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Reproductive biology and postembryonic development in the basal earwig *Diplatys flavicollis* (Shiraki) (Insecta: Dermaptera: Diplatyidae)

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> Abstract

Based on captive breeding, reproductive biology including mating, egg deposition and maternal brood care, and postembryonic development were examined and described in detail in the basal dermapteran *Diplatys flavicollis* (Shiraki, 1907) (Forficulina: Diplatyidae). The eggs possess an adhesive stalk at the posterior pole, by which they attach to the substratum. The mother cares for the eggs and offspring, occasionally touching them with her antennae and mouthparts, but the maternal care is less intensive than in the higher Forficulina. The prelarva cuts open the egg membranes with its egg tooth, a structure on the embryonic cuticle, to hatch out, and, simultaneously, sheds the cuticle to become the first instar. The number of larval instars is eight or nine. Prior to eclosion, the final instar larva eats its own filamentous cerci, with only the basalmost cercomeres left, and a pair of forceps appears in the adult. The present observations were compared with previous information on Dermaptera. The adhesive substance is an ancestral feature of Dermaptera, and the adhesive stalk may be a characteristic of Diplatyidae. The attachment of the eggs and less elaborate maternal brood care are regarded as plesiomorphic in Dermaptera. The number of larval instars in *D. flavicollis* (eight or nine) is remarkably larger than that in the higher Forficulina (generally four or five) and also exceeds that in another representative of basal Dermaptera or Pygidicranidae (six or seven). The largest number of larval instars among Dermaptera having been found in *D. flavicollis* confirms the perception of Diplatyidae being very primitive earwigs.

> Key words

Dermaptera, Forficulina, Diplatyidae, *Diplatys*, reproductive biology, mating, egg deposition, egg tooth, maternal brood care, postembryonic development.

1. Introduction

Dermaptera comprises the 11 families Karschiellidae, Diplatyidae, Pygidicranidae, Apachyidae, Anisolabididae, Labiduridae, Forficulidae, Spongiphoridae, Chelisochidae, Arixeniidae, and Hemimeridae (Haas & Klass 2003), and about 2,000 species have been described (Sakai 1996). The Hemimeridae and Arixeniidae have curious features specialized to their epizoic way of life, and are often dealt with as independent suborders, i.e., Hemimerina and Arixeniina, respectively. The majority of Dermaptera (the other nine families) are typical earwigs, belonging to the "Forficulina" (Jarvis et al. 2005). The Karschiellidae, Diplatyidae, and Pygidicranidae display plesiomorphic states in many characters and are called the "basal Dermaptera", which are most likely paraphyletic (Haas & Klass 2003; Klass 2003). The six remaining forficuline families possess many derived features and are grouped into the "higher Forficulina". The monophyly of this group is well supported, though the Hemimeridae and Arixeniidae probably have to be included,

as they are likely related to different families of the "higher Forficulina" (HAAS & KUKALOVÁ-PECK 2001; KLASS 2001; HAAS & KLASS 2003; JARVIS et al. 2005).

The knowledge on the biology of Forficulina is fragmentary (MATZKE & KLASS 2005). Furthermore, most reports concern the higher Forficulina, while the information on the biology of basal Dermaptera is very scarce. Recently, MATZKE & KLASS (2005) studied the biology and postembryonic development of some basal earwigs, providing a comprehensive description of a pygidicranid, *Tagalina papua* de Bormans, 1903. Although they also provided notes on the biology of an unidentified diplatyid and other authors (GREEN 1898; KAMIMURA 2004) including ourselves (SHIMIZU & MACHIDA 2009) have also published observations on different aspects of the life history of diplatyid dermapterans, information on diplatyid biology remains sketchy. Here we describe the reproductive biology and postembryonic development of *Diplatys flavicollis* (Shiraki, 1907).

