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Larval Development of the Mangrove Fiddler Crab *Austruca albimana* (Kossmann, 1877) (Crustacea: Brachyura: Ocypodidae) Under Laboratory Conditions

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Larvae of the mangrove fiddler crab *Austruca albimana* (Kossmann, 1877), hatched from an ovigerous female collected from the mangroves of Sumariat, Jazan Province, Saudi Arabia in the southern Red Sea, were reared in the laboratory. Four zoeal and a megalopal stages were recorded, and their morphological features are described herein for the first time. The setations of the cephalothoracic appendages of the zoeas of *A. albimana* and their congeners exhibit several variations that help differentiate larvae of this genus easily from other meroplankton. However, a character of phylogenetic significance – minute spines on the forks of the telson of pleon – is common to larvae of this genus. These minute spines were studied with the aid of scanning electron microscope images. There were five common morphological features between *A. albimana* and other fiddler crab megalope, including *Minuca burgersi*, *Leptuca uruguayensis* and *Leptuca thayeri*. These features were a deflexed front, rounded to obtuse frontal margin, seven-segmented antennal flagellum, unsegmented endopod of maxilla and three cincinnuli on the endopods of pleopods. Two zoeal morphological features described in this study and other studies (*i.e.*, the absence of lateral spines on carapace [vs. their presence in species of *Uca*, *Afruca* and *Ocypode* in the Ocypodinae] and the presence of a maximum of four pairs of inner setae on the telson of pleon [vs. presence of more than four pairs of setae in species of *Uca*, *Afruca* and *Ocypode*]) support the taxonomic amendment of transferring *Uca* spp. and *Afruca* spp. crabs from Gelasiminae to Ocypodinae.

Key words: Fiddler crabs, Gelasiminae, Megalopa, Ocypodinae, Red Sea, Zoea.

BACKGROUND

Fiddler crabs inhabit muddy, muddy-sandy or muddy-intertidal zones, especially in the mangroves of tropical and subtropical regions (Crane 1975). In Saudi Arabia, mangroves have a discontinuous distribution along the 1,700-km Red Sea coast (Saifullah 1996). Three species of fiddler crabs have been recorded from the mangroves of Saudi Arabia: *Cranuca inversa* (Hoffmann 1874), *Austruca albimana* (Kossmann, 1877) and *Tubuca alcocki* Shih, Chan & Ng, 2018. The most studied *Tubuca alcocki* has been mentioned in several ecological reports of the Red Sea (*e.g.*, Por and Dor 1975; Tubbs and Hogarth 1986; Vine 1986; Mandura et al. 1987).

Austruca Bott, 1973 widely distributed in the Indo-West Pacific, includes 13 species (Shih et al. 2009 2016; Rosenberg 2019; Shih and Poupin 2020). *Austruca albimana* is distributed from the Red Sea to the south-eastern Persian Gulf and has sympatric coexistence with

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two congeners, *Austruca annulipes* (H. Milne Edwards, 1837) and *Austruca iranica* Pretzmann, 1971. In the southern Red Sea of Saudi Arabia, *A. albimana* co-occurs with *C. inversa* and *T. alcocki* in the mangroves of Jazan, and with *C. inversa* in Sumariat mangroves, Jazan (Kumar 2019).

Although several taxonomic studies of fiddler crab zoea have been conducted (Zhang and Shih 2022), studies from the western Indian Ocean are few in number (Table 1). Anger (1991) and Spivak and Cuesta (2009) studied the effects of salinity, particularly the cumulative effect of salinity and temperature, on the development of brachyuran larvae. Insecticides such as fenoxycarb and dieldrin affect the development of xanthid larvae (Epifanio 1971 1972 1973; Cripe et al. 2003). In highly polluted sites at Piles Creek, Linden, New Jersey, USA, the survival rate of *Minuca pugnax* in the early benthic stages (Smith, 1870) was found to have been affected (Bergey and Weis 2008). This is a matter of concern because the reduced survival of early benthic stage crabs shrinks the population size of the fiddler crabs in mangroves, since as at this stage crabs settle into the intertidal areas inhabited by older conspecifics (Armendariz 2005). This reduction may severely affect the health and survival of mangroves as their burrows promote nutrient turnover (Bertness 1985) and accelerate decomposition of organic matter by supplying oxygen to the anoxic mangrove subsurface organic sediments (Mokhtari et al. 2013).

Phylogenetic studies of brachyuran crabs revealed that larval morphological data rather than adult morphological data concur more with molecular data (Hultgren et al. 2009). In the phylogeny of fiddler crabs, the larval morphological features also play a crucial role (Shih et al. 2016).

Comprehensive identification keys of brachyuran larvae are necessary to identify meroplankton up to the species level and to understand spatial-scale biodiversity (Bento 2017; Clark and Paula 2003). Most available descriptions are inaccurate and do not meet requirements for comparative studies (Clark et al. 1998). On the Red Sea coast of Saudi Arabia, only the larvae of *C. inversa* have been described (Al-Aidaroos 2013), and among the 13 species of *Austruca*, only the larval stages of *A. iranica* (Hashmi 1968; Ghory and Siddique 2006) (as *A. annulipes*) (see Apel 2001) and *Austruca lactea* have been partially described (Terada 1979).

In this study, all the larval stages of *A. albimana* are described and compared with the larvae of other fiddler crabs. Some taxonomically significant morphological features found in those larvae are also discussed in detail.

MATERIALS AND METHODS

An ovigerous female of *A. albimana* was collected on 8 March 2018 from the mangroves of Sumariat (17°29'15.3312"N, 42°15'9.7452"E), Jazan Province, Saudi Arabia (Fig. 1). The crab was reared in an ESPEC walk-in type environmental chamber at the Faculty of Marine Sciences, King Abdulaziz University at 28°C under a 12-h light/dark photoperiod. Soil collected from the habitats of fiddler crabs was sprinkled at the base of the container, and the crab was found feeding on organic matter. The larvae hatched on 17 March 2018. Six batches of 50 larvae each were reared in 1-L containers, each with 800 mL of seawater with a salinity of 35 psu at 28°C. All zoeal stages were fed with rotifers (50/mL). Water was changed every other day. Antibiotics were not used.

Ten larvae from each stage were preserved in 70% ethanol and dissected using a Leica M80 microscope in polyvinyl lactophenol. A Leica 6000B phase-contrast stereomicroscope equipped with camera lucida (5–40× objective lenses) was used for drawings and setal counting. The following measurements were made. For zoeal stages, CL: distance from the base of the rostral spine to the posterior margin of the carapace; RDL: distance between the tips of the dorsal and rostral spines. For the megalopa: CW: maximum distance across the carapace; CL: maximum distance along the carapace. Setal counts were made from the proximal to distal portions. Setal numbers are represented for appendages from basis to endopod (Clark et al. 1998; Clark and Cuesta 2015). The first zoea has been

Table 1. Morphological descriptions of the first zoeas of fiddler crabs available from the western Indian Ocean

Species	Reference	No. of larval stages described	Collection site of the berried female
Austruca albimana	this study	Zoeas 1–4, megalopa	Sumariat mangrove, Jazan, Saudi Arabia
A. iranica	Ghory and Siddique 2006	Zoea 1	Sandspit Beach, Karachi, Pakistan
A. iranica	Hashmi 1968	Zoeas 1 and 2	Karachi, Pakistan
Cranuca inversa	Al-Aidaroos 2013	Zoea 1	Ras-Hatiba Bay, Dahban, Saudi Arabia
Gelasimus hesperiae	Hashmi 1968	Zoea 1	Karachi, Pakistan
Tubuca alcocki	Ghory and Siddique 2006	Zoea 1	Sandspit Beach, Karachi, Pakistan

morphologically described completely, and, for the following stages, only changes from the previous stages were noted. The berried female crab (CW, 9 mm) and complete larval stages were deposited into the King Abdulaziz University Museum (KAUMM 879–884).

For the study involving scanning electron microscopy (SEM), the pleons of zoeas II and IV were fixed in 2.5% glutaraldehyde followed by washing three times with sodium cacodylate. Subsequently, the samples were dehydrated successively in 30%, 50%, 70%, 90% and 100% ethyl alcohol. The appendages were air-dried and placed on a thin layer of conductive carbon tape stuck on the specimen stub. Afterwards, the pleons were coated with a thin layer of gold using an Auto Fine Coater for 30 seconds at 30 mA and approximately 3.5 Pa (K550X, 50/60 Hz; Quorum Technologies Ltd, Ashford, UK). Thereafter, the specimen stub was loaded into the microscope and SEM images were taken at 2–5 kV (FEI Quanta 250, FP 2012/14, Czech Republic) (Hayat 2000).

RESULTS

Family Ocypodidae Rafinesque, 1815
Austruca albimana (Kossmann, 1877)

(Figs. 1–15)

Zoea I

Size (mean ± sd): CL = 0.3 ± 0.05 mm; RDL = 0.59 ± 0.09 mm.

Carapace (Fig. 2a): Smooth; rostrum short, dorsal spine small, curved posteriorly, smaller than rostrum; lateral spines absent; ventral margin without setae; eyes sessile.

Antennule (Fig. 3a): Endopod absent; exopod unsegmented with 2 long, 3 short aesthetascs.

Antenna (Fig. 4a): Biramous. Protopodal process bilaterally spinulate up to distal margin; exopod with two terminal simple setae.

Mandible (Fig. 5a): Incisor with five blunt teeth, molar process present, posterior margin with three teeth; palp absent.

Maxillule (Fig. 6a): Epipod seta absent; coxa with 2 subterminal plumodenticulate, 3 terminal cuspidate setae; basis with 5 terminal setae (4 cuspidate, 1 plumodenticulate); endopod 2-segmented, distal segment with two plumodenticulate terminal setae.

Maxilla (Fig. 7a): Coxa bilobed, proximal lobe with 2 cuspidate, 1 plumodenticulate setae, basis with 2 plumodenticulate setae; basis bilobed, proximal segment with 4 cuspidate terminal setae, distal segment with 3 plumodenticulate terminal setae; endopod bilobed with 1+2 terminal plumose setae; scaphognathite with 4 plumose setae.

First maxilliped (Fig. 8a): Basis with 2+2+3+2 sparsely plumose setae; endopod 5-segmented with 2 (plumose), 2 (plumose), 1 (plumose), 2–3 (plumose), 5 (2 plumose subterminal, 3 plumodenticulate terminal) setae; exopod 2-segmented, distal segment with 4 natatory plumose setae.

Second maxilliped (Fig. 9a): Basis with 1+1+1+1 plumose setae; endopod 3-segmented with 0,0,5 (3 simple, 2 plumodenticulate setae); exopod bisegmented with 4 terminal plumose setae.

