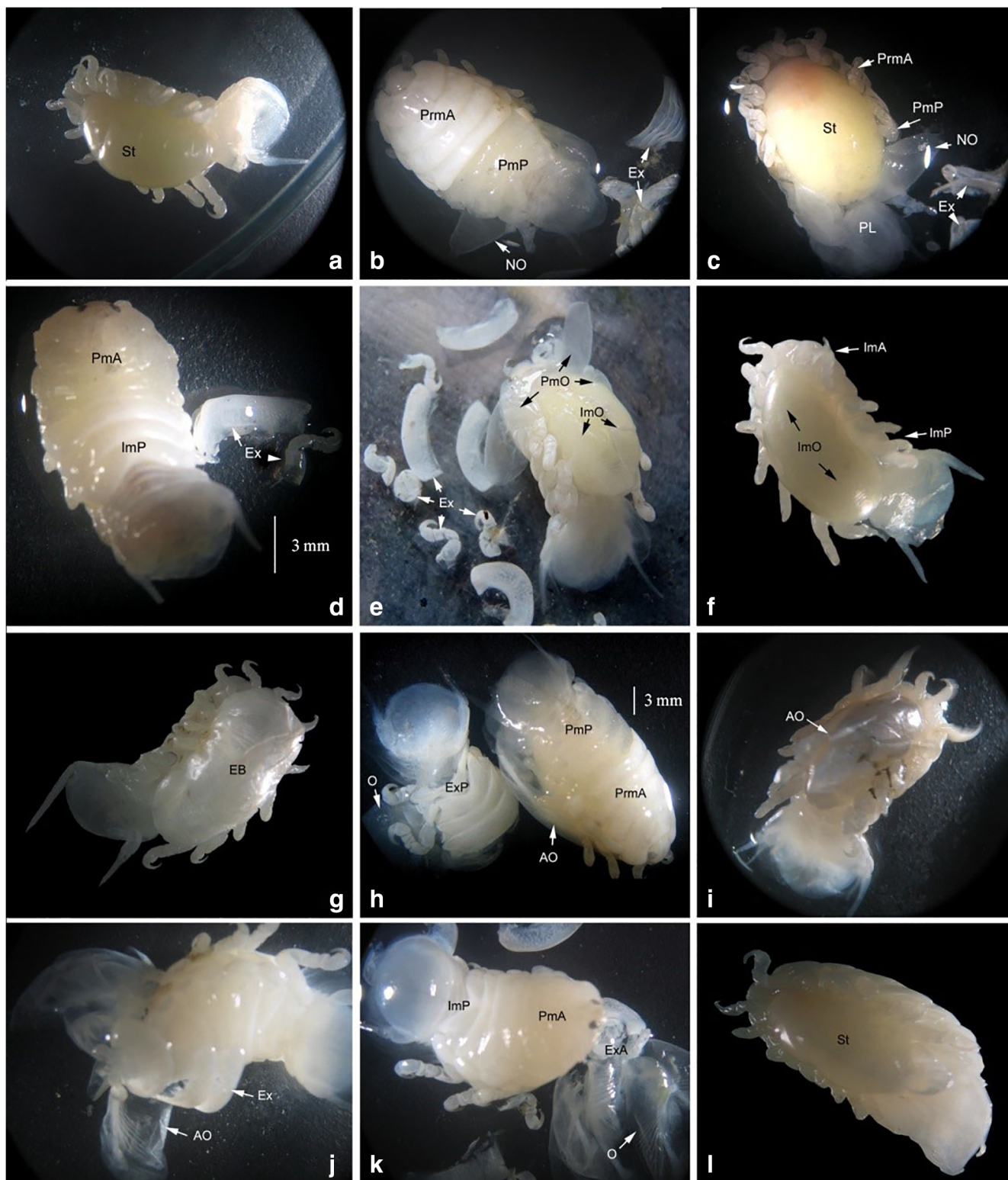
After the manca I was released, females carrying the old oostegites (brood plates) underwent biphasic molting through which old oostegites were removed; ecdysis of posterior half resulted in the removal of one pair of oostegites (endopodite of 6th pereopod). Remaining three pairs of oostegites were removed by the subsequent anterior half ecdysis (Fig. 7G-L). This was followed by another biphasic molt resulting in the formation of new set of oostegites for receiving the next clutch of eggs.

Discussion

Present study reveals that while the free living manca I of *M. renardi* undergoes monophasic molt, all other infective life cycle stages including manca II, juvenile, male, transitional and female strictly follow the biphasic molt cycle (Fig. 1).

The cymothoid, *M. renardi* follows the general pattern of biphasic molt reported in free living isopods such as *Ligia* sp., *Porcellio* sp., *Limnoria* sp., *Cirolana* sp., *Idotea* sp. and *Ascellus* sp. in which the posterior half of the body molts first followed by the anterior half (Tait 1917; Carlisle 1956; George 1972). *M. renardi* exhibits biphasic molting only during their infestation stages beginning with the manca II, juvenile, male, transitional and female. The manca I, however, undergoes monophasic molt in agree with the pattern shown by the isopod, *Glyptonotus* (George 1972) and other crustaceans (Sudha 1992; Suganthi 1996; Supriya 2011; Sudha et al. 2012).