Diplatys flavicollis is distributed in the Iriomote and Ishigaki Islands, the Southwest Islands of Japan and in Taiwan (SHIRAKI 1928; ICHIKAWA & KOHNO 1999). It is the only diplatyid occurring in Japan. *D. flavicollis* is found under stones or in leaf litter near streams in evergreen broad-leaved forests. When frightened, they rush to escape. Their body length is 1–1.5 cm, with females slightly larger than males. Their abdomen is cylindrical, and narrowest in the middle in the males (Fig. 1A,B). Larval cerci are filamentous and multi-segmented (Fig. 1C,C') – a feature that in Dermaptera is limited to larvae of Diplatyidae and Karschiellidae (BURR 1911). The cerci of *D. flavicollis* larvae are nearly twice as long as the body, but the cerci in adults are reduced to single-segmented, short forceps (Fig. 1A,A',B,B').

2. Material and methods

We collected about 150 larvae and 12 adults of *Diplatys flavicollis* in April and October 2007, April 2008, and July 2010, at Sokobaru River on Ishigaki Island, Okinawa Prefecture, Japan. The specimens were then kept in the laboratory at 18–25°C. The wild-caught larvae were reared separately in cylindrical plastic cases (height 5 cm, diameter 8 cm) with moistened soil (Fig. 2A). The wild-caught adults were reared separately in square plastic cases (height 3 cm, length 10 cm) with moistened soil, on which a square glass plate (5 mm thick, 6 cm long) was placed as a refuge (Fig. 2B). For mating, a pair collected from the field or a pair raised to adulthood in the laboratory was kept in a single case for several days. The larvae and adults were fed dried anchovies, dead *Drosophila*, and a compound of yeast extracts, chlorella extracts, carrot powder, goldfish food and powdered dried silk worm pupae (commercially available fishing bait). Various biological aspects of *D. flavicollis* were documented by photographs taken with a Nikon E-8400 or Olympus E-620 digital camera.

For counting larval instars and to obtain larvae with the instar identified, we used captive breeding. We inspected the larvae every several days under a Leica MZ12 stereomicroscope, for counting the number of antennomeres. To record the external morphological characteristics of each instar, we anesthetized larvae with the instar identified by CO_2 and took photographs using a Leica MZ12 equipped with the Nikon E-8400. Some of the larvae of each instar were anesthetized with diethyl ether vapor, fixed with FAA fixative (ethyl alcohol : formalin : acetic acid = 15 : 5 : 1) for 3 days and stored in 70% ethyl alcohol. The fixed specimens were used to determine: (1) body length, (2) antennal lengths (right and left), (3) head length and (4) width, (5) pronotum length and (6) width, (7) cercal lengths (right and left), (8) numbers of antennomeres (right and left), (9) numbers of ommatidia (right and left), and (10) numbers of cercomeres (right and left).

For scanning electron microscopic observations, full-grown embryos, which were dissected out of the eggs in a physiological saline Ephrussi-Beadle Ringer's solution (0.75% NaCl + 0.035% KCl + 0.021% $CaCl_2$), and newly hatched larvae were fixed with an alcoholic Bouin's fixative (saturated picric acid ethyl alcohol solution : formalin : acetic acid = 15 : 5 : 1) for 12 h and stored in 70% ethyl alcohol. The fixed specimens stored in 70% ethyl alcohol were hydrated in a graded ethyl alcohol series, postfixed with 1% OsO_4 for 1 h, again dehydrated in a graded ethyl alcohol series, dried with a critical point dryer TOUSIMIS Samdri®-PVT-3D, coated with gold, and observed under a scanning electron microscope TOPCON SM-300.

3. Results

3.1. Mating, egg deposition and eggs

Pairs of *Diplatys flavicollis* mate repeatedly, with the copulation lasting several hours (SHIMIZU & MACHIDA 2009). The mating is of the end-to-end type, with the pair twisting their postabdomina (Fig. 3), as re-

