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Reproductive biology and postembryonic development of a polyphagid cockroach *Eucorydia yasumatsui* Asahina (Blattodea: Polyphagidae)

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Abstract

Reproductive biology, including mating behavior, ootheca deposition, ootheca rotation, and postembryonic development, were examined and described in a Japanese polyphagid, *Eucorydia yasumatsui* Asahina, 1971. *E. yasumatsui* lacks elaborate pre-copulation behaviors, in contrast to most cockroaches. On encountering a female, the male rushes to her, chases her, touching her with his antennae, and finally the pair initiates “tail-to-tail” copulation. The ootheca bears a well-developed, serrated keel along its dorsal median line and a flange on its anterior end, which is grasped with the female’s paraprocts while she carries the ootheca. The ootheca formed in the vestibulum emerges from her caudal end, with its keel upwards. Several hours later, she rotates the ootheca clockwise by 90°, viewed from the female’s side, into a horizontal position. After rotation, she carries the ootheca, maintaining this horizontal position for a few days, and then deposits it on the ground. The number of larval instars was 9 or 10 in females and 8 or 9 in males. Addition of annuli to the antennal flagellum occurs from the 2nd instar molting onwards, and annular division occurs both in the 1st annulus of the flagellum (meriston) and in the annulus following it (called “meristal annulus” from the 3rd instar on): one to several annuli from the former and a single annulus from the latter are added. Sexes can be distinguished from the 3rd instar on according to the changes of the postabdominal structures. Regarding exposed structures, in the female the posterior margin of abdominal coxosternum VIII becomes incised medially, the abdominal coxosterna VIII and IX retract, and the styli of segment IX disappear. The male does not undergo marked externally visible changes.

Key words

Blattaria, Blattodea, Polyphagidae, *Eucorydia*, reproductive biology, mating behavior, ootheca, postembryonic development.

1. Introduction

In cockroaches or “Blattaria,” about 450 genera and 3,500 species have been described. Many classifications have been proposed for Blattaria. Substantial phylogenetic work on cockroaches has been initiated by McKittrick (1964), who compared 85 genera of blattarians, referring mainly to complex morphological structures such as the female and male genitalia (partly including the musculature) and the proventriculus (a part of the foregut), and also to a few biological traits such as reproductive biology and oviposition behavior. She proposed a novel classification into Blattoidea (= Blattidae + Cryptocercidae) and Blaberoidea (= Polyphagidae + Blattellidae + Blaberidae). McKittrick & Mackerras (1965) further studied Tryonicinae and assigned it to Blattidae. Roth (1967, 1970) made a comprehensive comparison of the structure and rotation of the ootheca, and interpreted the data in the context of McKittrick’s system. In several older papers (but not in McKittrick 1964) the Isoptera (termites) were suspected to be a taxon subordinate in cockroaches, i.e., to be highly derived eusocial cockroaches (e.g., Cleveland et al. 1934 based on comparisons of the life history, brood care and intestinal flagellate fauna).

Phylogenetic work in recent years, based on morphology and DNA sequences (or both), revealed at least seven principal lineages of “Blattaria”: Cryptocercidae + Isoptera, Blattidae, Lamproblattidae, Tryonicidae, Polyphagidae (= Corydiidae), Nocticolidae, and Blaberoidea (including only Blaberidae and, paraphyletic with regard to the former, Blattellidae (= Ectobiidae)) (Klass 1997; Klass & Meier 2006; Lo et al. 2007; Inward et al. 2007; Pellens et al. 2007; Ware et al. 2008; Klass et al. 2008; Murienne 2009; Beccaloni & Eggleton 2011; Djernæs et al. 2012, submitted). The subordinate position of termites in “Blattaria” was consistently confirmed, and the monophyletic group including both is usually called “Blattodea”. However, the relationships among these seven major lineages have remained highly controversial, as seen from the aforementioned papers. For reconstruction of the phylogeny in Blattodea and for a closer understanding of the evolution of the life history of this group, the accumulation of knowledge on the biology of each major lineage of blattodeans is strongly desired. In the present study, we describe the reproductive biology and postembryonic development of a Japanese polyphagid, *Eucorydia yasumatsui* Asahina, 1971 (Fig. 1).

2. Materials and methods

2.1. Collection and rearing

Eleven larvae of *Eucorydia yasumatsui* (Fig. 1A−C), which is endemic to the Yaeyama Islands of Okinawa Prefecture, were collected in Komi, Iriomote Island, Taketomi, Okinawa Prefecture in April 2008. These larvae were kept in plastic cases (14 cm in diameter and 6.5 cm high) with a moistened soil bottom at room temperature (18−24°C) and fed on grained food for goldfish (Hikari-Flake Goldfish; Kyorin), a grained chlorella tablet (Chlorella; Fancl), a grained beer yeast tablet (EBIOS; Asahi Food & Healthcare), and a grained balanced food (CalorieMate; Otsuka Pharmaceutical) at the ratio of 9 : 3 : 3 : 1, respectively. From wild-caught larvae, we succeeded in establishing a culture of *E. yasumatsui* (Fujita et al. 2011).

2.2. Observation of postembryonic development

We reared 105 hatched larvae separately in 8 × 5 × 2 cm plastic cases at room temperature (18−24°C). To count the total number of larval instars, it was checked every few days whether each larva had molted, as evidenced by exuvia.

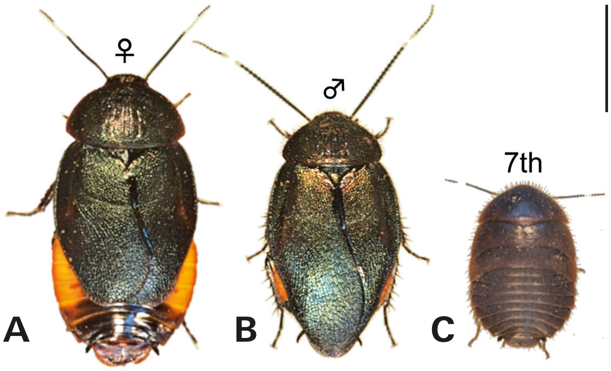

Fig. 1. Female (**A**), male (**B**) and 7th instar larva (**C**) of *Eucorydia yasumatsui* Asahina, 1971, from Fujita et al. (2011: fig. 1). Scale bar = 0.5 cm.

For observation of the external morphology of each instar, larvae were anesthetized by CO_2 and photographed using a Leica MZ12 stereomicroscope equipped with an Olympus E-620 digital camera. We measured the body length on the photographs.

Some larvae of each instar were fixed in 70% ethyl alcohol for detailed observations and measurements. For sketches of the external morphology of each instar, we used a Leica MZ12 equipped with a drawing attachment. The following measurements were made for each instar: (1) pronotum length along median line and (2) greatest width, (3) metathoracic tergal length along median line and (4) along wing bud length (i.e., metathoracic paranotal length), (5) the total number of annuli of the antennal flagellum (a in Fig. 11A), (6) the number of annuli in the white zone (b in Fig. 11A), (7) the percentage of the number of annuli in the white zone relative to the total number of annuli (%), (8) the position of the white zone (center of the zone) relative to the total flagellar length from the flagellum base (%), and (9) the number of annuli distal to the white zone (c in Fig. 11A).

A 2nd instar larva just before molting was fixed in 70% ethyl alcohol, and its antenna was removed and processed into 2-μm-thick methacrylate sections according to Machida et al. (1994a,b). Sections were stained with 1% Delafield hematoxylin, 0.5% eosin G for 1h and a 0.5% fast green FCF 100% ethyl alcohol solution for 1 min.

3. Results and discussion

3.1. Mating behavior

On encountering a female, the male rushes to her, and then chases her, frequently touching her with his antennae. After chasing her for a short time, the female stops walking, and the male turns 180° behind her, taking an opposite-linear position to the female, and they initiate "tail-to-tail" copulation, which lasts for a few hours (Fig. 2A,B). No tergal gland is formed in the males of *Eucorydia yasumatsui* (Fig. 4A,B), and the partners never take positions in the same direction during the precopulation stage with the female sitting on the back of the partner, as is often observed in other cockroaches. Fig. 2B clearly shows that the female's subgenital plate covers that of the male during copulation.

Data on mating behavior are so far available only for members of the lineages Blattidae (mainly *Periplaneta*) (Roth & Willis 1952; Barth 1970; Kitamura & Takahashi 1973), Cryptocercidae (Nalepa 1988), Blaberoidea (*Byrsotria*, *Blaberus*, *Leucophaea*, *Blattella*, *Pycnoscelus*, *Gromphadorhina*, *Panchlora* etc.) (Roth & Willis 1952, 1954, 1958; Barth 1961; Willis 1966; Roth & Barth 1967; Barth 1968), and Polyphagidae (Livingstone & Ramani 1978). It is well known that most cockroaches show elaborate mating behavior, which is composed of: (1) male raising his wings (if present) in front of the female; (2) female stepping slightly onto the back of the male and feeding on the tergal-gland secretion produced by the male, with the male usually simultaneously grasping the female's crescent sclerite, composed of the basivalvulae and interbasivalvula, with his left genital hook; then (3) the male moving posterior and clasping the female's caudal end with his phallomeres; and (4) finally the pair taking a tail-to-tail position. In the pycnosceline blaberid *Pycnoscelus surinamensis* (Linnaeus, 1758) (= *P. indicus*) (Roth & Barth 1967), the male is attracted by the female pheromone and tries to mount the female. If the female is receptive, she raises her caudal end towards the male, and the male clasps the female's caudal end with his genitalia. Then, the male dismounts from the female, and the pair takes a tail-to-tail position.

Compared to the above-mentioned cases, the mating behaviors of some blaberids and the polyphagid *Therea petiveriana* (Linnaeus, 1758) are less elaborate. In the oxyhaloine blaberid *Gromphadorhina portentosa* (Schaum, 1853) (Barth 1968), on encountering the female, the male touches her body with his antennae and starts antennal fencing with the female. Subsequently, the female and male mutually stroke their bodies with their antennae, and the male walks around the female, hissing, produced by an explosion of air from abdominal spiracle II. Finally, the male orients so that his abdominal tip is opposed to that of the female and achieves a genital connection merely by backing up to the female. In the panchlorine blaberid *Panchlora irrorata* Hebard, 1925, on contact, both the female and male engage in antennal fencing. Then, the male moves close to the female's side and rocks sideways periodically. After a period of rocking, the male turns his body 180º behind her and copulates (Willis 1966). The process of antennal fencing and male sideways rocking is lacking in *Panchlora nivea* (Linnaeus, 1758) (Roth & Willis 1958). In the polyphagid *T. petiveriana* (Livingstone & Ramani 1978), the male rushes to the female. Then he starts to chase her, touching her with his antennae, and the excited male repeats his characteristic vertical jerks, touching the female's cerci with his antennae. Finally, the male turns 180° behind her, taking an opposite linear position to the female, and they initiate "tail-to-tail" copulation. In spite of the male's activeness, the female is always passive, without any positive actions towards her counterpart. The mating behavior of *Eucorydia yasumatsui* revealed herein may well resemble that in panchlorine and oxyhaloine blaberids and in *T. petiveriana* in that the female is always passive, without any positive actions towards her counterpart.