The characteristic changes in the epidermal growth related to monophasic molt were reflected in all the appendages of the manca I (Figs. 2-4) of *M. renardi* and were akin to that of other crustaceans undergoing the monophasic mode of molting. However, in other subsequent life cycle stages of the parasite (*M. renardi*), noticeable molt changes were limited in the maxillule (Fig. 5). During the molt cycle, the matrix of the appendages of the manca I of *M. renardi* showed resemblance to those of free living decapod crustaceans to a great extent. At intermolt stage, pleotelson and uropod rami of manca I do not possess setae and spines and dactylus of pereopods is toothless. The premolt changes in these appendages include the gradual but complete retraction of epidermis from the cuticular layer, translucent matrix along with the reduction hemocyte number and visibility of protruded juvenile setae. The antennae and the first three pereopods developing juvenile aesthetascs and the toothed juvenile dactylus, respectively are the characteristic changes when the premolt stage attains its late stage (D₄). The observed average time period for the



completion of the event of ecdysis in the manca-1 of *M. renardi* was 15 min; the duration is quite short compared to that of other crustaceans in which the duration of the event is reportedly more than 45 min (Sudha 1992; Syama 2009; Supriya et al. 2017).

Biphasic premolt changes (D_0 - D_4) in manca II of *M. renardi* was seen when it permanently settled in the branchial cavity of its host. The molting of the posterior half in the manca II develops the rudimentary 7th pereopod at pereonite 7 and by the completion of anterior half results in the

◀ **Fig. 7** Life cycle stages (transitional to female) of *M. renardi* showing biphasic premolt changes and ecdysis. a–f: transitional stage under oostegition molt: a- D₁; b- posterior half molted dorsal view, c- posterior half molted ventral view; d- anterior half molted dorsal view, e- anterior half molted ventral view; f- female after oostegition molt (g–l) female under de-oostegition molt: g- D₁; h- posterior half molted dorsal view; i- posterior half molted ventral view; j- after anterior half molt; k- after anterior half molt; l- female after de-oostegition molt (ventral view). St- sternites, Ex- exuvium, PrmA - premolt anterior half, PmP - post molt posterior half, PmA - postmolt anterior half, PmO - premolt oostegites, ImO- intermolt oostegites, NO- new oostegites, PL- pleopod, ImP- intermolt posterior half, ImA- intermolt anterior half, PmO- post molt oostegites, ImO - intermolt oostegites, EB- empty brood, AO- anterior oostegites, ExP- exuvium of the posterior half, ExA- exuvium of the anterior half, O- oostegites

formation of juvenile characterized by the presence of seven toothed and spined pereopods, including the newly formed rudimentary 7th one. Molting of posterior and anterior halves of the juveniles of *M. renardi* leads its transformation into adult male with all seven spineless and toothless functional pereopods and a functional penis. The setae present in the uropodal rami and pleotelson of the juvenile were completely disappeared in the postmolted juvenile (adult male). Through the same pattern of biphasic molting, the males sequentially transformed into the transitional stage which undergo biphasic transitional-transitional molt followed by transitional-female molt, by the time transitional completely lose their male features such as penis and appendix masculina in the 2nd pleopod and transformed into functional females possessing oostegites or brood plates (Trilles 1968, 1969, 1994; Sindermann 1990; Grabda 1991; Leonardos and Trilles 2003).

In oniscid isopod *Ligia oceanica* after a premolt period of 6–7 days, a complete separation takes place between the 4th and 5th thoracic segments, the tergites of the 5th, 6th and 7th segments splits longitudinally and the animal extracts itself from the hind part of the cuticle by a series of writhing movements; in this species, the exuvium sheds as fragments (Tait 1917). In *M. renardi* the exuvia of both anterior and posterior region are found in fragments as reported in *L. oceanica*. In this free living isopod, the time interval between the anterior and posterior molting extends between 1 and 6 days and shedding of the exoskeleton of the posterior half takes 10–12 min (Tait 1917; Carlisle 1956; George 1972). In *M. renardi*, exuviation of anterior half ensues within 2–3 days after the posterior half ecdysis.

To conclude the present study on the molting in *M. renardi* is significant inasmuch as it appears as the first report on the occurrence of monophasic and biphasic molts in the life cycle of crustaceans in general and in a parasitic isopod in particular. The precise microscopic characterization of these two diverse molting patterns made during the present study would be helpful to design the future work on physiology and endocrinology of molting in isopods by adopting advanced techniques. This in turn would pave the way to explore the significance of biphasic molting in the obligatory parasitic life of isopods.

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Author's Contribution APT worked on the topic and prepared the first draft of the manuscript. SK drew out the concept, supervised the work, interpreted the results, corrected and finalized the manuscript. All authors read and approved the final manuscript.

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Compliance with Ethical Standards

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

Ethical Approval This article does not contain any studies with animals which require ethical approval.

Sampling and Field Studies Permission from the competent authority is not required as the specimens (parasitic isopods and the host fish) sampled for the present study were not in the scheduled list of protected animals.

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