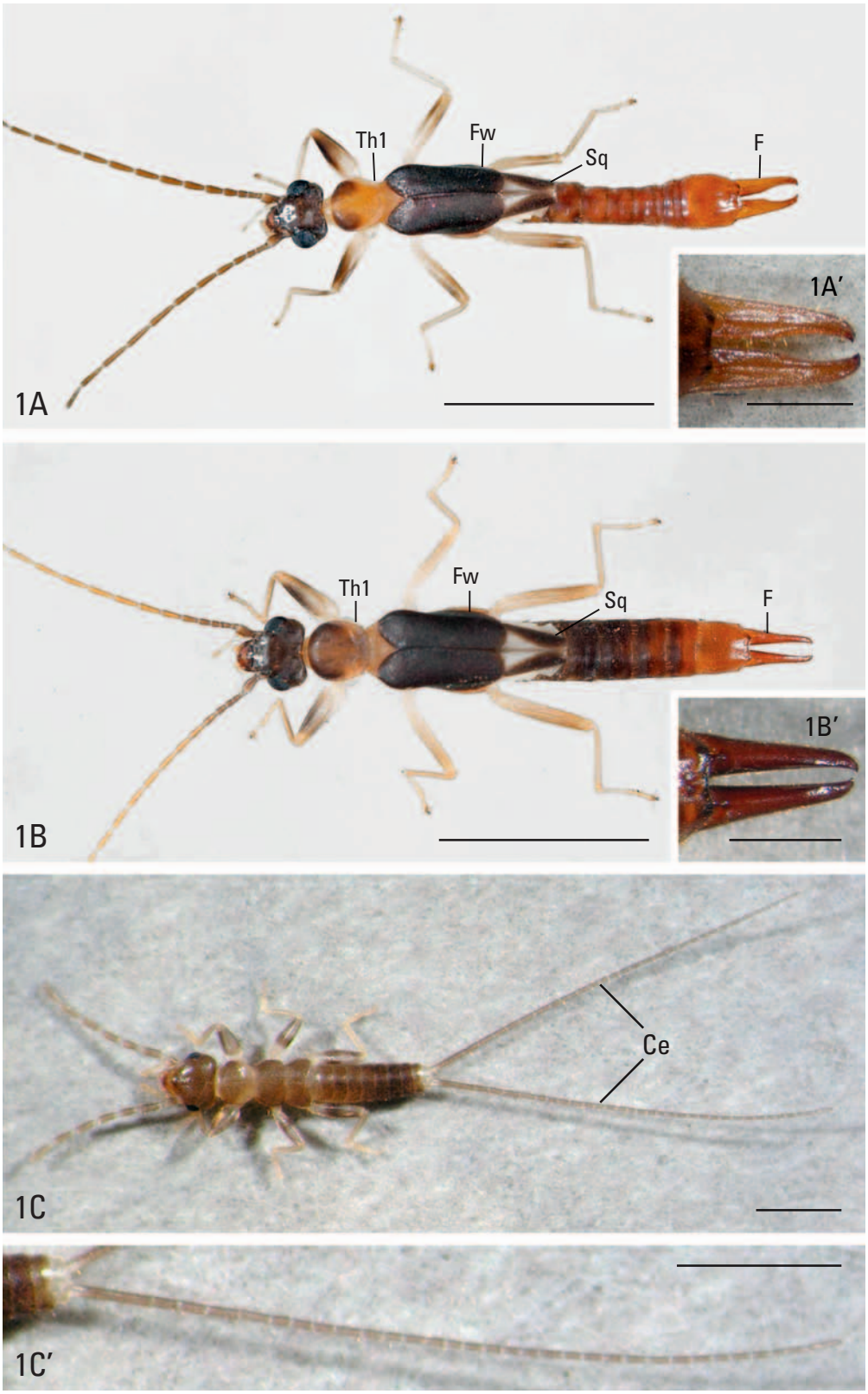
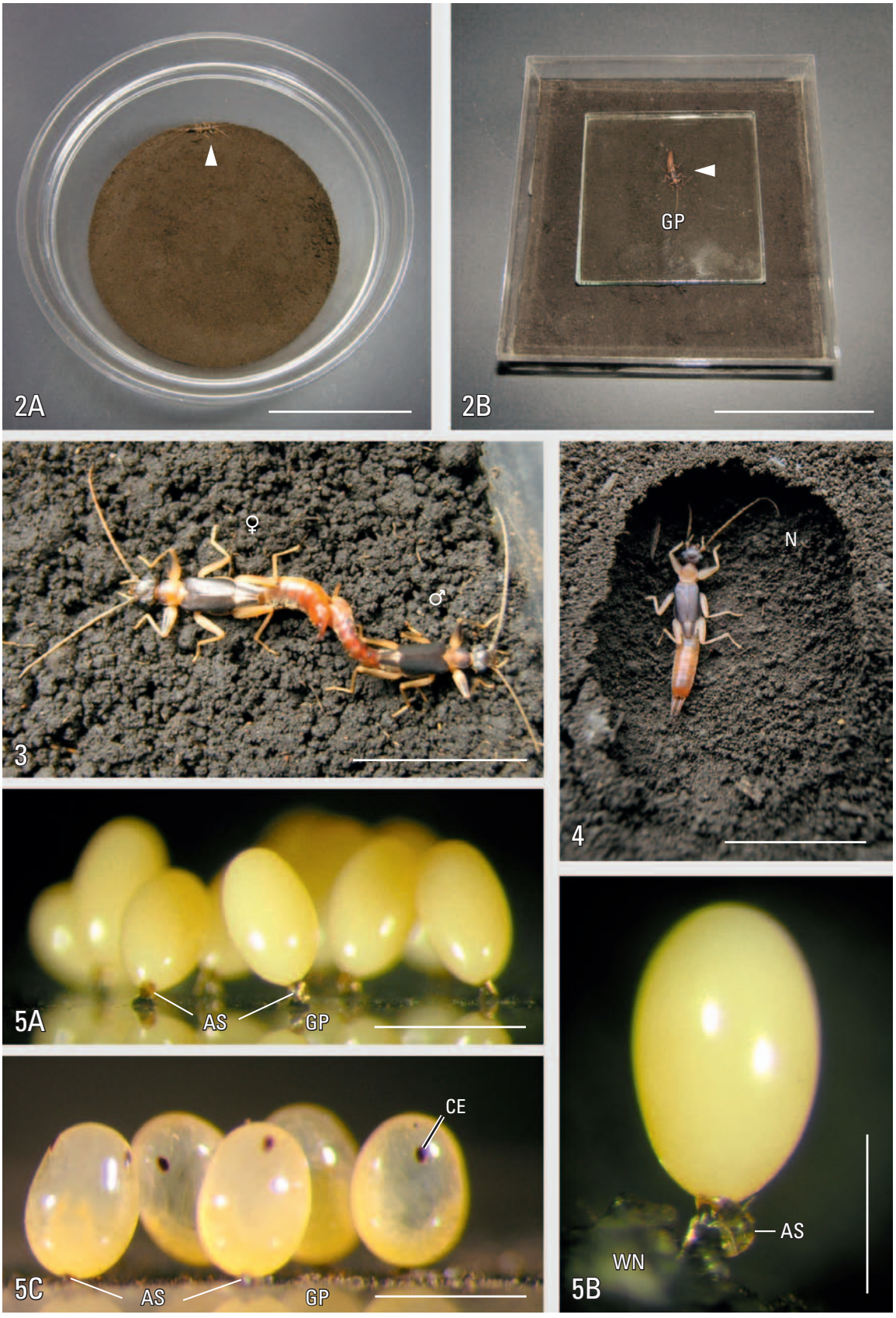