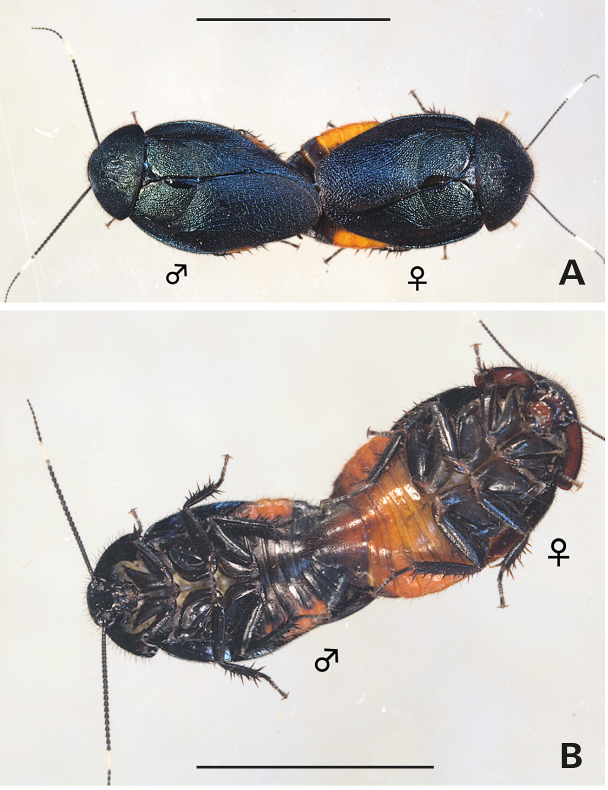

Fig. 2. Mating of *Eucorydia yasumatsui*. Dorsal (**A**) and ventral (**B**) views. Females and males take a linear "tail-to-tail" position when they copulate. Scale bars = 1 cm.

As for Polyphagidae, the males of *Melestora* and *Compsodes* have been reported to have a tergal gland on abdominal tergum IV (Hebard 1921; Princis 1952; Roth 1969), while no tergal gland is found in *Therea* (Livingstone & Ramani 1978) and *Eucorydia* (present study). As mentioned, the latter two genera without tergal glands show simple mating behavior. Careful examinations of the mating behaviors of polyphagids with tergal glands are desired.

3.2. Structure, deposition and handling of ootheca

A few days after copulation, the females of *Eucorydia yasumatsui* produce their oothecae (Fig. 3A,B). The brownish ootheca bears a well-developed, serrated keel

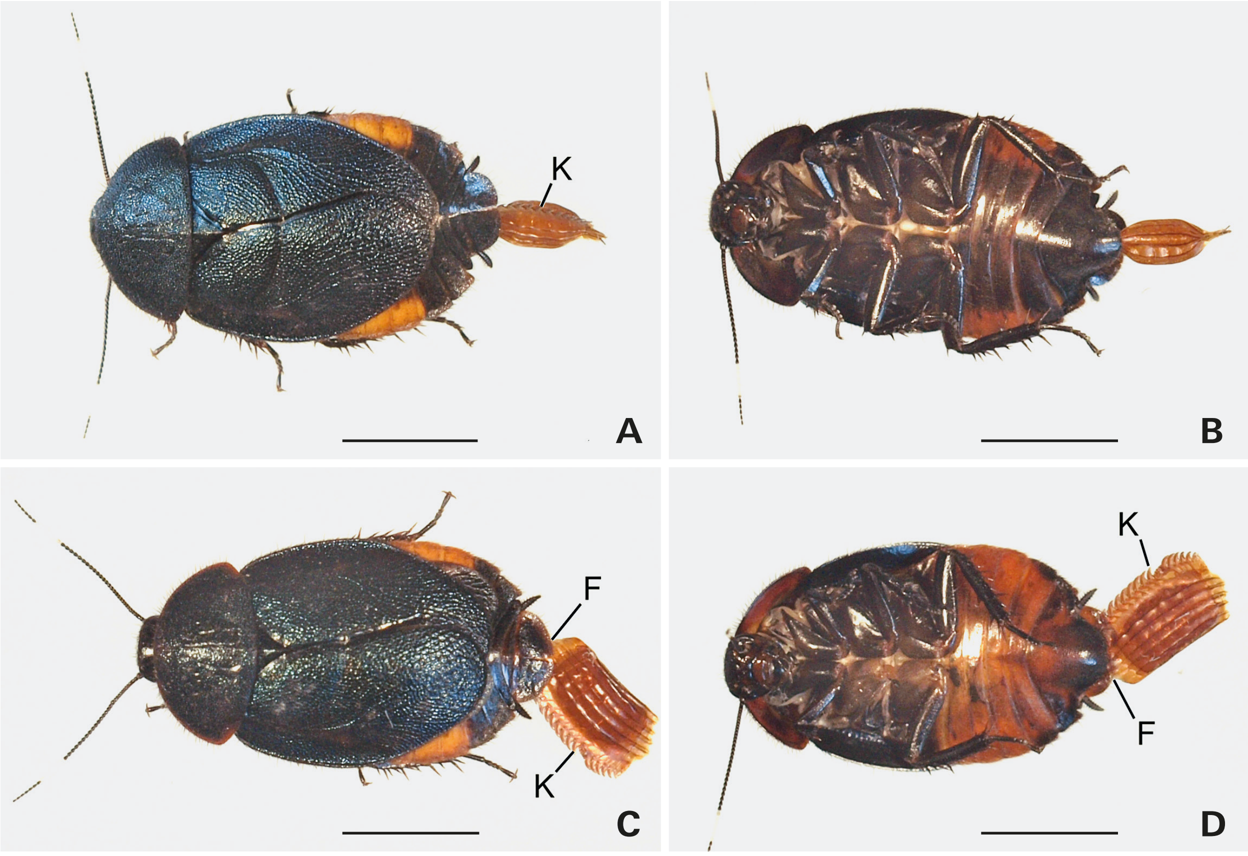

Fig. 3. Oviposition of *Eucorydia yasumatsui*. Female deposits the ootheca with its keel (K) upward, dorsal (**A**) and ventral (**B**) views. The ootheca is then rotated by 90° with its flange (F) grasped by the caudal end of the female, dorsal (**C**) and ventral (**D**) views. Scale bars = 5 mm.

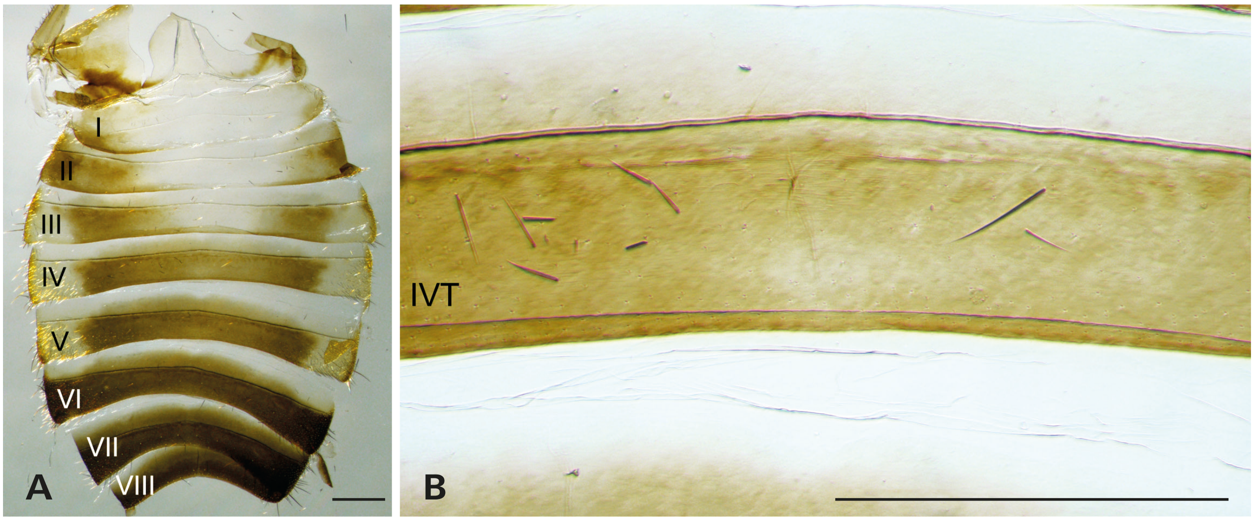

Fig. 4. Abdominal terga of an *Eucorydia yasumatsui* male. **A**: I^st^ to VIII^th^ abdominal terga. No tergal gland is found. **B**: Enlargement of the IV abdominal tergum. The tergal gland reported for polyphagids are present exclusively in the IV abdominal tergum. Scale bars = 1 mm.

along its dorsal median line, 5 longitudinal ridges running symmetrically on both lateral sides and a triangular flange on its anterior end, which is grasped with the female's caudal end while she carries the ootheca (Fig. 5A–C). About 30 respiratory canals are found on the inner side of each serration of the keel, and they open into a common respiratory canal, which leads to the egg chamber (Fig. 5D,E). The ootheca contains 5–10 eggs (8.1 ± 1.3, n = 20), which are arranged in 2 rows in the ootheca. The dorsoventral axis of the ootheca corresponds to the anteroposterior axis of the eggs contained, and the eggs are in the ootheca with their dorsal side facing to the oothecal wall. The ovary of *E. yasumatsui* is composed of 4 pairs of ovarioles (data not shown).