Pleon (Fig. 10a): Five somites; somite II with pair of anteriorly directed dorsolateral processes; somite III with pair of posteriorly directed dorsolateral processes; somite IV broader than others, posterolateral margin

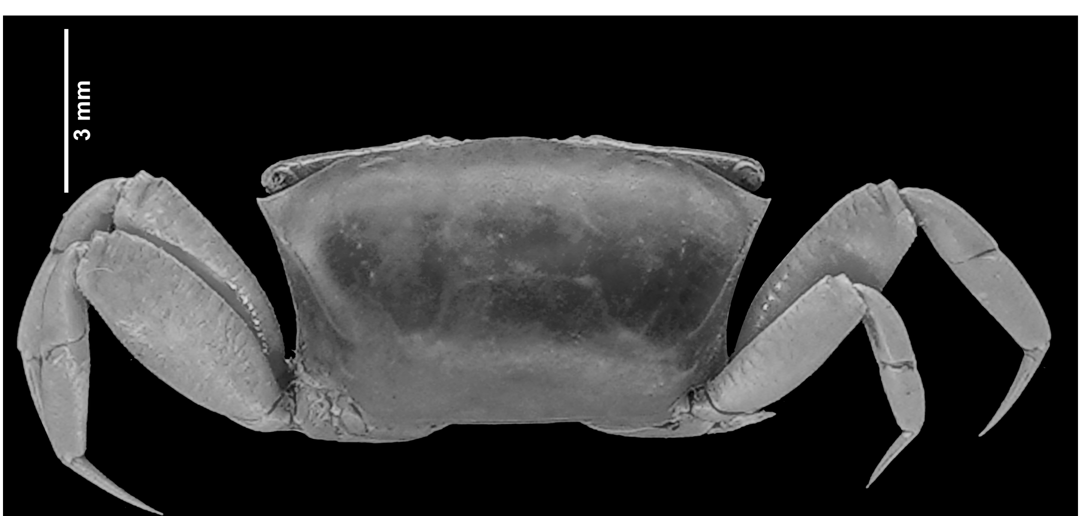

Fig. 1. *Austruca albimana* (Kossmann, 1877), dorsal view of the berried female.

overlapping with Vth somite; somite I without seta; somites II–V with pair of posterodorsal simple setae.

Telson (Fig 10a): Inner margin with 3 pairs of setae; minute spines on lateral sides of forks of telson.

Zoea II

Size (mean ± sd): CL = 0.35 ± 0.02 mm; RDL = 0.8 ± 0.05 mm.

Antenna (Fig. 4b): Endopod bud present.

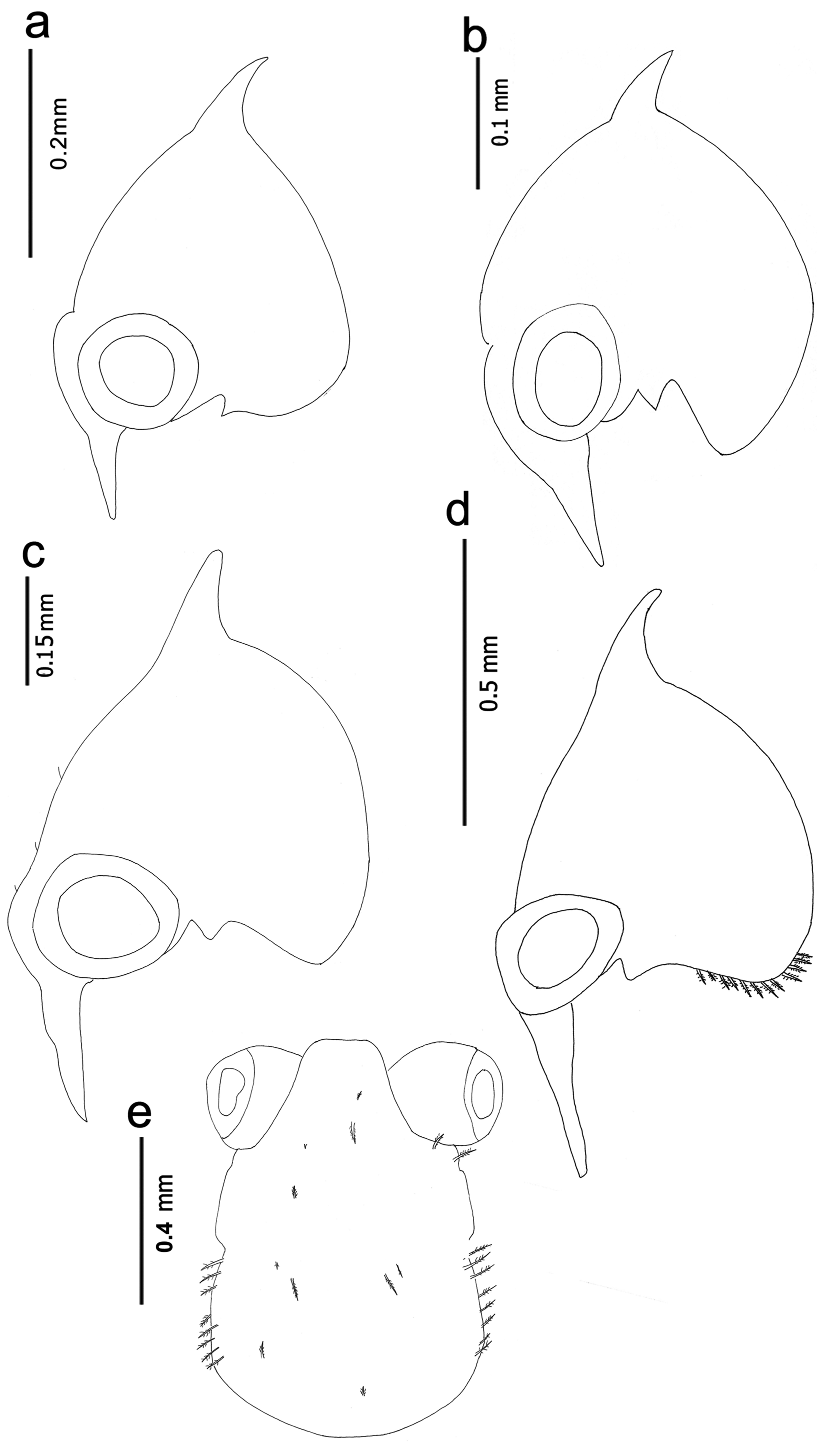

Fig. 2. *Austruca albimana* (Kossmann, 1877), lateral view of carapace: a) zoea I; b) zoea II; c) zoea III; d) zoea IV; e) dorsal view of carapace of megalopa.

Mandible (Fig. 5b): Incisor with six blunt teeth, all margins of molar process toothed.

Maxillule (Fig. 6b): Basis with 5 cuspidate, 1 plumodenticulate setae; epipod seta present.

Maxilla (Fig. 7b): Coxa bilobed, proximal lobe with 1 cuspidate, 4 plumodenticulate setae, distal lobe with 3 plumodenticulate setae; basis bilobed, proximal segment with 1 cuspidate, 5 plumodenticulate setae, distal segment with 1 cuspidate, 3 plumodenticulate setae; scaphognathite with 8 plumose setae.

First maxilliped (Fig. 8b): Endopod with 2,2,1,3,6 (2 subterminal plumose, 4 terminal plumodenticulate) setation; exopod with 6 natatory setae.

Second maxilliped (Fig. 9b): Exopod with 6

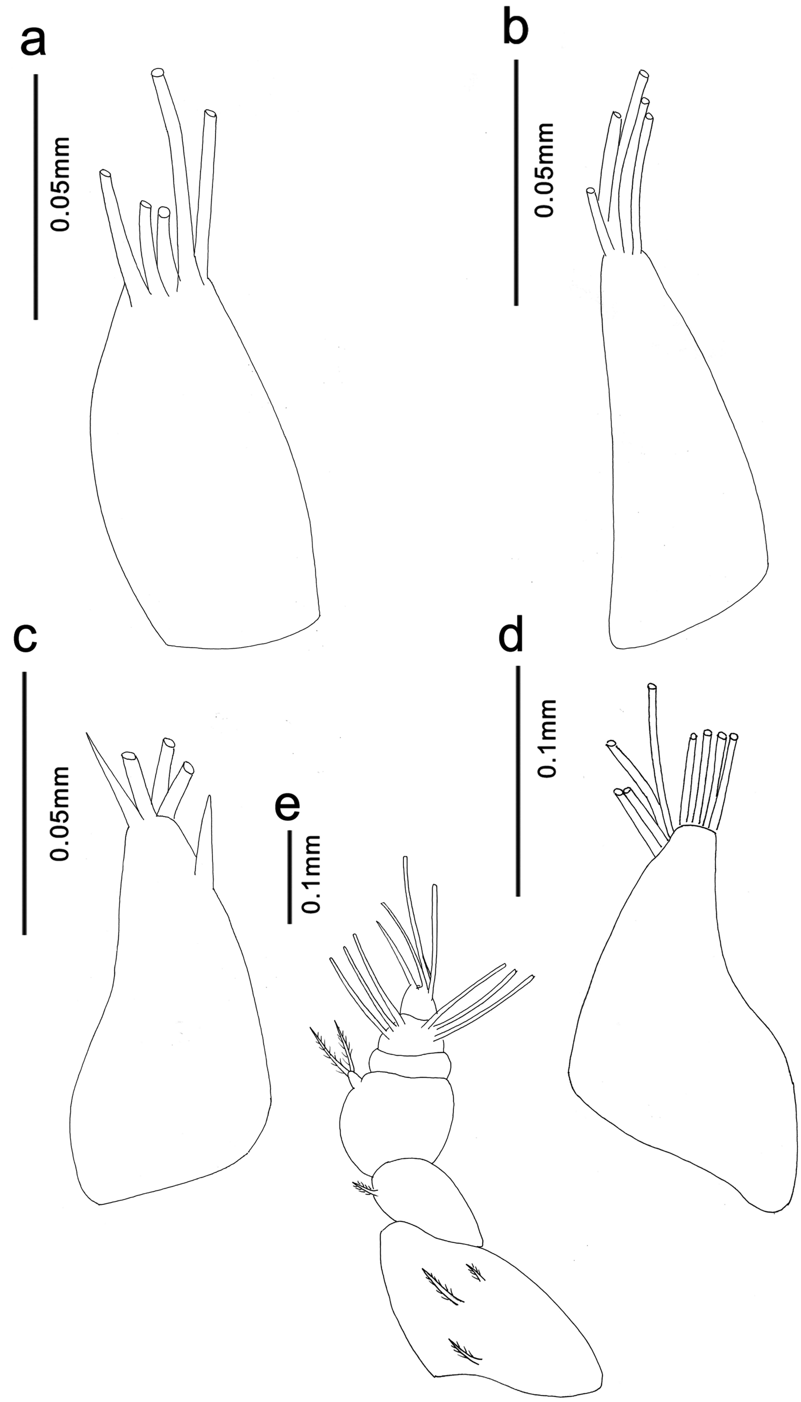

Fig. 3. *Austruca albimana* (Kossmann, 1877), antennule: a) zoea I; b) zoea II; c) zoea III; d) zoea IV, e) megalopa.

natatory setae.

Pleon (Figs. 10b; 13 a, b): Pleopod buds appear.

Zoea III

Size (mean ± sd): CL = 0.57 ± 0.05 mm; RDL = 0.9 ± 0.09 mm.

Carapace (Fig. 2c): Small hairs on anterodorsal margin.

Antennule (Fig. 3c): Three aesthetascs, two spines.

Antenna (Fig. 4c): Endopod about one half length of protopod.