Fig. 1. *Diplatys flavicollis* (Shiraki, 1907). **A**: Male adult. **A'**: Enlarged view of forceps. **B**: Female adult. **B'**: Enlarged view of forceps. **C**: First instar larva. **C'**: Enlarged view of cercus. Ce = cerci; F = forceps (adult cerci); Fw = forewing; Sq = squama of hindwing; Th1 = prothorax. Scale bars = A, B: 5 mm; A', B', C, C': 1 mm.

ported for the same species by Kamimura (2004). Digging the soil with her mouthparts and legs, the female builds a nest under the glass plate (Figs. 2B, 4). The females who have built a nest never forage for food, and only eat if food is placed in their nests. Several days after the nesting, the females start to lay



Figs. 2–5. Rearing, mating, nesting and egg deposition in *Diplatys flavicollis* (Shiraki, 1907). **2**: Rearing. 2A: Larvae. The arrowhead shows the single larva in the case. 2B: Adults. The arrowhead shows a female nesting beneath the glass plate (GP). **3**: Mating. **4**: Female in a nest (N) made beneath the glass plate, which was removed to show the details of the nest. **5**: Eggs. 5A: Freshly deposited eggs stuck to glass plate (GP) by the adhesive stalk (AS). 5B: Enlargement of an egg deposited on and stuck to the wall of the nest (WN) by the adhesive stalk (AS). 5C: Eggs containing full-grown embryos whose compound eyes (CE) are visible near the anterior pole; AS = adhesive stalk; GP = glass plate. Scale bars = 2A,B: 5 cm; 3, 4: 1 cm; 5A,C: 1 mm; 5B: 500 μm.

eggs. The oviposition lasts several days, and females lay 30–60 eggs under these conditions.