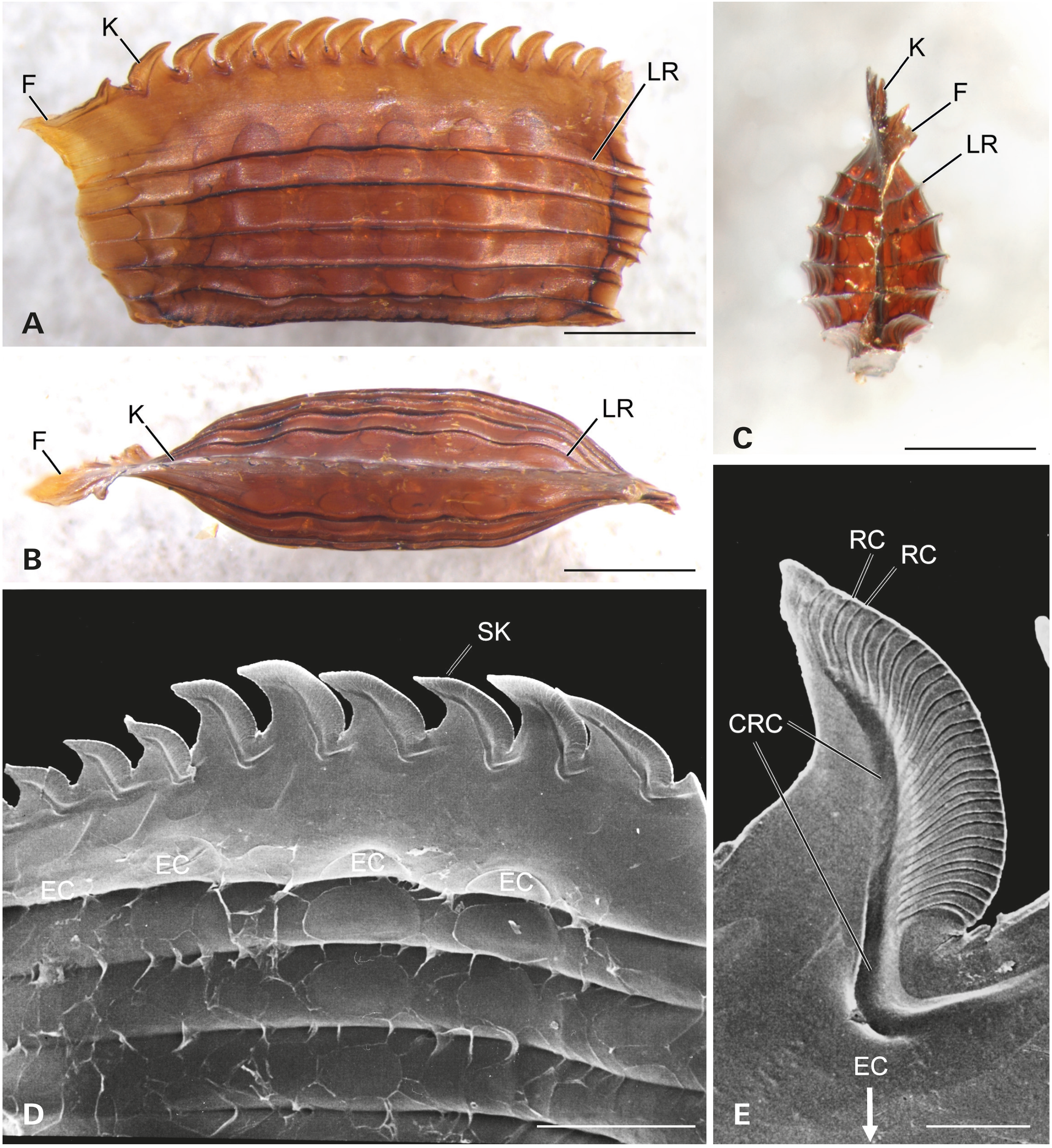

Fig. 5. Oothecae of *Eucorydia yasumatsui*. **A**–**C**: Lateral (**A**), dorsal (**B**) and anterior (**C**) views of ootheca. F = flange; K = keel; LR = longitudinal ridge. **D**: SEM of inner surface of oothecae. EC = egg chamber, SK = serration of keel. **E**: SEM of inner surface of keel serration. The respiratory canals (RC) come into a common respiratory canal (CRC), which leads to the egg chamber (EC). Scale bars = A–C: 1 mm; D: 500 µm; E: 100 µm.

In cockroaches, the number of eggs varies according to species, from 6 to about 50 (Hinton 1981). Roth (1968) summarized the number of eggs per ootheca, i.e., 8–15 in *Therea petiveriana*, 7–13 in *Polyphaga aegyptiaca* (Linnaeus, 1758), and 6 in *Arenivaga* (*Psammoblatta*) *cerverae* (Bolívar, 1886). We may say that in polyphagids the number of eggs per ootheca is fairly low, i.e., 5–10, including *Eucorydia yasumatsui* as revealed herein.

McKittrick (1964) suggested that there are two types of keels in Polyphagidae, i.e., the serrated (e.g., *Polyphaga aegyptiaca* and *Arenivaga* (*Psammoblatta*) *cerverae*) and smooth (e.g., *Arenivaga* (*Arenivaga*) spp., *Homoeogamia mexicana* Burmeister, 1838, and *Therea petiveriana*) types, and the keel structure of *Eucorydia yasumatsui* falls in the former type. Roth (1968) examined and described the respiratory system inside the keel of some polyphagid species. In *P. aegyptiaca,* each tooth of the keel has numerous canals, which open externally and run down to a common respiratory canal leading into a large egg chamber containing eggs (see Roth 1968: fig. 60).

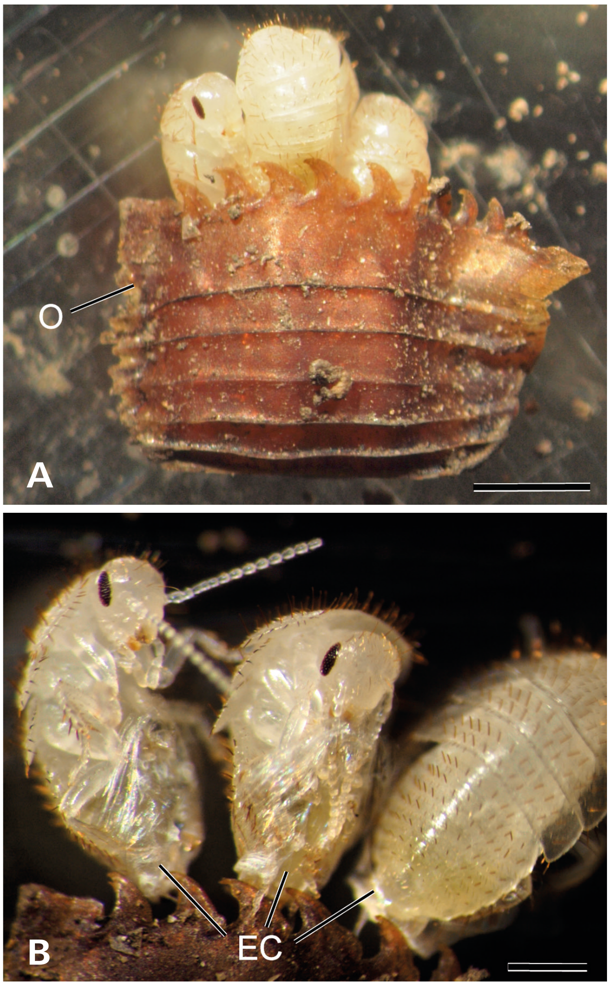

Fig. 6. Hatching of *Eucorydia yasumatsui*. Prelarvae during escape from the ootheca (O) (**A**) and shedding the embryonic cuticle (EC) to become 1st instar larvae (**B**). Scale bars = A: 1 mm; B: 0.5 mm.

The respiratory system of *P. aegyptiaca* closely resembles that of *E. yasumatsui* (present study). On the other hand, *A.* (*P.*) *cerverae* differs from *E. yasumatsui* in that each tooth has an opening at its tip, and just below each opening is an elongated air cell, which simply opens into the space above the egg.

The ootheca of *E. yasumatsui*, which was formed in the mother's vestibulum (space above the subgenital plate, see Klass 1998: fig. 1), emerges from her caudal end, with its keel upwards (Fig. 3A,B). Several hours later, she rotates the ootheca clockwise by 90° (n = 15) viewed from the female's side, so that it takes a horizontal position (Fig. 3C,D). The flange is less frequently straightened, but is basically bent to either side (Fig. 5B,C). After rotation, she carries the ootheca for a few days, maintaining this horizontal position, and then deposits it on the ground. The ootheca is ever exposed, never hidden within the mother's vestibulum.

McKittrick (1964) and Roth (1967, 1970) provided important data for comparison: In all examined cockroaches, the ootheca is produced in the vestibulum and the completed parts are gradually shifted out posteriorly, held in a keel-up position. In most cockroach lineages, the ootheca is simply dropped when completed or a little later. In the examined Polyphagidae and advanced Blaberoidea (essentially Blattellinae, Nyctiborinae, Ectobiidae, and Blaberidae), however, the ootheca is rotated by 90° (with the keel directed laterally), and the female continues to carry it. In the Blaberoidea concerned, at least the anterior part of the rotated ootheca (containing some of the eggs) is deeply sunken in the vestibulum, which allows the mother to supply the ootheca with water; in some Blattellinae and all Blaberidae it is even more or less completely retracted into an anteriorly expanded ventral cavity of the vestibulum (brood sac), which allows the transfer of nutrients from mother to ootheca (the basis for ovoviviparity or even viviparity).

In the rotating Polyphagidae, which are exclusively oviparous, the female holds the flange of the ootheca with her caudal end, no parts of the ootheca being harbored in the vestibulum. In regard to the length of the flange and rotation of the ootheca, two types are distinguished in Polyphagidae: (1) in e.g., *Arenivaga* (*Psammoblatta*) *cerverae* and *Polyphaga aegyptiaca*, the ootheca has a long flange or "handle," which is held vertically between the paraprocts, and the female does not rotate the ootheca; (2) in e.g., *Arenivaga* (*Arenivaga*) spp. and *Therea petiveriana*, the flange is relatively shorter, and the female rotates the ootheca. We found that *E. yasumatsui* also represents the latter type. However, as mentioned above, *E. yasumatsui* shares similarities in the respiratory system with *P. aegyptiaca*, which represents the former type. The issue regarding the similarities between *E. yasumatsui* and *P. aegyptiaca* remains a subject to be addressed in the future.

3.3. Postembryonic development

3.3.1. Hatching and molting

The entire keel splits apart, and all larvae, which have no egg tooth, synchronously hatch from the ootheca. First, prelarvae, covered with a thin, transparent embryonic cuticle, tear the chorion and emerge from the seam along the midline of the keel by peristaltic movement (Fig. 6A). Subsequently, prelarvae shed the embryonic cuticle and become 1st instar larvae (Fig. 6B), which soon leave the ootheca.

At molting, a longitudinal mid-dorsal fissure occurs in the thoracic exoskeleton, reaching the head to bifurcate, and the next instar emerges, basically the same as in other insects (Fig. 7A,B).