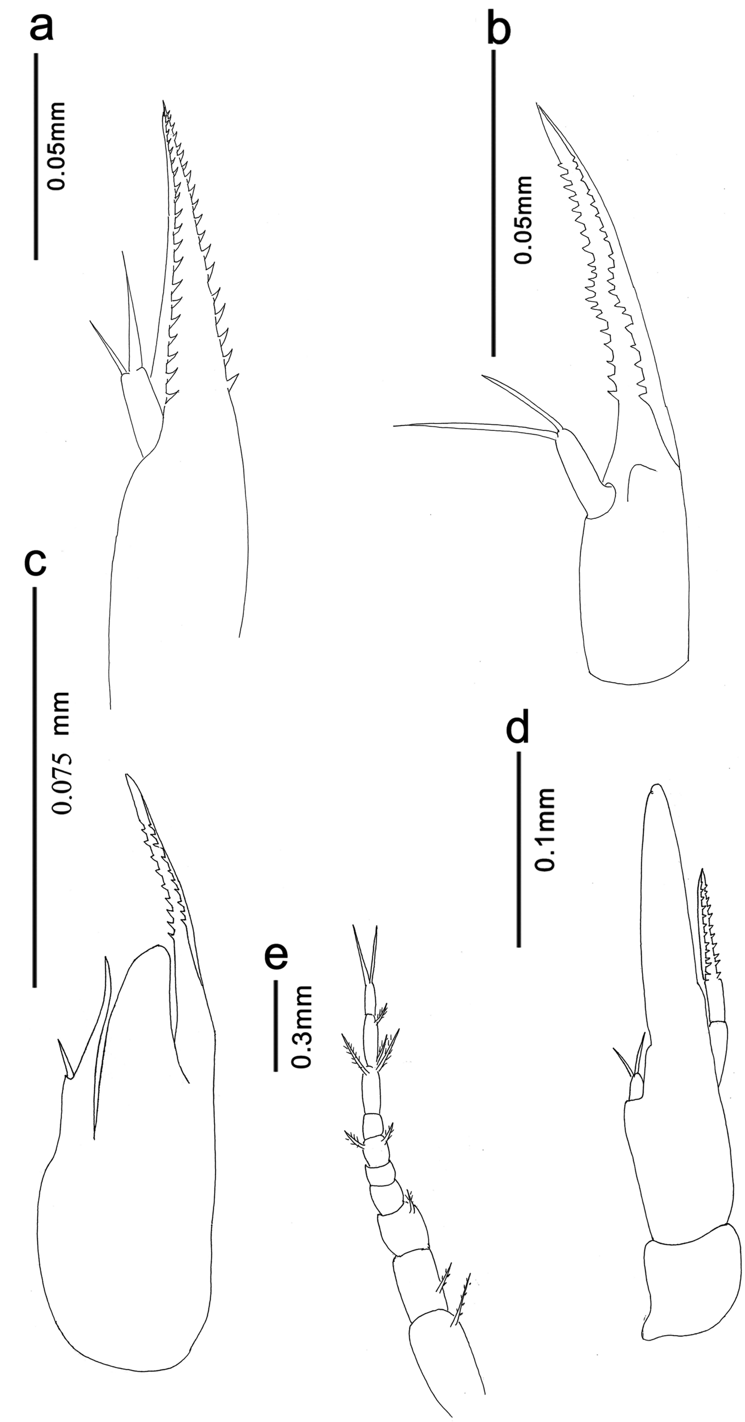

Fig. 4. *Austruca albimana* (Kossmann, 1877), antenna: a) zoea I; b) zoea II; c) zoea III; d) zoea IV; e) megalopa.

Mandible (Fig. 5c): Incisor with around eight blunt teeth, posterior margin of molar process with large tooth, other margins smooth.

Maxillule (Fig. 6c): Coxa with 2 cuspidate, 2 plumodenticulate, 1 simple setae; basis with 7 cuspidate, 2 plumodenticulate setae.

Maxilla (Fig. 7c): Proximal segment of coxa with 4 plumodenticulate, 1 cuspidate setae, distal segment with 3 cuspidate setae; proximal segment of basis with 3 cuspidate, 2 plumodenticulate setae, distal segment with

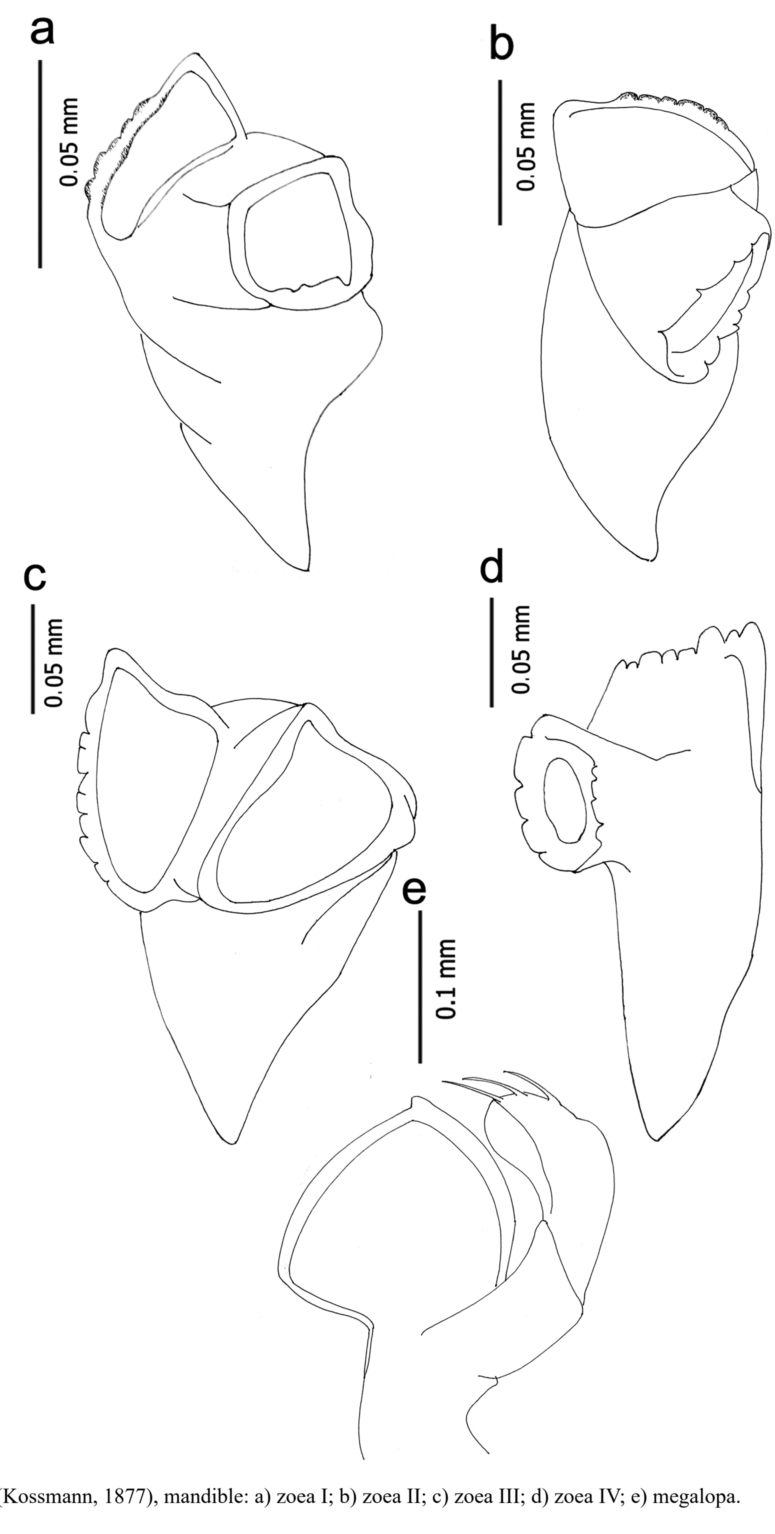

Fig. 5. *Austruca albimana* (Kossmann, 1877), mandible: a) zoea I; b) zoea II; c) zoea III; d) zoea IV; e) megalopa.

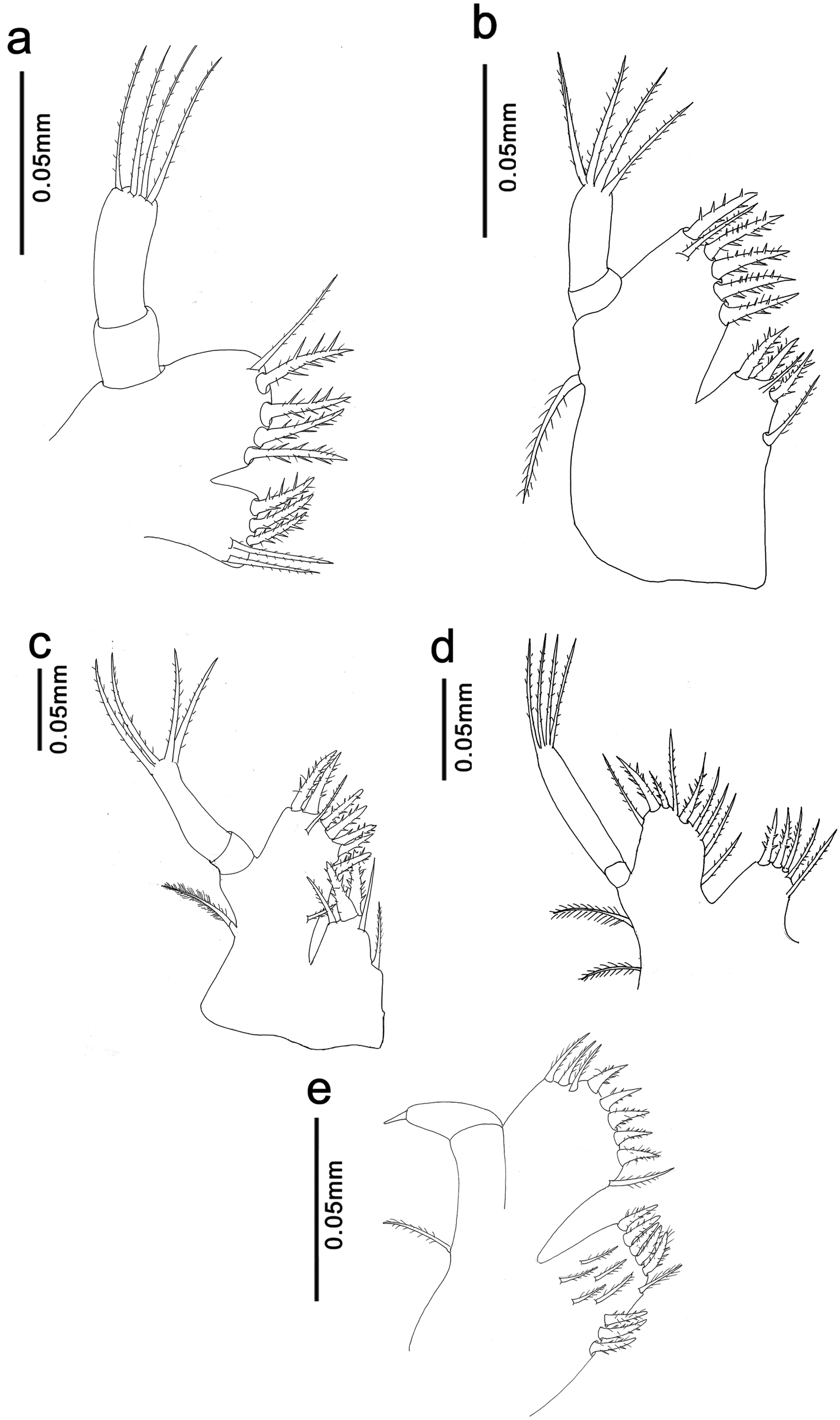

Fig. 6. *Austruca albimana* (Kossmann, 1877), maxillule: a) zoea I; b) zoea II; c) zoea III; d) zoea IV; e) megalopa.

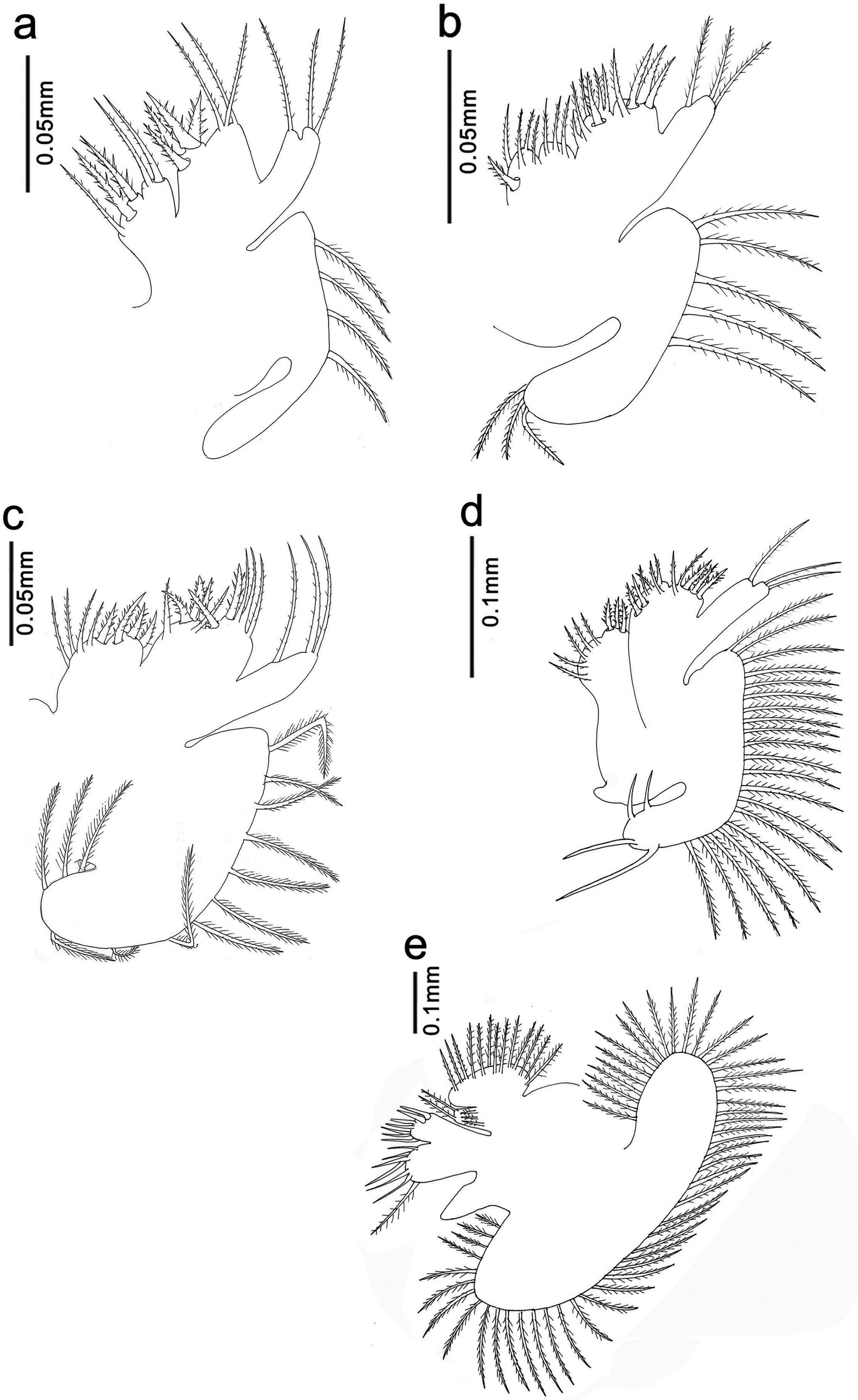

Fig. 7. *Austruca albimana* (Kossmann, 1877), maxilla: a) zoea I; b) zoea II; c) zoea III; d) zoea IV; e) megalopa.

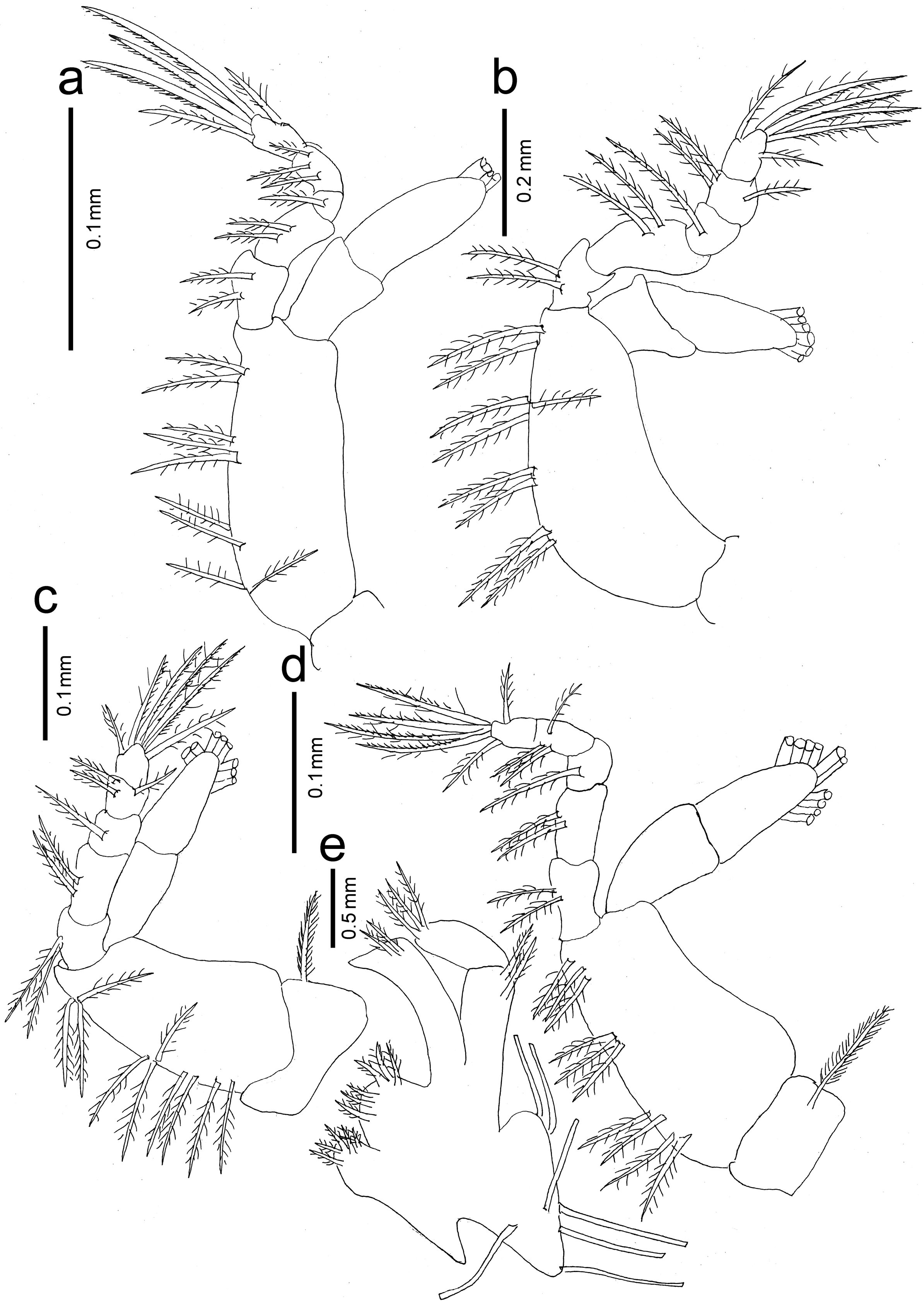

Fig. 8. *Austruca albimana* (Kossmann, 1877), first maxilliped: a) zoea I; b) zoea II; c) zoea III; d) zoea IV; e) megalopa.

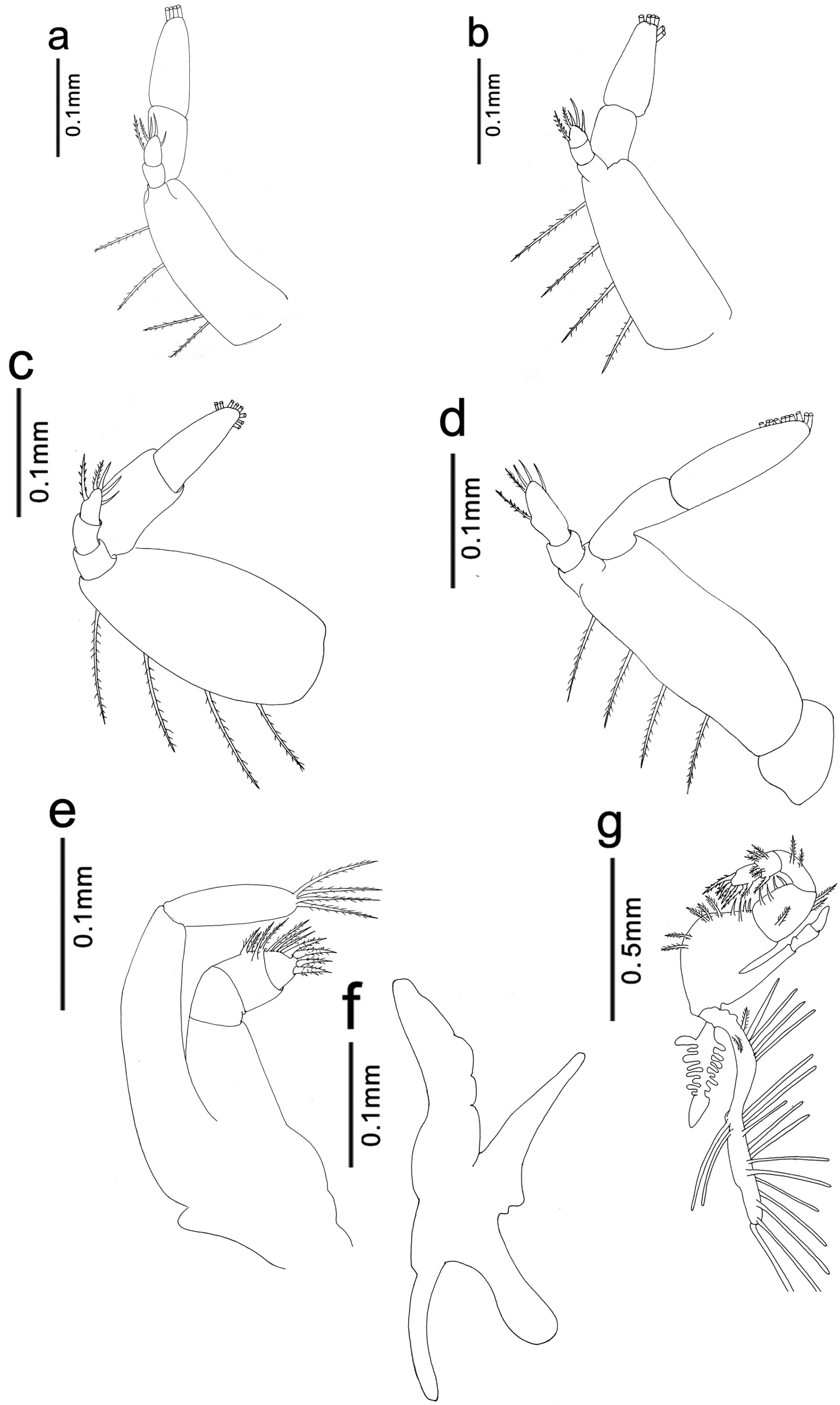

Fig. 9. *Austruca albimana* (Kossmann, 1877), second maxilliped: a) zoea I; b) zoea II; c) zoea III; d) zoea IV; e) megalopa; f) third maxilliped of zoea IV; g) third maxilliped of megalopa.