3.3.2. Number of larval instars

We separately reared 105 hatched larvae in a plastic case at room temperature (18−24°C), and raised 22 individuals to adulthood (9 females and 13 males). In females,

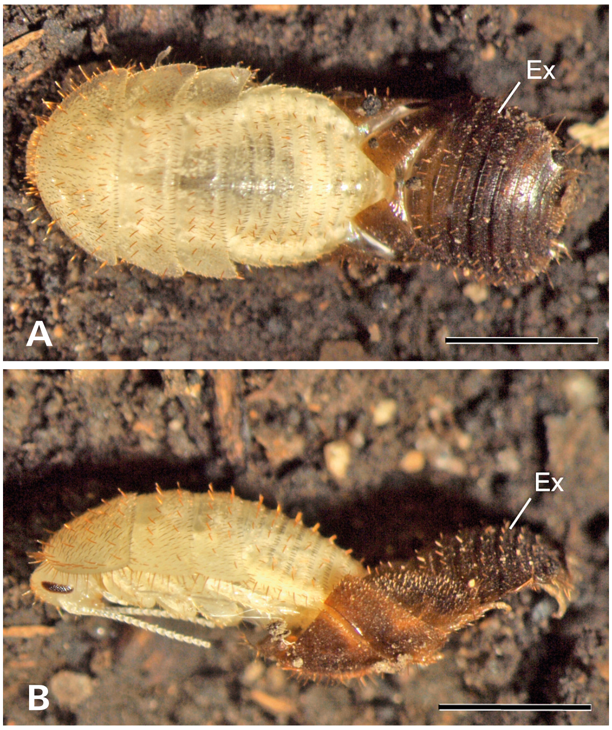

Fig. 7. Molting of *Eucorydia yasumatsui*. Molting of a 5th instar larva, viewed from dorsal (**A**) and lateral (**B**). Ex = exuvia. Scale bars = 5 mm.

the number of larval instars was 9 in 8 individuals, and 10 in the other, whereas in males it was 8 in 6 individuals, and 9 in 7 individuals. Table 1 shows the life histories of the female and male individuals examined. The duration (with mean and SD) of the larval period (i.e., from hatching of the ootheca to the emergence of adults) was 591 – 679 days (625 ± 25 days; n = 9) in females, and 562 – 645 days (608 ± 24 days; n = 13) in males.

Esperk et al. (2007a) reviewed published case studies on the number of larval instars in insects, with the following numbers for cockroaches: Blattidae, ranging from 6 – 8 instars in *Eurycotis floridana* (Walker, 1868) (Willis et al. 1958) to 9 – 14 instars in *Periplaneta americana* (Linnaeus, 1758) (Willis et al. 1958; Mira & Raubenheimer 2002); Cryptocercidae, 7 instars in *Cryptocercus punctulatus* Scudder, 1862 (Cleveland 1934); Blattellidae, ranging from 3 – 5 in *Diploptera punctata* (Eschscholtz, 1822) (Willis et al. 1958; Woodhead & Paulson 1983; Holbrook & Schal 1998) to 8 – 10 in *Pycnoscelus surinamensis* (Willis et al. 1958); for more details refer to Esperk et al. (2007a). There has been no information on the number of larval instars in Polyphagidae, and the present study on *Eucorydia yasumatsui* provides the first data.

The number of larval instars in insects is often put into a phylogenetic context. In Dermaptera, it was suggested that larger and smaller numbers of larval instars represent the plesiomorphic and apomorphic states, respectively (Matzke & Klass 2005; Shimizu & Machida 2011). In cockroaches, as listed above, the total number of larval instars considerably varies from around five to a dozen, but without any pattern distinguishing systematic groups; in this sense, the markedly small number of 3 – 5 in *Diploptera punctata* is in strong contrast to up to 10 in its blaberid relative *Pycnoscelus surinamensis*. This indicates that the number of larval instars in cockroaches is of little phylogenetic relevance. The number in *E. yasumatsui* falls in the range evident from the above-mentioned examples.

3.3.3. Measurements and changes of external features

Fig. 8A and B are series of images of female and male instars, respectively: every photo shows the same female or male from the 22 individuals raised to adulthood (see 3.3.2.), except for those of the 8th instar female and 7th instar male, which were supplemented by specimens dipped in alcohol: due to a technical problem we failed to obtain any (or sufficient) data on the 7th and/or 8th instar. It is known that individuals gradually increase in size according to the instar. A photographic record of growth was also made for the other 20 individuals. Body parts (pronotum, metathorax and antennal annuli) were measured and counted in dipped samples for each instar. Based on the information from these photographs and direct observations and measurements of 65 dipped samples from the 105 individuals selected from captive breeding, the postembryonic development of *Eucorydia yasumatsui* was followed and examined in detail. It was revealed that sexes can be distinguished from the 3rd instar according to differences in postabdominal structures.

1. Coloration. The larvae are brownish. The adults become blackish, and the pronotum and forewings (tegmina) turn metallic dark blue. The adults have orange-colored areas on the abdomen, but their extension is highly variable among individuals. Basically, there is a pair of orange areas in the middle abdominal segments, as shown for the female in Fig. 3B and for the male in Figs. 2B and 8B, but in the extreme, almost the entire abdomen is orange, as shown for the females in Figs. 2B, 3D and 8A.

2. Body length. The body lengths of each instar and each sex were measured using the photographic records of the 22 individuals raised to adulthood (Table 1). Data on the 7th and/or 8th instar were supplemented using dipped specimens, see above (Table 2).

The growth changes of body length in females and males with different numbers of larval instars are shown in Fig. 9A – D: females with 9 or 10 instars, and males with 8 or 9 instars. In all four groups, the growth rate of the body length seemed to increase up to the instar before the penultimate larva, but to decrease from the last one or two larval to adult stages, as clearly shown in Fig. 9B,C. This fall of the growth rate may be because energy consumption gradually changes from body enlargement to internal reproductive maturation in the last phase of

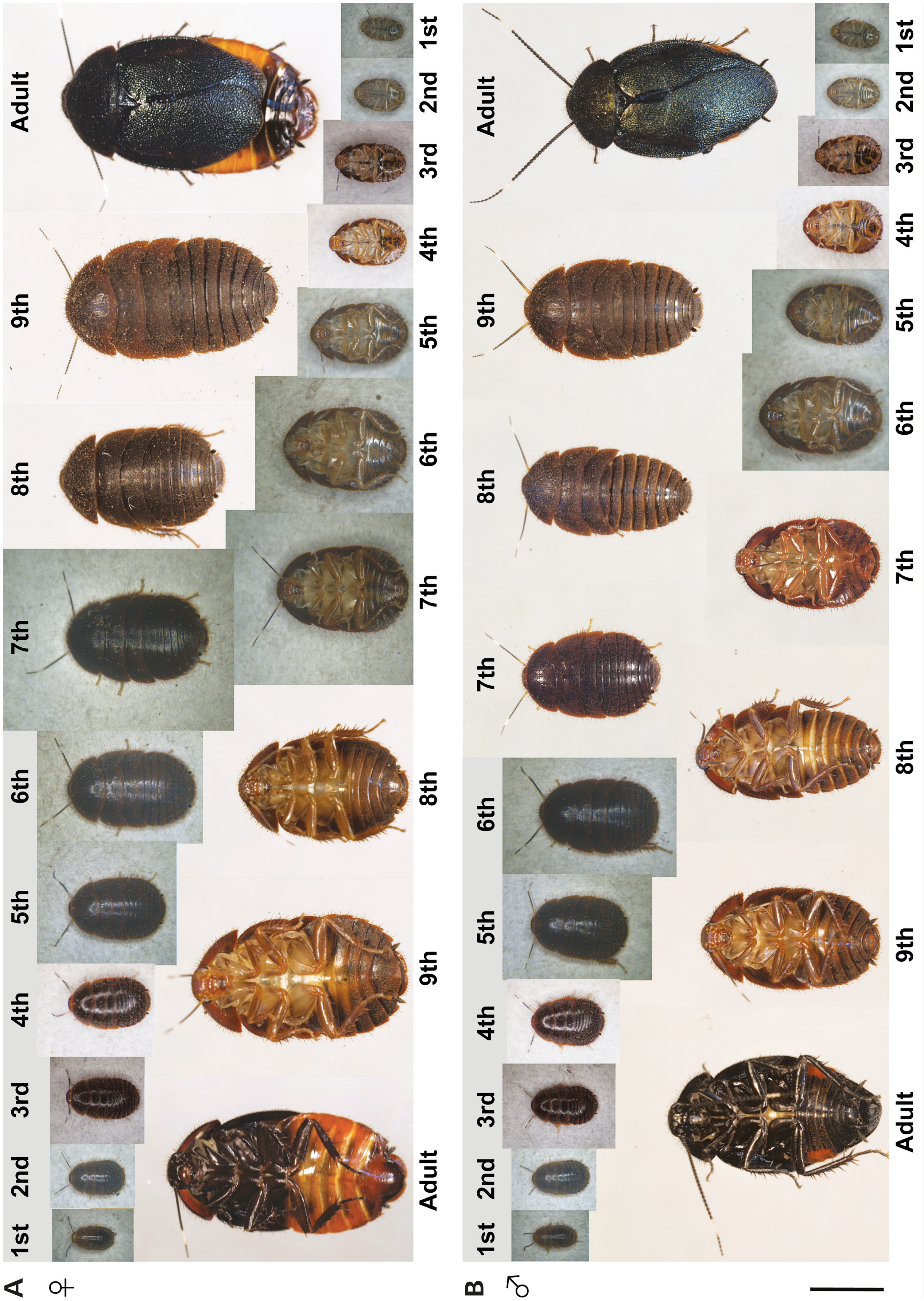

Fig. 8. Photographic records of postembryonic developmental stages of *Eucorydia yasumatsui*, following the 1st to 9th instars and adults. Basically the same female (**A**) and male (**B**) were photographed, except for the 8th instar female larva and 7th instar male, which were supplemented by dipped specimens. Scale bar = 5 mm.