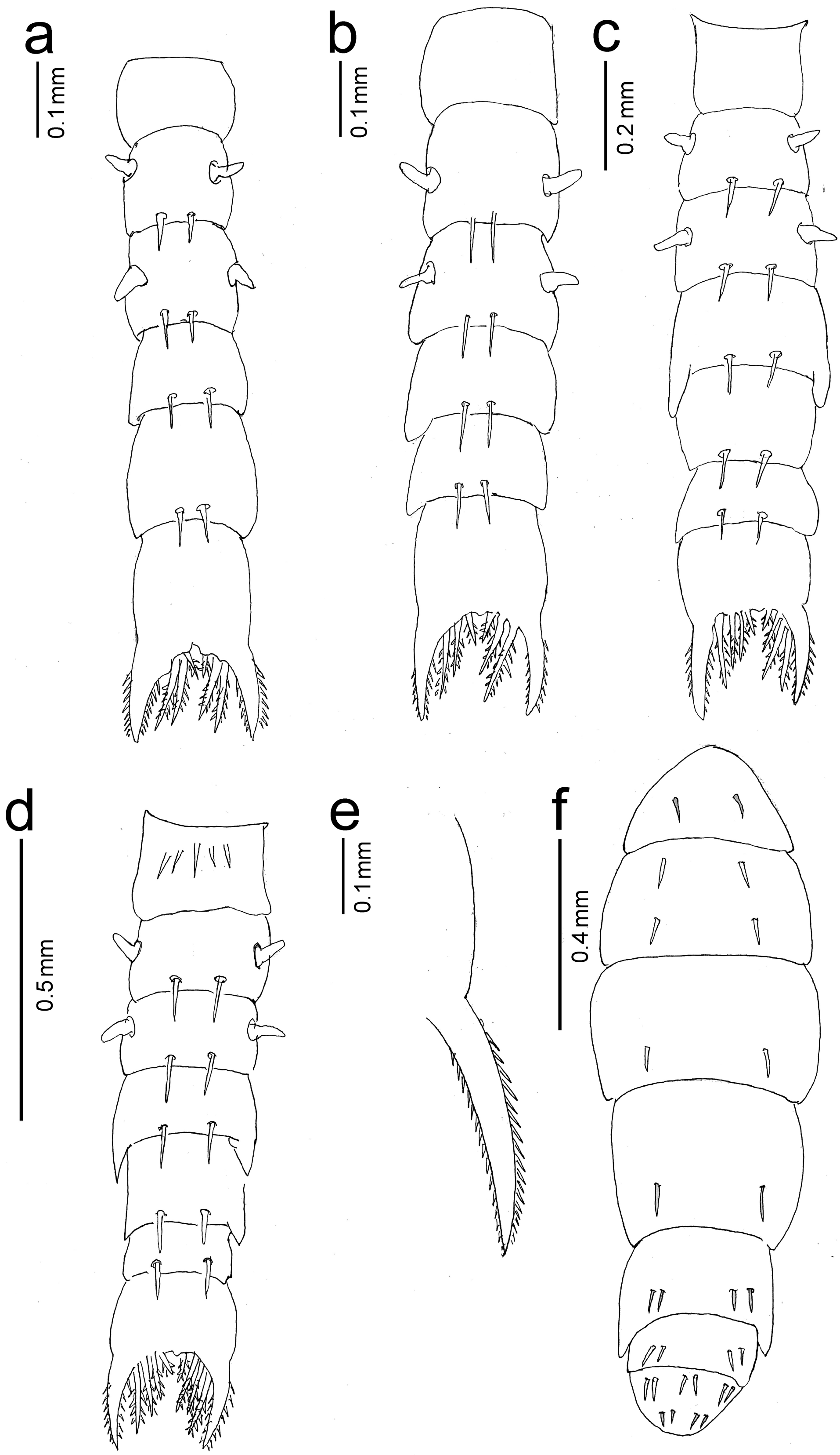

Fig. 10. *Austruca albimana* (Kossmann, 1877), dorsal view of pleon: a) zoea I; b) zoea II; c) zoea III; d) zoea IV; e) fork of the telson of zoea IV; dorsal view of pleon: e) megalopa.

2 cuspidate, 3 plumodenticulate setae; scaphognathite with 13 plumose setae.

First maxilliped (Fig. 8c): Coxal seta; basis with 2,2,3,3 plumose setae; exopod with 8 plumose natatory setae.

Second maxilliped (Fig. 9c): Exopod with 8 plumose natatory setae.

Pereiopods (Fig. 11a). Segmentation incomplete.

Pleon (Fig. 10c): Six somites; somites III–V with well-developed posterolateral processes; pleopod buds more developed.

Telson (Fig. 10c): Inner margin with four pairs of setae.

Zoea IV

Size (mean ± sd): CL = 0.6 ± 0.05 mm; RDL = 1.4 ± 0.1 mm.

Carapace (Fig. 2d): Twelve pairs of ventral setae.

Antennule (Fig. 3d): Eight aesthetascs arranged in two groups (4+4).

Antenna (Fig. 4d): Endopod longer than exopod.

Mandible (Fig. 5d): Incisor with eight teeth, all margins of molar process toothed.

Maxillule (Fig. 6d): Two epipodal setae; coxa with 2 cuspidate, 3 plumodenticulate (1 subterminal, 2 terminal) setae; basis with 3 terminal cuspidate, 6 plumodenticulate setae (3 subterminal).

Maxilla (Fig. 7d): Proximal lobe of coxa with 5 plumodenticulate setae, distal segment with 3 cuspidate setae; proximal lobe of basial with 2 cuspidate, 4 plumodenticulate setae, distal segment with 3 cuspidate, 2 plumodenticulate setae; scaphognathite with 24 plumose setae (20 Plumose, 4 simple).

First maxilliped (Fig. 8d): Exopod with 10 plumose natatory setae.

Second maxilliped (Fig. 9d): Exopod with 10 plumose natatory setae.

Third maxilliped (Fig. 9f): Present, not well developed.

Pereiopods (Fig. 11b): Well developed, segmented.

Pleon (Figs. 10d, e, 14a, b, 15): Somite I with 5 dorsal setae; pleopods well developed.

Megalopa

Size: CW = 0.86 mm; CL = 1.1 mm.

Carapace (Fig. 2e): Longer than broad; sparsely setose dorsally, posterolateral margins with few setae; rostral spine truncated, naked; eyes stalked.

Antennule (Fig. 3e): Peduncle 3-segmented with 3,1,0 plumose setae; endopod small, unsegmented with 2 plumose, distal setae; exopod three-segmented with 0, 6 (aesthetascs), 4 (3 aesthetascs, 1 seta) setation.

Antenna (Fig. 4e): 3-segmented peduncle with 1,1,1 plumose setae; flagellum 7-segmented with 0,0, 2,0,2,2,2 setae, segments 1–6 with plumose setae, 7th segment with simple setae.

Mandible (Fig. 5e): Palp two-segmented; distal segment with 3 terminal simple setae.

Maxillule (Fig. 6e): Coxa with 8 cuspidate, 6 plumodenticulate setae; basis with 5 cuspidate, 2 plumose and 2 plumodenticulate setae; endopod bisegmented, distal segment terminates with seta; single protopod plumose seta.

Maxilla (Fig. 7e): Coxa bilobed, proximal segment with 13 setae, distal segment with 5 setae, all plumodenticulate; basis bilobed, proximal segment with 7 simple setae, distal segment with 6 simple, 1 plumose setae; endopod unsegmented without setae; scaphognathite with 51 plumose setae.

First maxilliped (Fig. 8e): Coxa, basis with 5, 6 plumodenticulate setae, respectively; endopod with 2 subterminal setae; exopod 2-segmented, proximal segment with two distal setae, distal segment with 3 setae, all plumose; epipod with 7 long setae.

Second maxilliped (Fig. 9e): Endopod 4-segmented with 0, 0, 4 (all plumodenticulate), 7 (4 cuspidate, 3 plumodenticulate) setation; exopod 2-segmented, distal segment with 4 plumose setae.

Third maxilliped (Fig. 9g): Protopod naked; endopod 5-segmented with 9 (5 plumodenticulate, 4 simple), 7 (4 simple, 3 plumodenticulate), 2 (plumodenticulate), 6 (plumodenticulate), 5 cuspidate setae; exopod 3-segmented without setation, epipod with 20 (18 simple, 2 plumose) setae.

Pereiopods (Fig. 11c–g): Inner margins of fused basis, ischium, merus, superior border of carpus of chelae with 1 or 2 spines each; fingers cross each other; inner margins of segments of pereiopods II–IV with few spines; coxa of Vth pereiopods with three stout plumose setae; superior margins of carpus and propodus with 1 or 2 spines; tips of dactyl with 3 long setae.

Pleon (Fig. 10f): Six somites; somites I, III, IV with 1 pair of setae each, somite II with 2 pairs of setae, one each on anterior and posterior borders, V and VI with two pairs of posterior setae each; somite III with 3 pairs of setae; somite V with well-developed lateral processes.

Telson (Fig. 10f): Tip rounded: 5 pairs of plumose setae; three pairs anteriorly, two pairs posteriorly.

Pleopods (Fig. 12a–d): Endopods of somites I–V with three cincinnuli each, pleopod of somite VI without endopod; exopods of pleopods of somite II–VI with 13S, 12S, 14S, 12S plumose setae, respectively.

Uropod (Fig. 12e): Exopod with 9 plumose setae, protopod with plumose seta.

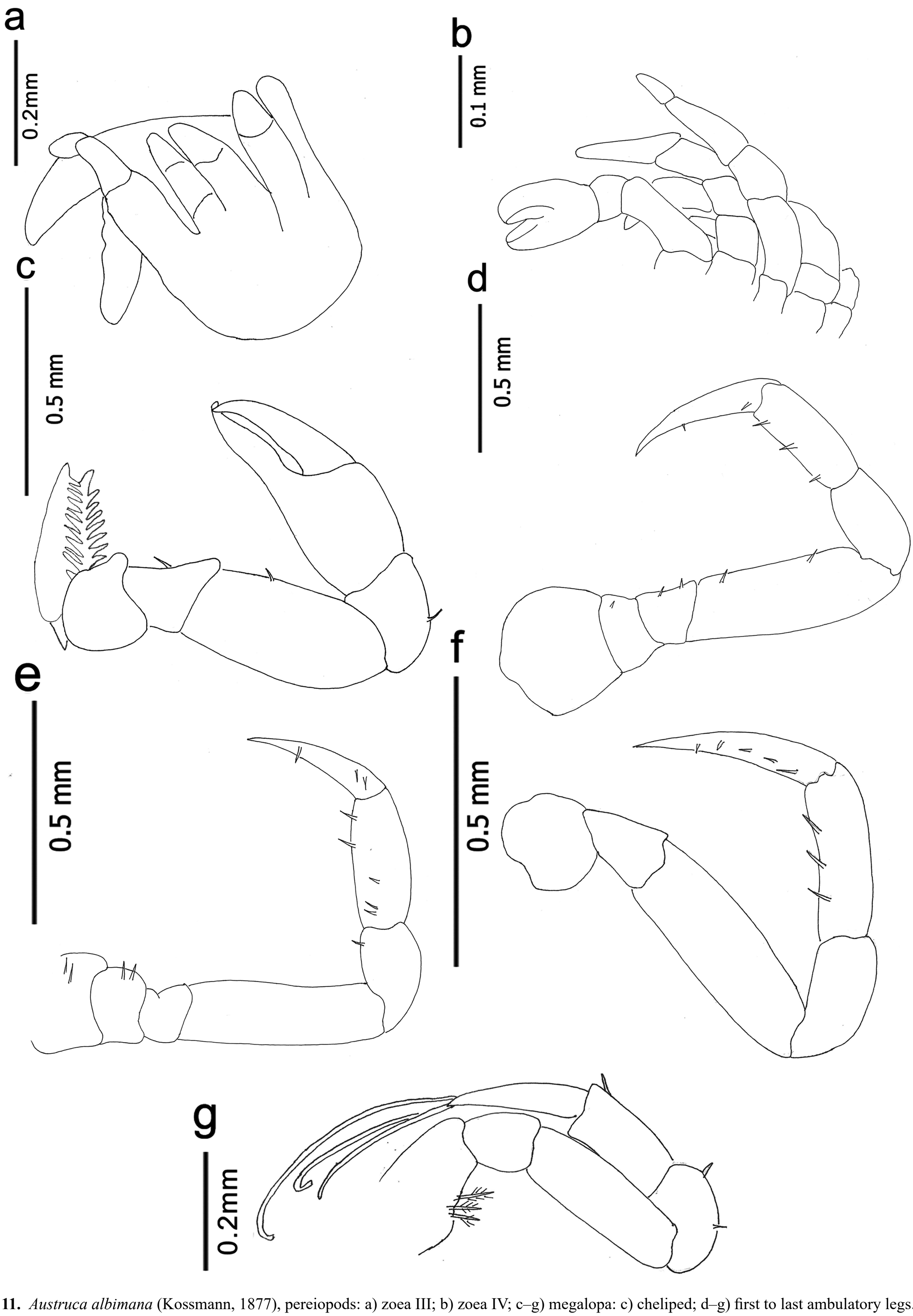

Fig. 11. *Austruca albimana* (Kossmann, 1877), pereiopods: a) zoea III; b) zoea IV; c–g) megalopa: c) cheliped; d–g) first to last ambulatory legs.

DISCUSSION

Four zoeal stages and one megalopal stage were recorded during the larval development of *A. albimana*. Some fiddler crabs exhibit more than four zoeal stages: *A. lactea* and *L. thayeri* (five) (Terada 1979; Anger et al. 1990) and *Minuca burgersi* (six) (Rieger 1998a).

Several environmental factors have been thought to influence the number of zoeal stages in brachyuran crabs, *e.g.*, salinity, temperature, photoperiodicity,

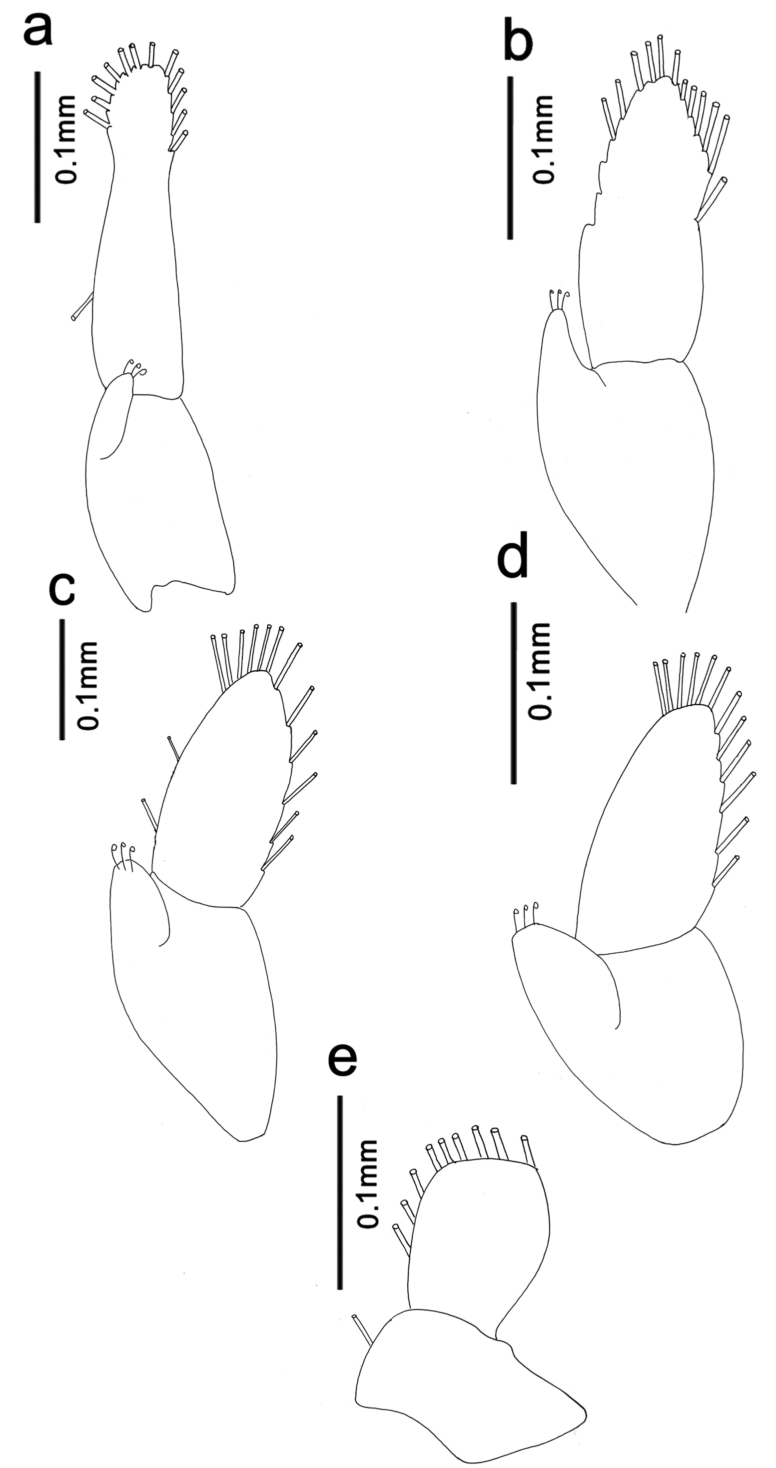

Fig. 12. *Austruca albimana* (Kossmann, 1877), megalopa; a–e) pleopods II–VI.

prophylactic usage and food availability (Gardner and Northam 1997; Gardner and Quintana 1998; Al-Aidaroos et al. 2014). Crabs living in highly specialised habitats exhibit abbreviated development to reduce the chances of larval dispersion (Rabalais and Gore 1985). Although this statement has proven true in *A. albimana*—it inhabits a specialised ecosystem, mangroves and has just four zoeal stages—other fiddler crabs of this habitat have up to six zoeal stages (Anger et al. 1990; Rieger 1997 1998a b; Batisteli 2003). Temperature is another important factor in determining the number of larval stages of crustaceans (Anger 2001). In five species of *Coenobita* (hermit crabs), the total zoeal stages tended to decrease with increasing temperature (Hamasaki et al. 2020). In our study, the zoeas were reared at a higher temperature, 28°C, which generally might cause a reduction in zoeal stages.

In this study, the zoea I of *A. albimana* can be well differentiated from those of the other two congeneric species. The antennule of *A. albimana* has five aesthetascs, while the other two species have two aesthetascs and a spine. Both the coxa and the basis of maxillule of *A. albimana*, *A. iranica* (Hashmi 1968) and *A. lactea* (Terada 1979) have five setae each. However, the zoea I of *A. iranica* described by Ghory and Siddique (2006) had only four setae (Table 2). Similarly, intrageneric variations can be seen in the setations of the maxilla and maxillipeds I and II of the first zoeas of

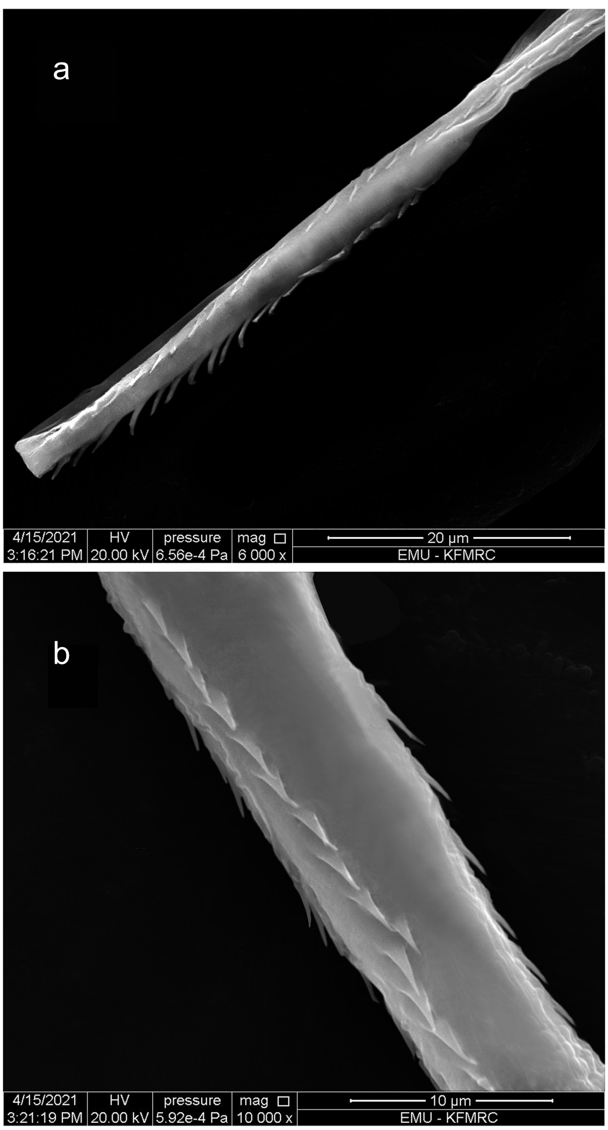

Fig. 13. *Austruca albimana* (Kossmann, 1877), SEM images of the telson of zoea II; a) at magnification 6000×; b) at magnification 10000×.