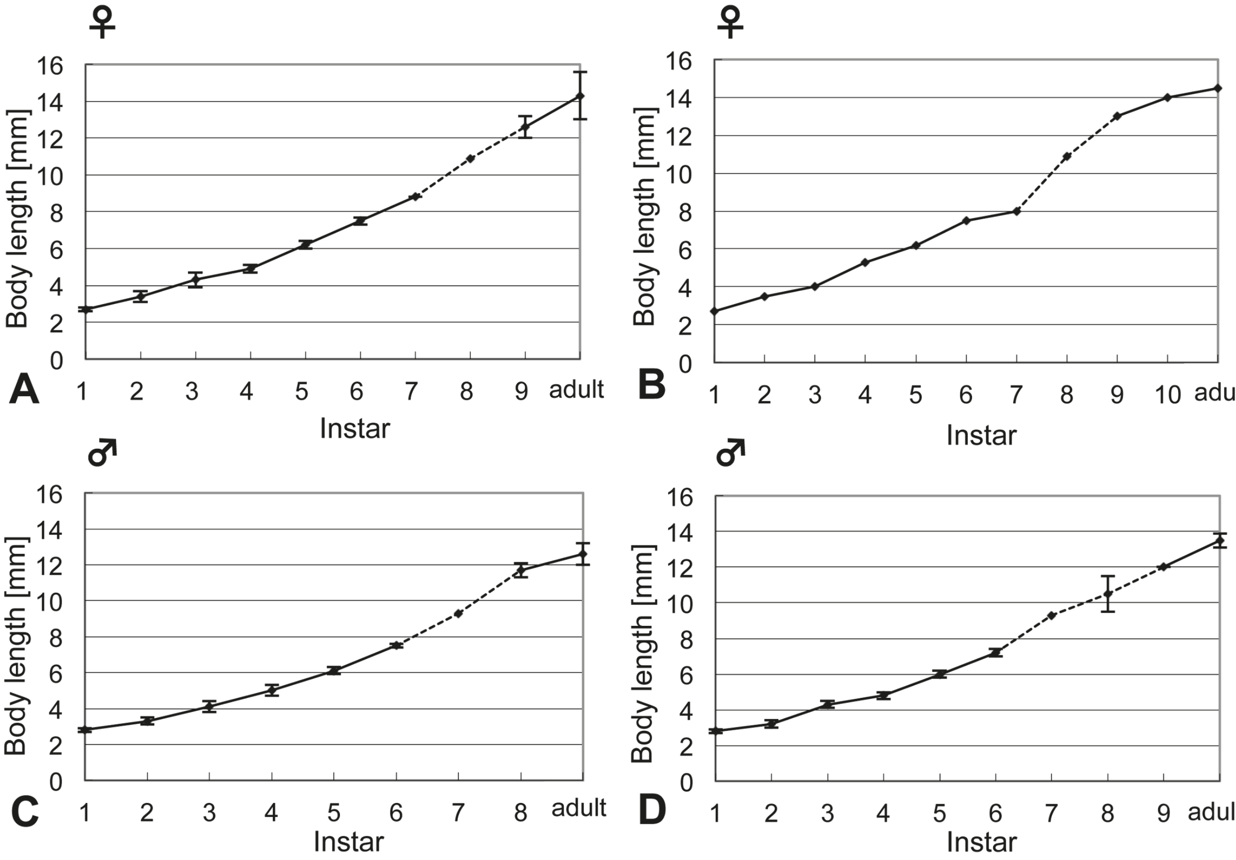

Fig. 9. Growth changes of body length in both sexes during postembryonic development of *Eucorydia yasumatsui*. **A**: Females with 9 larval instars. **B**: A female with 10 larval instars. **C**: Males with 8 larval instars. **D**: Males with 9 larval instars. Measurements were obtained from photographic data of larvae and adults (see Table 1). The data on the 7th and/or 8th instar of both sexes are supplemented by dipped specimens, connected by broken lines in each graph (see Table 2).

postembryonic development. Comparing the body sizes of adults with different instar numbers, no significant differences were found between them: see Table 1 and also compare Fig. 9A and 9B for females and Fig. 9C and 9D for males.

As described, in *Eucorydia yasumatsui*, the number of larval instars is 9 or 10 in females and 8 or 9 in males. As shown in Table 1, females and males are about 14.5 – 15 mm and 13 – 14 mm in body length, respectively. Esperk et al. (2007b) reviewed the sexual size dimorphism in insects related to the total number of instars using published case studies including several cockroach species (Blaberidae: *Diploptera punctata*, *Leucophaea maderae*, *Nauphoeta cinerea*, *Opisthoplatia orientalis*; Blattellidae: *Blattella germanica*, *B. vaga*; Blattidae: *Blatta orientalis*). According to them, at least concerning cockroaches, females have a larger number of instars and larger body sizes than males. Their generalization concerning the sexual size dimorphism in cockroaches applies to *E. yasumatsui*.

3. Pronotum. Both the length and width of the pronotum increased along with progressive growth, and the length to width ratio (L/W) was approximately 0.4 – 0.5 (Table 3), without significant changes during postembryonic development.

4. Wing buds. As shown in Fig. 8, the posterior dorsal margins of pterothoracic segments of larvae are concave. Concavity increased gradually with successive instars (Fig. 8). This may be related to the development of the paranotal region or wing buds. For documentation of the growth of wing buds, we measured the lengths of the mesonotum in the median (TL) and paranotal (lateral, including the wing bud) regions (PL) in each instar of both sexes (Table 4). Both TL and PL increased with progressive growth as well as the PL/TL ratio, and the increases of PL and PL/TL were marked, seemingly due to the growth of wing buds. However, even PL and PL/TL were not differentiated well enough to distinguish successive instars.

Fig. 10 shows the paranotal regions of the pterothorax of a female larva of the final instar (in this case, the 9th instar), in which newly formed venation is clearly observed as light-colored branchings.

5. Antennae. The number of flagellomeres (annuli) increases during development. We counted the number of annuli of the entire flagellum (a in Fig. 11A), of the white zone (appearing first in the 2nd instar: b in Fig. 11A), and of the part distal to the white zone (c in Fig. 11A) for each instar of both sexes (Table 5). The flagellum of the 1st and 2nd instars comprises 11 annuli. An addition

Table 1. Duration of each instar and change of body length in 9 females and 13 males of *Eucorydia yasumatsui*. The data of body length marked by an asterisk (*) were supplemented from alcohol-dipped specimens (see text and Table 2). Data are in 4 groups according to the sex and total instar number: A, B, C and D are females with 9 larval instars, female with 10 larval instars, males with 8 larval instars and males with 9 larval instars, respectively. ND = no data.

	Sex	Individual	1st instar		2nd instar		3rd instar		4th instar		5th instar		6th instar		7th instar		8th instar		9th instar		Adult	
			Period of instar (day)	Body length (mm)	Period of instar (day)	Body length (mm)	Period of instar (day)	Body length (mm)	Period of instar (day)	Body length (mm)	Period of instar (day)	Body length (mm)	Period of instar (day)	Body length (mm)	Period of instar (day)	Body length (mm)	Period of instar (day)	Body length (mm)	Period of instar (day)	Body length (mm)	Period of instar (day)	Body length (mm)
A	♀	**1**	37	2.6	30	3.0	29	4.3	36	4.7	64	5.9	102	7.6	113	ND	84	ND	104	13.0	—	ND
		2	34	2.7	29	3.4	37	4.4	35	5.0	104	6.5	150	7.6	77	ND	92	ND	121	12.0	—	ND
		3	39	2.6	25	3.1	33	4.0	33	5.2	72	5.9	139	7.5	101	ND	64	ND	152	12.5	—	ND
		4	34	3.0	25	3.4	34	4.4	31	4.7	53	6.2	135	7.6	95	ND	100	ND	108	13.0	—	15.0
		5	30	2.9	32	3.5	38	4.3	33	5.1	51	6.1	72	7.4	138	8.8	104	ND	144	13.0	—	ND
		6	26	2.7	32	3.4	27	3.7	40	4.6	72	6.3	116	7.1	82	ND	65	ND	131	12.0	—	15.0
		7	29	2.8	24	4.1	25	4.1	49	5.1	108	6.4	120	7.3	79	ND	57	ND	132	12.0	—	12.0
		8	31	2.6	35	3.2	32	4.9	35	4.8	64	6.1	108	7.7	110	ND	94	ND	111	13.5	—	15.0
		mean ± SD	32.5 ± 4.3	2.7 ± 0.2	29.0 ± 4.0	3.4 ± 0.3	32.0 ± 5.0	4.3 ± 0.4	37.0 ± 6.0	4.9 ± 0.2	74.0 ± 21.0	6.2 ± 0.2	114.0 ± 23.0	7.5 ± 0.2	99.0 ± 21.0	8.8	83.0 ± 18.0	10.9 ± 0.4*	125.0 ± 17.0	12.6 ± 0.6	—	14.3 ± 1.5

	Sex	Individual	1st instar		2nd instar		3rd instar		4th instar		5th instar		6th instar		7th instar		8th instar		9th instar		10th instar		Adult	
			Period of instar (day)	Body length (mm)	Period of instar (day)	Body length (mm)	Period of instar (day)	Body length (mm)	Period of instar (day)	Body length (mm)	Period of instar (day)	Body length (mm)	Period of instar (day)	Body length (mm)	Period of instar (day)	Body length (mm)	Period of instar (day)	Body length (mm)	Period of instar (day)	Body length (mm)	Period of instar (day)	Body length (mm)	Period of instar (day)	Body length (mm)
B	♀	**1**	33	2.7	28	3.5	43	4.0	33	5.3	59	6.2	93	7.5	99	8.0	82	10.9 ± 0.4*	71	13.0	88	14.0	—	14.5

	Sex	Individual	1st instar		2nd instar		3rd instar		4th instar		5th instar		6th instar		7th instar		8th instar		Adult	
			Period of instar (day)	Body length (mm)	Period of instar (day)	Body length (mm)	Period of instar (day)	Body length (mm)	Period of instar (day)	Body length (mm)	Period of instar (day)	Body length (mm)	Period of instar (day)	Body length (mm)	Period of instar (day)	Body length (mm)	Period of instar (day)	Body length (mm)	Period of instar (day)	Body length (mm)
C	♂	**1**	37	2.8	26	3.4	34	4.2	33	4.6	58	5.8	109	7.5	182	ND	116	12.0	—	13.0
		2	31	2.6	25	3.1	38	4.3	35	4.8	102	6.1	137	7.3	91	ND	136	12.0	—	12.0
		3	34	2.9	27	3.0	37	4.5	34	5.5	162	6.5	100	ND	97	ND	151	ND	—	11.5
		4	26	2.7	32	3.4	30	3.9	53	5.0	218	6.1	94	ND	56	ND	83	11.5	—	13.0
		5	ND	2.7	ND	ND	25	3.8	33	5.2	65	6.2	150	7.5	100	ND	138	12.0	—	13.0
		6	29	3.0	28	3.4	40	4.1	33	4.9	ND	6.0	ND	7.6	91	ND	144	11.0	—	13.0
		mean ± SD	31.4 ± 4.3	2.8 ± 0.1	27.6 ± 2.7	3.3 ± 0.2	34.0 ± 5.6	4.1 ± 0.3	36.8 ± 8.0	5.0 ± 0.3	121.0 ± 68.1	6.1 ± 0.2	118.0 ± 24.3	7.5 ± 0.1	112.2 ± 39.2	9.3 ± 0.3*	137.0 ± 13.1	11.7 ± 0.4	—	12.6 ± 0.7

Table 1 continued.

	Sex	Individual	1st instar		2nd instar		3rd instar		4th instar		5th instar		6th instar		7th instar		8th instar		9th instar		Adult	
			Period of instar (day)	Body length (mm)	Period of instar (day)	Body length (mm)	Period of instar (day)	Body length (mm)	Period of instar (day)	Body length (mm)	Period of instar (day)	Body length (mm)	Period of instar (day)	Body length (mm)	Period of instar (day)	Body length (mm)	Period of instar (day)	Body length (mm)	Period of instar (day)	Body length (mm)	Period of instar (day)	Body length (mm)
D	♂	**1**	36	3.0	26	3.3	29	4.5	39	5.0	58	6.3	128	7.5	105	ND	74	ND	95	12.0	—	13.0
		2	34	2.7	24	3.3	32	ND	34	5.1	64	6.2	131	7.3	100	ND	72	ND	105	12.0	—	13.0
		3	31	2.8	29	3.0	32	ND	33	4.8	50	5.9	150	6.9	125	ND	52	ND	118	12.0	—	13.5
		4	34	2.7	36	3.2	29	4.2	37	4.6	56	5.9	150	7.1	106	ND	49	ND	148	12.0	—	ND
		5	31	2.6	25	3.3	42	3.9	28	5.0	57	5.9	128	7.2	95	ND	76	ND	133	12.0	—	14.0
		6	26	2.8	34	3.0	32	4.3	28	4.5	50	5.7	126	6.9	105	ND	74	ND	155	12.0	—	14.0
		7	28	3.0	28	3.4	39	4.4	30	4.9	52	6.1	141	7.4	97	ND	88	ND	135	12.0	—	ND
		mean ± SD	31.4 ± 3.6	2.8 ± 0.2	28.9 ± 4.6	3.2 ± 0.2	33.6 ± 5.0	4.3 ± 0.2	32.7 ± 4.3	4.8 ± 0.2	55.3 ± 5.1	6.0 ± 0.2	136.3 ± 10.6	7.2 ± 0.2	104.7 ± 9.9	9.3 ± 0.3*	69.3 ± 13.9	10.5 ± 1.0*	123.6 ± 18.5	12.0 ± 0.0	—	13.5 ± 0.5

Table 2. Body length of female 8th instar and male 7th and 8th instar larvae of *Eucorydia yasumatsui*, supplemented by alcohol-dipped specimens.