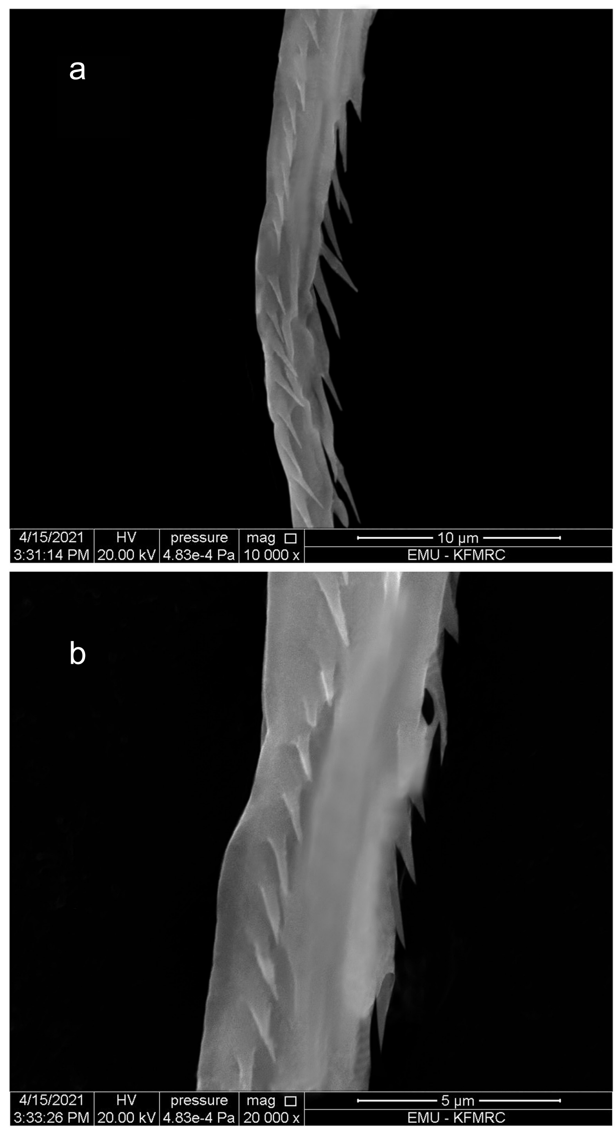

Fig. 14. *Austruca albimana* (Kossmann, 1877), SEM images of the telson of zoea IV; a) at magnification 10000×; b) at magnification 20000×.

Austruca. These variations can help identify the larvae of *Austruca* spp.

One important character, several minute spines on the forks of the telson, has been found in the zoeas of all *Austruca* spp. (Hashmi 1968; Terada 1979; Ghory and Siddique 2006; this study; Figs. 12–14). This characteristic suggests that this genus is monophyletic. It has long been understood that larval morphological features reflect phylogenetic relationships (Rice 1983; Hultgren et al. 2009).

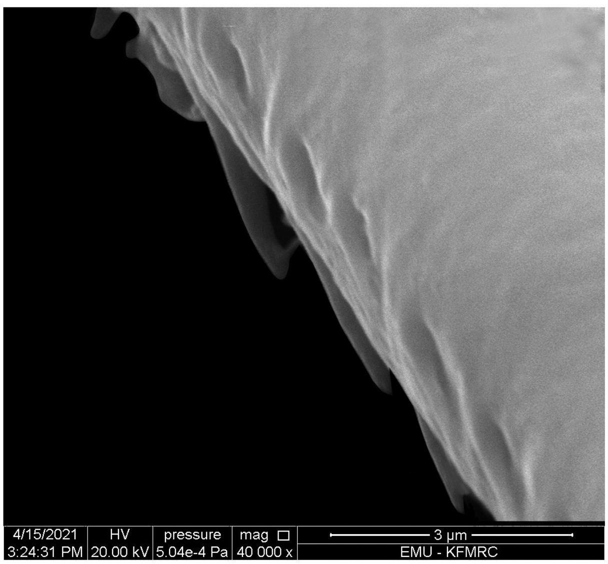

Fig. 15. *Austruca albimana* (Kossmann, 1877), SEM images of the telson of zoea IV at magnification 40000×.

Several morphological features are similar among the first zoeas of different species in Gelasiminae: presence of two aesthetascs and a spine in the antennule (*A. iranica*, *A. lactea*, *Gelasimus hesperiae*, *L. thayeri*, *M. burgersi* and *T. alcocki*); presence of two setae on the exopods of antenna (*A. iranica*, *C. inversa*, *G. hesperiae* and *T. alcocki*); presence of five setae on each of the coxa and basis of the maxillule (*A. iranica*, *A. lactea*, *C. inversa*, *G. hesperiae*, *L. thayeri*, *Leptuca uruguayensis*, *M. burgersi*, *Minuca mordax*, *Minuca rapax*, *Minuca vocator* and *T. alcocki*); presence of 5+4 setal pattern on the basis of maxilla; presence of 2+2+3+2 and 2,2,1,2,5 setation on the basis and endopod of maxilliped I, respectively and the occurrence of 0,0,5 setation on the endopod of maxilliped II (Table 2).

Bento and Paula (2018) have listed some morphological features of the first zoeas of four species of fiddler crabs collected from the western Indian Ocean, *A. occidentalis* (as *A. annulipes*) (see Naderloo et al. 2016), *Gelasimus hesperiae* (as *G. vocans*) (see Crane 1975), *T. urvillei* and *Paraleptuca chlorophthalmus*. The larvae of Bento and Paula (2018) and our study have several common morphological features (Table 4). That is, the ratio of the length of the dorsal spine to the length of the carapace is 1/3 for *A. annulipes*, *G. hesperiae* and *T. urvielli*, and the setation on the basis of first maxilliped is 2+2+3+2 for *A. albimana*, *G. hesperiae* and *T. urvielli*. Likewise, minute spines are found in the forks of telson of *A. annulipes*,

Table 2. Morphological differences between the first zoeas of *Austruca albimana* (Kossmann, 1877) (present study) and other related fiddler crabs. *Ghory and Siddique 2006; [†]Hashmi 1968; [‡]Anger et al. 1990; [+]De Souza et al. 2013

	Antennule		Antenna	Maxillule		Maxilla			Maxilliped I		Maxilliped II	Each fork of telson
	AE	SP	EXS	COS	BAS	COS	BAS	SCHS	BAS	ENS	ENS	LSP
Austruca albimana	5	-	2	5	5	3+2	4+3	4	2+2+3+2	2,2,1,3,5	0,0,5	-
*A. iranica**	2	1	2	4	5	3+3	5+3	3	2+2+2+2	2,2,1,2,1+4	0,0,2+2	SMSP
A. iranica[†]	2	1	2	5	5	2+3	5+4	4	7	2,2,1,2,4+1	0,0,5	1
A. lactea	2	1	ND	5	5	1+3	4+4	4	12?	2,2,1,2,5	0,0,5	-
Cranuca inversa	4	-	2	5	5	5+3	5+4	4	2+2+3+3	2,2,1,2,5	0,0,5	-
Gelasimus vocans	2	1	2	5	5	2+4	5+4	4	8	2,2,1,2,4+1	0,0,5	SMSP
Leptuca thayeri[‡]	2	1	3	4	5	3+3	3+5	4	1+1+2+2	0,1,1,2,4 (5)	0,0,4	-
L. thayeri[+]	2	2	2+2SP	5	5	4+3	5+4	4	2+2+3+2	0(2),0(2),0(1),2,4(5)	0,0,5	-
L. leptodactylus	3	1	-	6	5	3+5	5+4	4	8	1,2,1,2,5	0,1,5	-
L. uruguayensis	3	2	3	5	5	3+3	5+4	5	9	2,2,1,2,5	0,0,5	-
Minuca burgersi	2	1	3	5	5	3+3	4+4	4	9	2,2,1,2,5	0,0,5	-
M. mordax	3	3	3	5	5	4+3	5+4	5	9	2,2,1,2,5	0,0,5	-
M. rapax	2	2	3	5	5	4+3	5+4	4	2+2+3+2	2,2,1,2,5	0,0,5	1
M. vocator	2	2	3	5	5	3+3	5+4	5	9	2,2,1,2,5	0,0,5	-
Tubuca alcocki	2	1	2	5	5	3+3	5+4	3	2+2+3+2	2,2,1,2,1+4	0,0,2+2	SMSP

AE, aesthetascs; BAS, basial setae; COS, coxal setae; DS, dorsal setae; EXS, exopod seta/e; ENS, endopodal setae; LSP, lateral spine; ND, no data; SCHS, scaphognathite setae; SMSP; small spines; SP, spine/s.

A. albimana and *G. hesperiae*. These morphological similarities in early zoeal stages are common in several brachyuran larvae at the genus level, and variations become more apparent in the later stages (De Souza et al. 2013).

Morphological descriptions are fewer for later zoeal stages because of high mortality during larval rearing; this hampers better larval comparisons. Twelve posterolateral setae are seen on the ventral margin of the carapace of the fourth zoeal stage of *A. albimana* (this study), and these setae are present from zoea III onwards in *L. thayeri* (4 in zoea III, 6 in zoea IV) and from zoea II onwards in *M. burgersi* (1 in zoea II, 2 in zoea III, 7 in zoea IV) (Anger et al. 1990; Rieger 1998a). In the fourth zoeal stage, the number of plumose setae on the scaphognathite of the maxilla is higher for *Austruca* sp. (24 in *A. albimana*, 17–20 in *A. lactea*) and *Leptuca* sp. (24 in *L. uruguayensis*) (Table 3).

MXPI, first maxilliped; FTA, forks of the telson; CL, length of carapace; ND, no data; RDL, the length of carapacial dorsal spine; SANT, size of antenna; SRS, rostral spine length.