	Male 7th instar (n = 4)	**Female** 8th instar (n = 2)	**Male** 8th instar (n = 3)
Range of body length [mm]	9 – 9.7	10.6 – 11.1	9.4 – 11.1
Mean ± SD	9.3 ± 0.3	10.9 ± 0.4	10.5 ± 1.0

of annuli occurs from the 2nd instar molting onwards, increasing up to ca. 40 in adults. The number of flagellar annuli increases by division of the basalmost annulus in the flagellum (meriston) and of the immediately following one, which is called the "meristal annulus" from the 3rd instar on. From the meriston, 1 to several new annuli are added at molt (Fig. 11B). The meristal annulus divides into 2 annuli (doublets) in subsequent moltings (Fig. 11B): the annulus designated as "2" in the 2nd instar could also be designated as "MA", but it cannot be done so, because the addition of annuli does not occur from the 1st to 2nd instar and so the annulus was not a derivative from the meriston of the 1st instar larva. In the doublets derived from a meristal annulus, the proximal annulus is shorter and slightly lighter colored (open star in Fig. 11B), the distal annulus is longer and slightly darker (solid star in Fig. 11B). Doublet annuli in the 3rd instar, which were derived from the annulus next to the meriston in the 2nd instar larva, likewise consist of proximal slightly lighter-colored and distal slightly darker-colored annuli (3rd and 4th annuli of 3rd instar larva in Fig. 11B): the 2nd flagellomere next to the meriston in the 2nd instar larva could be homologized with the meristal annulus of 3rd to 9th instar larvae.

Fig. 12A is a differential interference contrast micrograph of part of an antenna of the 2nd instar larva just before molting. In Fig. 12B, an enlargement of Fig. 12A, 2 annuli are observed to be prepared both in the meriston and 2nd flagellomere. The annuli under formation in the meriston and 2nd flagellomere are bounded by wavy lines (arrowheads in Fig. 12B): these 2 new annuli within the meriston of the 2nd instar become the meriston and meristal annulus of the 3rd instar. Fig. 12C is a histological section of the opposite antenna of the same individual as shown in Fig. 12A,B. The cuticle of the 2nd instar larva is much decreased in thickness, and the cuticle of the next 3rd instar larva is under secretion. Two new annuli under formation, the divisions of which are shown by arrowheads in Fig. 12C, corresponding to the "wavy lines" indicated by arrowheads in Fig. 12B, are observed both in the meriston and 2nd flagellomere of the 2nd instar. The 3rd-instar cuticle under formation has a folded appearance, and strong setae are found under formation (arrow in Fig. 12C). Thus, in the individual shown in Fig. 12, the flagellum increases into 13 annuli by the addition of 1 annulus each from the meriston and the next annulus.

Table 3. Measurements of pronotum length and width of each larval instar in *Eucorydia yasumatsui*. ND = no data.

Instar	Sex	**Pronotum length** (PL) (average) [mm]	**Pronotum width** (PW) (average) [mm]	**PL/PW** (average)
1	– (n = 7)	0.52 – 0.74 (0.63)	1.28 – 1.38 (1.33)	0.39 – 0.56 (0.47)
2	– (n = 8)	0.76 – 0.90 (0.82)	1.64 – 1.70 (1.68)	0.45 – 0.54 (0.49)
3	♀ (n = 5)	1.04 – 1.12 (1.06)	2.12 – 2.20 (2.18)	0.45 – 0.53 (0.49)
	♂ (n = 4)	0.92 – 1.24 (1.05)	1.72 – 2.24 (2.08)	0.46 – 0.55 (0.51)
4	♀ (n = 1)	1.20	2.64	0.45
	♂ (n = 4)	1.04 – 1.52 (1.22)	2.60 – 2.72 (2.67)	0.40 – 0.58 (0.46)
5	♀	ND	ND	ND
	♂ (n = 3)	1.36 – 1.40 (1.39)	3.20 – 3.72 (3.40)	0.38 – 0.44 (0.41)
6	♀ (n = 2)	1.60 – 1.72 (1.66)	3.84 – 3.92 (3.88)	0.41 – 0.48 (0.43)
	♂ (n = 2)	1.52 – 1.60 (1.56)	3.88 – 4.24 (4.06)	0.39 – 0.51 (0.45)
7	♀	ND	ND	ND
	♂ (n = 6)	1.76 – 2.08 (1.97)	4.00 – 4.96 (4.67)	0.37 – 0.52 (0.43)
8	♀ (n = 2)	2.24 (2.24)	5.52 – 5.76 (5.64)	0.39 – 0.41 (0.40)
	♂ (n = 4)	1.84 – 2.72 (2.24)	4.64 – 6.00 (5.42)	0.37 – 0.47 (0.42)
9	♀ (n = 4)	2.56 – 3.20 (2.94)	6.24 – 6.48 (6.36)	0.41 – 0.50 (0.46)
	♂ (n = 1)	2.56	6.08	0.42
Adult	♀ (n = 5)	2.60 – 3.30 (2.90)	5.90 – 6.30 (6.10)	0.41 – 0.53 (0.48)
	♂ (n = 5)	2.40 – 2.80 (2.58)	5.50 – 6.10 (5.68)	0.41 – 0.49 (0.45)

Table 4. Measurements of metathoracic tergal length along the median line and paranotal length of each larval instar in *Eucorydia yasumatsui*. ND = no data.

Instar	Sex	**Mesothoracic tergal length** along median line (TL) (average) [mm]	**Mesothoracic paranotal length** (PL) (average) [mm]	**PL/TL** (average)
1	– (n = 7)	0.28 – 0.30 (0.30)	0.42 – 0.48 (0.44)	1.40 – 1.60 (1.50)
2	– (n = 8)	0.36 – 0.40 (0.38)	0.60 – 0.64 (0.62)	1.58 – 1.72 (1.64)
3	♀ (n = 5)	0.48 (0.48)	0.68 – 0.88 (0.80)	1.42 – 1.83 (1.67)
	♂ (n = 4)	0.44 – 0.52 (0.50)	0.60 – 0.88 (0.77)	1.36 – 1.69 (1.54)
4	♀ (n = 1)	0.64	1.04	1.63
	♂ (n = 4)	0.60 – 0.64 (0.61)	1.04 – 1.12 (1.08)	1.73 – 1.80 (1.77)
5	♀	ND	ND	ND
	♂ (n = 3)	0.76 – 0.84 (0.79)	1.36 – 1.60 (1.44)	1.79 – 1.90 (1.83)
6	♀ (n = 2)	0.88 – 0.92 (0.90)	1.72 (1.72)	1.87 – 1.95 (1.91)
	♂ (n = 2)	0.88 (0.88)	1.68 – 1.72 (1.70)	1.91 – 1.95 (1.93)
7	♀	ND	ND	ND
	♂ (n = 6)	0.96 – 1.20 (1.13)	1.84 – 2.40 (2.16)	1.77 – 2.08 (1.91)
8	♀ (n = 2)	1.36 (1.36)	2.40 – 2.56 (2.48)	1.76 – 1.88 (1.82)
	♂ (n = 4)	1.04 – 1.36 (1.26)	2.16 – 3.04 (2.66)	1.94 – 2.24 (2.11)
9	♀ (n = 4)	1.36 – 1.60 (1.56)	3.04 – 3.20 (3.16)	1.90 – 2.22 (2.03)
	♂ (n = 1)	1.44	3.20	2.22

Hockman et al. (2009) summarized the modes of antennal development among the polyneopteran taxa and recognized three modes. The 1st mode is the simplest and involves exclusively the division of the 1st annulus of the flagellum (meriston) into two or three annuli at each molt. This mode of antennal growth has been documented in the Isoptera (Fuller 1920), some Blattaria (Blattidae: Qadri 1938), and Plecoptera (Qadri 1938) and in Dermaptera (Davies 1966). The 2nd mode involves three types of annular zone of the flagellum, i.e., the

Table 5. Postembryonic changes of antennomeres in *Eucorydia yasumatsui*. ND = no data.

Instar	Sex	Number of total annuli mean ± SD (range of annuli number)	Number of annuli of white zone	Number of annuli distal to white zone	Ratio in number of annuli of white zone to the number of total annuli (mean (%) ± SD)	Relative position of white zone from base of antenna (mean (%) ± SD)
1	(n = 10)	11 ± 0 (1)	—	—	—	—
2	(n = 7)	11 ± 0 (11)	1	3	9.1 ± 0	68.5 ± 3.8
3	♀ (n = 10)	14 ± 0.9 (13 – 15)	1 – 2	2 – 4	12.2 ± 3.7	67.5 ± 2.0
	♂ (n = 2)	14.5 ± 0.7 (14 – 15)	1 – 2	3 – 4	10.5 ± 5.3	64.7 ± 2.7
4	♀ (n = 2)	17 ± 0 (17)	2	3	11.8 ± 0	73.1 ± 0
	♂ (n = 4)	17.5 ± 0.6 (17 – 18)	2 – 3	3 – 4	12.8 ± 2.6	72.7 ± 1.6
5	♀	ND	ND	ND	ND	ND
	♂ (n = 4)	20.3 ± 1.5 (19 – 22)	2 – 4	3 – 4	11.1 ± 1.8	72.3 ± 2.8
6	♀ (n = 4)	22.3 ± 1.0 (21 – 23)	2 – 3	4	12.4 ± 2.5	71.6 ± 0.9
	♂ (n = 2)	22.5 ± 0.7 (22 – 23)	3	3 – 4	13.3 ± 0.4	72.7 ± 0.3
7	♀	ND	ND	ND	ND	ND
	♂ (n = 7)	29.9 ± 1.9 (28 – 32)	2 – 4	2 – 5	10.5 ± 1.8	73.6 ± 2.9
8	♀ (n = 3)	32 ± 0 (32)	4	4 – 5	12.5 ± 0	74.9 ± 3.1
	♂ (n = 3)	34.3 ± 2.9 (31 – 36)	4 – 5	4 – 5	13.6 ± 0.6	80.4 ± 2.6
9	♀ (n = 9)	34.3 ± 0.9 (33 – 35)	4 – 6	4 – 5	14.5 ± 1.8	75.5 ± 1.5
	♂ (n = 4)	35.8 ± 0.5 (35 – 36)	4 – 5	5 – 6	12.0 ± 1.6	75.9 ± 0.8
Adult	♀ (n = 10)	37.6 ± 1.6 (36 – 40)	5 – 7	6 – 7	16.5 ± 1.8	71.4 ± 1.8
	♂ (n = 10)	37.0 ± 1.2 (35 – 39)	3 – 5	9 – 11	10.8 ± 2.1	69.8 ± 1.7

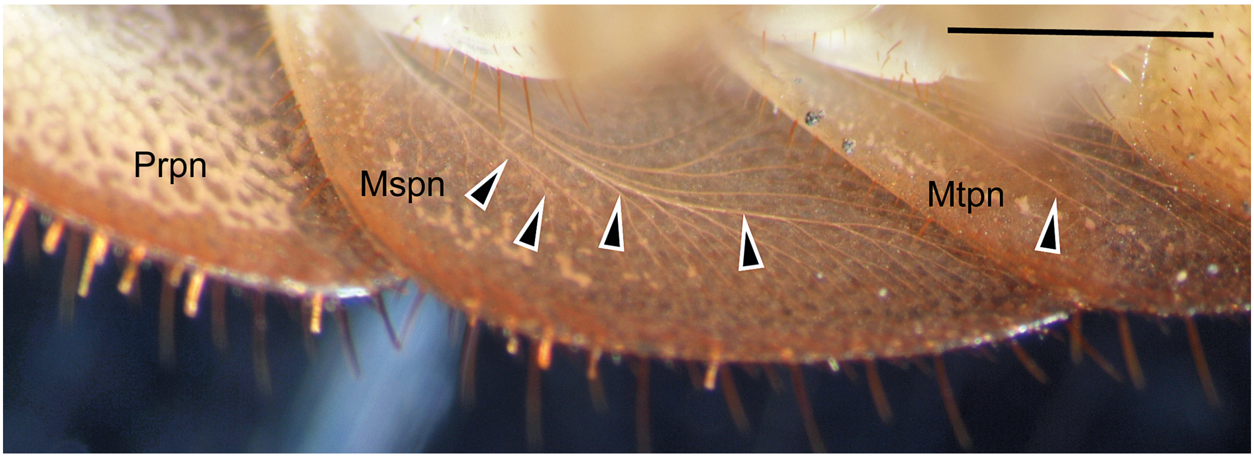

Fig. 10. Thoracic paranota of a female last instar (in this case, 9th instar) larva of *Eucorydia yasumatsui*, ventral view. Arrowheads show the venation of wing buds. Mspn = mesothoracic paranotum; Mtpn = metathoracic paranotum; Prpn = prothoracic paranotum. Scale bar = 1 mm.

basalmost meriston, meristal annulus which is derived from the meriston and undergoes once subdivision to produce singleton(s), and singletons which never divide. This mode of antennal growth is found in some Blattaria (Blattidae: Schafer & Sanchez 1973; Blaberidae: Schafer 1973, Blattellidae: Campbell & Priestley 1970) and Mantodea (Bugnion 1921). In the 3rd mode, the meristal annuli are not only derived from the division of the most basal annulus (meriston) but instead from several basal or even all annuli in the flagellum of the 1st instar. This mode of antennal growth is found in Orthoptera (Burnett 1951) and Phasmatodea (Roth 1917).

In the development of flagellomeres in cockroaches, as mentioned above, two modes have been reported: (1) in *Blatta orientalis* of Blattidae, lengthening of the flagellum is achieved by division of the 1st flagellomere (meriston) into 2 or 3 at each molt (Qadri 1938); (2) in *Periplaneta americana* of Blattidae (Schafer & Sanchez 1973), *Blattella germanica* of Blattellidae (Campbell & Priestley 1970) and *Leucophaea* (= *Rhyparobia*) *mad-*

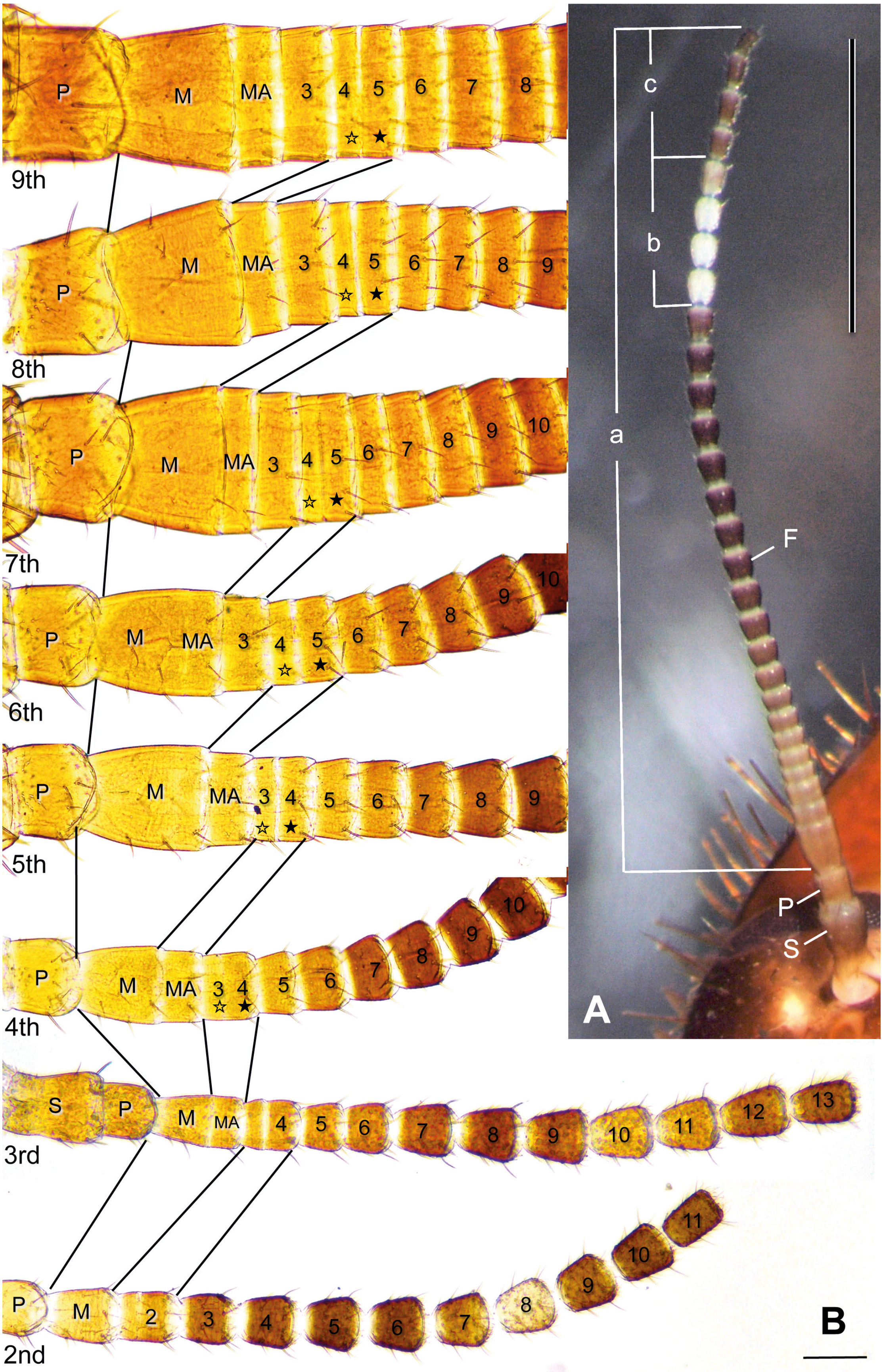

Fig. 11. Postembryonic changes of antennae of *Eucorydia yasumatsui*. **A**: Left antenna of a 7th instar larva. a, b and c show the entire flagellum, white zone and the region distal to the white zone, respectively. **B**: Proximal parts of antennae of the 2nd to 9th instar larvae. White and black stars respectively show the proximal and distal annuli produced from the meristal annulus at the previous molting. F = flagellomere; M = meriston; MA = meristal annulus; P = pedicellus; S = scapus. 1 – 13 = 1st to 13th flagellomeres. Scale bars = A: 1 mm; B: 100 µm.