Two morphological features observed in the larvae of *A. albimana* (this study) and other fiddler crabs, viz. the absence of lateral spines on the carapace and the presence of a maximum of four pairs of inner

Table 3. Morphological differences between the second, third and fourth zoeas of *Austruca albimana* (Kossmann, 1877) (present study) and other related fiddler crabs

	Antennule		Antenna	Maxillule		Maxilla			Maxilliped 1		Maxilliped I1	Each fork of telson
	AE	SP	EXS	COS	BAS	COS	BAS	SCHS	BAS	ENS	ENS	LSP
Zoea 2												
Austruca albimana	5	-	2	5	6	5+3	6+4	8	2+2+3+2	2,2,1,3,6	0,0,5	-
A. iranica	4	1	2	5	6	3+3	4+4	6	7	2,2,1,2,4+1	0,0,5	1
A. lactea	4	1	ND	5	5	3+2	4+3	8	12?	2,2,1,2,4+1	0,0,5	-
Leptuca uruguayensis	4	1	3	5	7	3+3	5+4	5	9	2,2,1,2,5	0,0,5	
Minuca burgersi	5	1	3	5	7	3+3	5+4	7	9	2,2,1,2,5	0,0,5	-
M. mordax	4	1	3	5	7	8+3	5+3	7	10	2.2,1,2,5	0,0,5	-
Zoea 3												-
Austruca albimana	3	2	2	5	9	4+2	5+5	13	2+2+3+3	2,2,1,3,6	0,0,5	-
A. lactea	2	3	ND	5	7	4+3	5+4	11	12?	2,2,1,2,6	0,0,5	-
Leptuca uruguayensis	4	-		5	7	4+3	5+4 (2SS)	12	9	2,2,1,2,6	0,0,5	
Minuca burgersi	5	-	3	5	7	3+6	5+4	11	2,2,2,3	2,3,1,2,6	0,0,5	-
M. mordax	4	1	3	5	7	4+3	5+4	10	8	2,2,1,2,6	0,0,5	
Zoea 4												-
Austruca albimana	8	-	2	5	9	5+3	6+5	24	2+2+3+3	2,2,1,3,6	0,0,5	-
A. lactea	3	2	ND	6	9	5+3	6+6	17–20	12?	2,3,1,2,6	0,0,5	-
Leptuca uruguayensis	5	-		5	12	5+4	6+5	24	9	2,2,1,2,6	0,0,5	
Minuca burgersi	5	-	3	5	10	5+3	5+5	14	2+3+1+2+1	2,3,1,2,6	0,0,5	-
M. mordax	6	-	3	6	10	5+3	5+5	13	9	2,3,1,2,6	0,0,5	

AE, aesthetascs; BAS, basial setae; COS, coxal setae; DS, dorsal setae; EXS, exopod seta/e; ENS, endopodal setae; LSP, lateral spine; ND, no data; SCH, scaphognathite setae; SP, spine/s; SS, small seta/e.

Table 4. Comparison of some of the morphological features of the first zoeas of the four species of fiddler crabs from the western Indian Ocean with *Austruca albimana* (Kossmann, 1877) (present study)

No.	Species name	RDL vs. CL	SRS vs. SANT	Spines on FTA	Setation on the basis of MXPI
1	*Austruca annulipes*	1/3	1/3 bigger than	Numerous, minute	1+2+3+2
2	*A. albimana* (present study)	1/4	4/5 bigger than	Numerous, minute	2+2+3+2
3	*Gelasimus vocans*	1/3	Twice the length of	Numerous small	2+2+3+2
4	*Paraleptuca chlorophthalmus*	1/6	1/4 length of	ND	3+2+3+2
5	*Tubuca urvielli*	1/3	Twice the length of	ND	2+2+3+2

CL, length of carapace; FTA, fork of telson; MXPI, maxilliped I; ND, no data; RDL, the length of carapacial dorsal spine; SANT, size of antenna; SRS, rostral spine length.

setae on the telson during the entire larval development, are suggested to have taxonomic significance at the subfamily level. These characteristics provide additional evidence indicating that species of *Uca* and *Afruca* belong to the subfamily Ocypodinae. The carapacial lateral spines are absent in the larvae of the subfamily Gelasiminae but present in those of *Afruca*, *Uca* and *Ocypode* species (Terada 1979; Rieger 1996 1997 1998a b; Kakati 2005; Negreiros-Fransozo et al. 2009; Spivak and Cuesta 2009; Jiang et al. 2014; this study). Moreover, a maximum of four pairs of inner setae are present on the telson of the zoeas of Gelasiminae even at the sixth stage (Terada 1979; Rieger 1996 1997 1998a; this study). Species of *Uca*, *Afruca* and *Ocypode*, however, have more than four pairs of setae on the telson of the later zoeal stages. This is a consistent feature similar to the presence of carapacial lateral spines (Kakati 2005; Negreiros-Fransozo et al. 2009; Spivak and Cuesta 2009; Jiang et al. 2014).

Only a few morphological descriptions are available for the megalopal stage of Gelasiminae (Table 4). Availability of more larval descriptions is

Table 5. Comparison of the morphological characteristics of the megalopae of *Austruca albimana* (Kossmann, 1877) (present study) and other related fiddler crabs

Morphological characters		*A. albimana* (present study)	*Leptuca thayeri* (Anger et al. 1990)
Carapace	CL	1.46–1.52 mm	1.10–1.29 mm
	CW	1.1–1.32 mm	0.85–1.04 mm
Antennule	Basal segment	3S	1S
	Peduncle	2 SEG (1,0S)	UNSEG (0S)
	Endopod	UNSEG (2S)	Absent
	Exopod	3 SEG (0, 6AE, 3AE+1S)	2 SEG (6AE, 4AE+2S)
Antenna	Peduncle	3 SEG (1,1,1S)	3 SEG (1,1,1S)
	Flagellum	7 SEG (0,0,2,0,2,2,2S)	7 SEG (0,0,2,1,3,1,3S)
Mandible	Palp	2 SEG (0,3S)	UNSEG (4S)
Maxillule	Coxa	14S	12S
	Basis	9S	19S
	Endopod	2 SEG (0,1S)	UNSEG (1S)
	Protopod	1S	1S
Maxilla	Coxa	13+5S	4+6S
	Basis	7+7S	8+8S
	Endopod	0	UNSEG (0S)
	SCH	51S	35S
	LSS	0	ND
Maxilliped I	Coxa	5S	6 S
	Basis	6S	6 S
	Endopod	UNSEG (2S)	UNSEG (2S)
	Exopod	2 SEG (2,3S)	2 SEG (2,4S)
	Epipod	7S	7S
Maxilliped II	Endopod	4 SEG (0,0,4,7S)	3 SEG (1,4,6S)
	Exopod	2 SEG (0,4S)	2 SEG (0,4S)
	Epipod	-	-
Maxilliped III	Protopodite	0S	3S
	Endopod	5 SEG (9,7,2,6,6S)	5 SEG (11–12, 10–11, 4–6, 5–8, 6–8S)
	Exopod	3 (0,0,0S)	2 SEG (1,5S)
	Epipod	20S	16S
Pleopod I	End Hooks	3	3
	Exopod	13S	14S
Pleopod II	End Hooks	3	3S
	Exopod	12S	14S
Pleopod III	End Hooks	3	3
	Exopod	14S	11S
Pleopod IV	End Hooks	3	3
	Exopod	12S	14S
Uropod	Exopod	9S	7S
	Protopod	1S	1S

a prerequisite for better larval comparisons (Rieger 1998a). A deflexed front, rounded to obtuse frontal margin, seven-segmented antennal flagellum, unsegmented endopod of maxilla and three cincinnuli on the endopod of pleopod are some of the characteristics common to the megalopae of Gelasiminae (Table 5). The morphology of the megalopae of other species of Gelasiminae should be studied further to confirm those characteristics as the key characteristics of this subfamily.

The megalopae of Gelasiminae can be easily distinguished from each other morphologically (Table 5). The posterolateral margins of *A. albimana* have a row of setae (this study) and this setation is extended to the posterior border in *M. burgersi* (Rieger 1998a), while this setation is absent in other species of Gelasiminae. Taxonomists should be cautious when considering this characteristic for comparing morphology of brachyuran larvae as it might have been overlooked in several previous works (Clark et al. 1998;

Table 5. (Continued)

Morphological characters		*L. uruguayensis* (Armendariz 2005)	*Minuca burgersi* (Rieger 1998a)
Carapace	CL	1.26–1.39 mm	ND
	CW	1.02–1.03 mm	ND
Antennule	Basal segment	1S	5S
	Peduncle	3 SEG (0,2,1S)	2 SEG (2,0S)
	Endopod	UNSEG (4S)	UNSEG (2S)
	Exopod	4 SEG (3,3,3–5AE, 3–5AE+2S)	3 SEG (0, 7 or 8, 4AE+1S)
Antenna	Peduncle	3 SEG (1,1,2S)	3 SEG (1,1,2S)
	Flagellum	7 SEG (0,0,2–3,1,3,2,3–4S)	7 SEG (0,0,3,0,4,1,2S)
Mandible	Palp	3 SEG (0,0,7–14–17S)	2 SEG (0, 4S)
Maxillule	Coxa	12–19S	16S
	Basis	18–20S	20S
	Endopod	2 SEG (1,4S)	2 SEG (1,2S)
	Protopod	0	2S
Maxilla	Coxa	2-3+14–15S	20S
	Basis	7-9+9–12S	9+8S
	Endopod	UNSEG (1–2S)	UNSEG (2S)
	SCH	46–49S	47S
	LSS	ND	3S
Maxilliped I	Coxa	10–11S	8S
	Basis	14–17S	7S
	Endopod	3 SEG (0,2,1S)	2SEG (2,3S)
	Exopod	2 SEG (3,5S)	2SEG (2,3S)
	Epipod	9S	7S
Maxilliped II	Endopod	5 SEG (1,1,1,5–6,7–8S)	4 SEG (0,1,4,7S)
	Exopod	2 SEG (1,5S)	2 SEG (1,4S)
	Epipod	2S	ND
Maxilliped III	Protopodite	15–21S	6S
	Endopod	5 SEG (11–12, 10–11, 4–6, 5–8,6–8S)	5 SEG (11,6,3,6,6S)
	Exopod	2 SEG (1–2, 4–5S)	2 SEG (1,4S)
	Epipod	31S	17S
Pleopod I	End Hooks	3	3
	Exopod	15S	16S
Pleopod II	End Hooks	3	3
	Exopod	16S	15S
Pleopod III	End Hooks	3	3
	Exopod	15S	14S
Pleopod IV	End Hooks	3	3
	Exopod	14S	14S
Uropod	Exopod	8S	9S
	Protopod		

AE, aesthetascs; End hooks, endopodal hooks; LSS, lateral setae; ND, no data; S, seta/setae; SCH, scaphognathite; S, segments; UNSEG, unsegmented.

De Souza et al. 2013). *Austruca albimana* is the only species with three segments in the exopod of the third maxilliped. Negreiros-Fransozo et al. (2009) reported the presence of a spine on both the basis of the chelipeds and third pereiopods of *Uca maracoani*. These spines are absent in the megalops of Gelasiminae (Anger et al. 1990; Rieger 1998a; Armendariz 2005; Negreiros-Fransozo et al. 2009; this study).

CONCLUSIONS

In this study, four zoeal and one megalopal stages were recorded in the larval development of *A. albimana*. In the different zoeal stages of the species of Gelasiminae, genus-level characteristics could not be identified, as no suites of characteristics are common to the congeners, and similar morphological features existed at the intergeneric level. However, exclusively in the different zoeal stages of *Austruca* spp., there are minute spines on the forks of the telson. This character is suggested to be of phylogenetic significance. Two morphological features were found in the zoeas of all fiddler crabs: (1) absence of lateral spines on the carapace; (2) presence of a maximum of four pairs of inner setae on the telson, even in the sixth-stage larvae. The congeners of fiddler crabs can easily be differentiated at the megalopal stage based on suites of morphological characteristics. Several morphological features are common to the megalopae of fiddler crabs. To confirm those features as key characteristics of this group, more extensive studies are necessary.

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