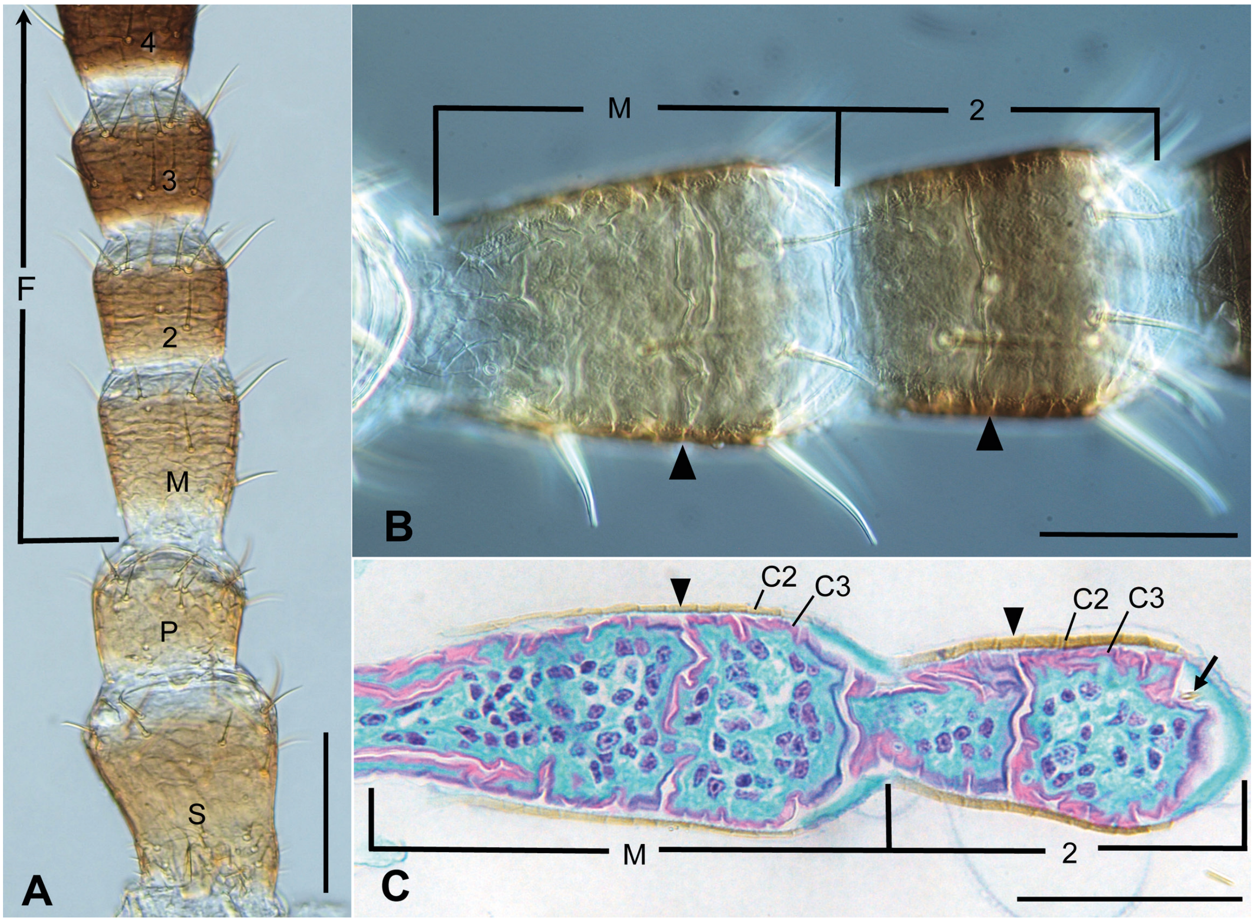

Fig. 12. Antennae of a 2nd instar larva of *Eucorydia yasumatsui* just before molting. Basal part (**A**) and its enlargement (**B**), differential interference contrast microscopy, and the histological section of the opposite antenna of the same individual as shown in **A** and **B** (**C**). See text. Arrowheads and arrow show the divisions of flagellomeres and a strong seta, respectively. C2, 3 = cuticles of the 2nd and 3rd instar larvae; F = flagellum; M = meriston of the 2nd instar larva; P = pedicellus of the 2nd instar larva; S = scapus of the 2nd instar larva; 2–4 = 2nd to 4th flagellomeres of the 2nd instar larva. Scale bars = A: 100 µm; B, C: 50 µm.

erae of Blaberidae (Schafer 1973) both the meriston and meristal annulus, which are derived from the meriston, divide and add annuli at each molt. In *B. germanica*, all the meristal annuli, derived from the meriston, divide and produce doublets at each molt (Campbell & Priestley 1970). The manner of annular addition of the flagellum in *Eucorydia yasumatsui* may be categorized in the latter case in the division of meristal annuli involved. The latter case is predominant in cockroaches and may be regarded as the "groundplan of the group". However, annular addition of the flagellum is achieved in termites only by division of the meriston (Fuller 1920). Flagellar annulation may have to be discussed in the framework of Blattodea.

As shown in Table 5, the number of annuli in the white zone increases from 1 in the 2nd instar to 5–7 in females and 3–5 in males in later instars. The number of annuli distal to the white zone also increases from 2 or 3 in earlier instars to 6 or 7 in females and 9–11 in males. The percentage of the number of annuli in the white zone relative to the total number of annuli is constantly 10–15% in the 3rd to 9th instars, excluding the markedly low value in 2nd instar larvae (9.1%) and high value in adult females (16.5%). The centre of the white zone is constantly located at ca. 70–80% of flagellum length (from the base), i.e., the distance from the flagellum base is approximately fixed throughout larval instars. The number of annuli in the white zone and that of annuli distal to the white zone increase with successive molts. Thus, an addition of annuli to these regions evidently occurs, but no division of annuli was found in these regions. This necessarily means that during development, with the progressive increase of the annular number of the white zone, the white coloration shifts to further proximal annuli, i.e., in successive instars previously dark annuli can become white (newly joining the white zone after a molt), and previously white annuli can become dark (changing from the white zone to the dark distal part). Accordingly, the absolute position of the white zone remains constant during development, but its relative position (i.e., position relative to particular structural elements = individual annuli) changes. The fixed percentages of the number of the annuli in the white zone (10–15%) and of the distance of the white zone from the flagellum base (70–80%) suggest that the white zone is shaped by a regulatory mechanism perhaps

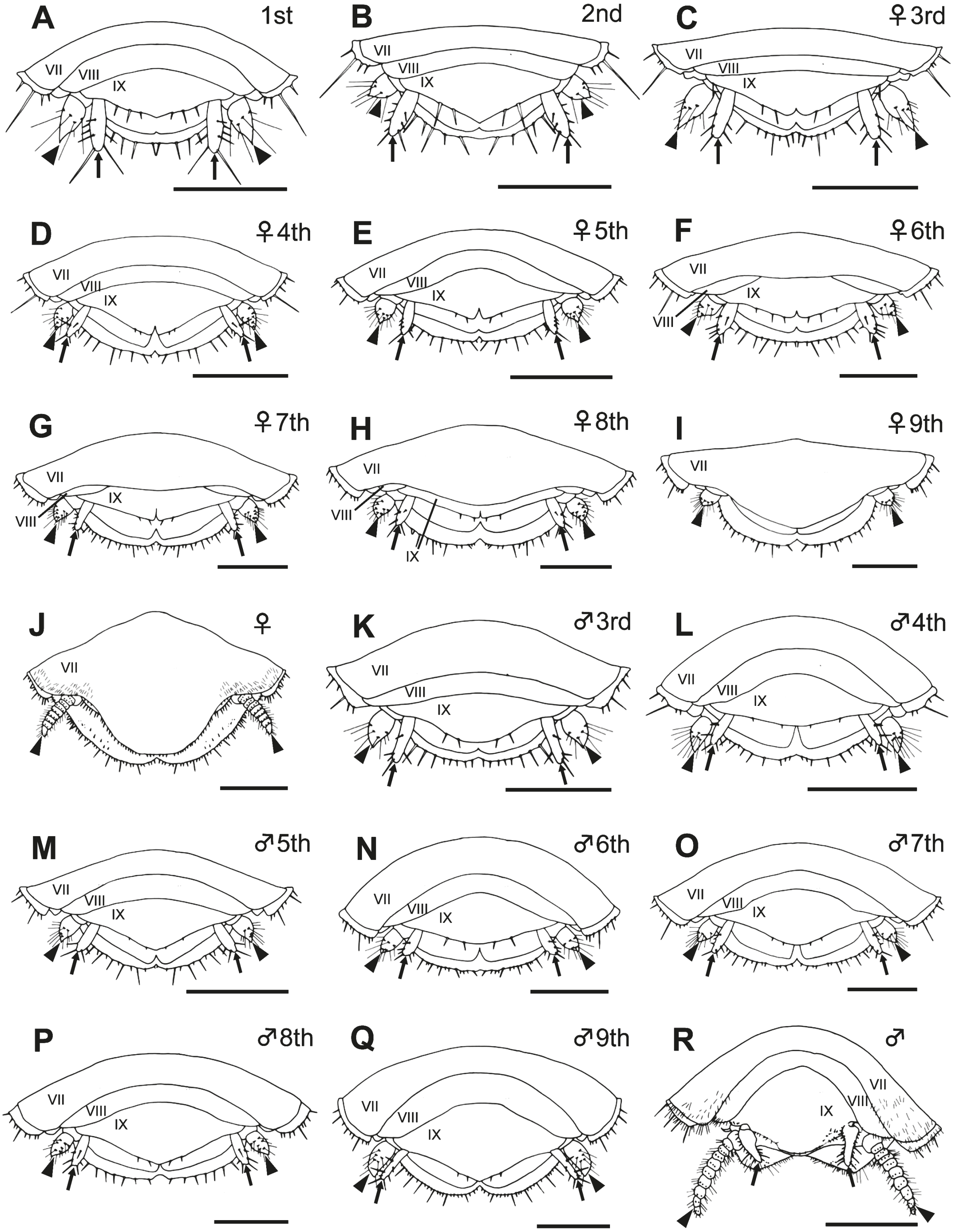

Fig. 13. Postabdominal segments of each instar larva and adult of *Eucorydia yasumatsui*, ventral views. **A**: 1st instar larva. **B**: 2nd instar larva. **C**−**J**: Female 3rd instar (**C**), 4th instar (**D**), 5th instar (**E**), 6th instar (**F**), 7th instar (**G**), 8th instar (**H**), 9th instar larvae (**I**), and adult (**J**). **K**−**R**: Male 3rd instar (**K**), 4th instar (**L**), 5th instar (**M**), 6th instar (**N**), 7th instar (**O**), 8th instar (**P**), 9th instar larvae (**Q**), and adult (**R**). Arrows and arrowheads show styli and cerci, respectively. VII−IX = 7th to 9th abdominal sterna. Scale bars = A−H, K−P: 500 µm; I, J, Q, R: 1 mm.

based on some proximodistal physiological gradient. The pigmentation responsible for the dark versus white color of annuli is located in the cuticle. Thus, if a gradient is present, it is likely to affect the distribution of pigmentation in the newly formed flagellomere cuticle of the various instars.

6. Structural changes in postabdominal segments. We only briefly examined the development of exposed ventral parts, but not that of the genitalia, which develop their great complexity in later instars, when they are covered by the subgenital plate (see Klass 1997: figs.109–142 for fully developed male genitalia and Klass 1998 for female genitalia of related taxa; McKittrick 1964 for the development of female genitalia).

1st and 2nd instar larvae are not sexually differentiated (Fig. 13A,B). Abdominal coxosterna VIII and IX are clearly observed from outside, and a pair of cerci and a pair of IXth-segmental styli are well visible at the caudal end. Sexes can be distinguished from the 3rd instar on. In females, a median notch appears on the posterior margin of abdominal coxosternum IX in 3rd instar larvae (Fig. 13C). The notch gradually deepens in 4th and 5th instars (Fig. 13D,E). Coxosternum VIII starts to become concave in the 5th instar (e.g., Fig. 13E), and in the 6th instar coxosternum VII starts to overgrow it (Fig. 13F). By an additional reduction of coxosternum VIII, coxosternum IX becomes also largely covered by the extending coxosternum VII in the 7th and 8th instars (Fig. 13G,H), and is completely covered by it in the last (9th or 10th) instar (Fig. 13I). In the last instar, the pair of styli of coxosternum IX disappears. Males do not undergo any marked changes in the postabdomen, as shown in Fig. 13K–R. Neither marked reduction of postabdominal coxosterna nor loss of the styli upon coxosternum IX occurs. The cercomeres are 8 or 9 in both female and male (Fig. 13J,R). We could not follow the annulation process of cerci in the postembryonic stages.

It is known that, in cockroaches, sexes can be distinguished from early instars according to changes of the postabdominal structures. As revealed in the present study, in *Eucorydia yasumatsui*, sexing is possible from the 3rd instar. It is possible from the 2nd instar in *Periplaneta americana* (Gould & Deay 1938) and *Blaberus discoidalis* (Manley 1969), and already at hatching in *Blattella germanica* (Ross & Cochran 1960). In the females of these cockroaches, as we described for *E. yasumatsui*, (1) first, a median notch appears on the posterior margin of coxosternum IX, (2) coxosterna VIII and IX are overgrown by coxosternum VII, and (3) in the final instar, the pair of styli upon coxosternum IX disappears (see McKittrick 1964 for details of the development of female genitalia in a few species). However, the males undergo no marked changes in the exposed parts of the postabdomen, i.e., neither noticeable reduction/extension of coxosterna nor loss of styli.

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