The eggs are ellipsoidal with approximately 1 mm long and 600 µm short diameters (in the freshly laid eggs), and ivory in color since the yellowish yolk is visible through the transparent egg membranes (Fig. 5A–C). At the posterior pole of the egg, there is a sticky stalk named the adhesive stalk by SHIMIZU & MACHIDA (2009), which is ca. 250 µm long (Fig. 5A,B). The orientation of the eggs is designated according to the orientation of the embryos just before hatching (i.e., at the postblastokinesis stage). Fig. 5C shows a photograph of eggs containing full-grown embryos. Note the position of the head with the compound eyes, i.e., the anterior of the embryo. We know that the adhesive stalk is opposite the anterior pole of the egg. The eggs are deposited in groups, forming a clutch, on the glass plate or wall of the nest and attached there by the adhesive stalk (Figs. 5A,C). At oviposition, the egg that emerges from the mother's genital opening immediately appears on the dorsal side of her body and lodges at the base of the forceps, passing through between and pushed up by the paired forceps (Fig. 6, 6'), and attaches to the substratum. The adhesive stalk is initially sticky, and we rarely observed the female moving the eggs by taking them in her mouthparts. However, the day after oviposition, the adhesive stalk lacks viscosity and becomes hardened; thereafter, the eggs could not be moved and rearranged. The eggs swell with development, 1.3-fold in short diameter and more than two-fold in volume: compare the newly deposited eggs in Fig. 5A and those containing full-grown embryos in Fig. 5C, both photographed at the same magnification.

3.2. Maternal brood care and hatching

The female attends the egg clutch (Fig. 7A). She does not take great care of the eggs as reported for higher Forficulina such as cleaning by licking, but occasionally touches the eggs with her antennae and mouthparts. As mentioned, for a short period after egg deposition, the adhesive stalk has not hardened, and we rarely observed the female rearranging the eggs by taking them in her mouthparts. Once the stalk has dried and hardened, the eggs cannot be moved. When disturbed by finger, the female usually counterattacks against it with her forceps. Excessive disturbance can lead the mother to eat her eggs. If the mother dies, the eggs become moldy.

The egg period was about three weeks at 18–25°C and 18–19 days at 25°C (n = 5). The embryos just before hatching are covered with the embryonic cuticle, beneath which the first instar larval cuticle has been prepared (data not shown). The frons of the full-grown embryo bears an egg tooth (Fig. 9A,A',B,B'), a large knob-like structure with a median denticulated ridge and a pair of horn-shaped, stout projections. The embryo cuts open the egg membranes by means of the egg tooth, and the prelarva hatches out. Simultaneously to hatching out, the prelarva sheds off the embryonic cuticle, which is caught by the egg membranes, and becomes the first instar larva. The frons of the first instar larva (Fig. 10,10') does not bear an egg tooth; this structure is thus derived not from the first instar larval cuticle but from the embryonic cuticle.

The first instar larvae are cared for by their mother (Fig. 7B). As with the eggs, she occasionally makes physical contact with the larvae with her antennae and mouthparts, and when disturbed, counterattacks with her forceps. Nearing molting, the first instar larvae gradually disperse and expand their range outside the nest, and the second instar larvae completely part from their mother to become independent.

3.3. Field observations on nesting

In the field, we encountered three cases of *Diplatys flavicollis* nesting at the banks of mountain streams. In two cases, females nested between rocks, one with eggs (Fig. 8, 8') and the other with eggs and newly hatched first instar larvae. Even in the latter case, we could count the number of eggs, because the egg exuviae were left on the rock. The number of eggs in these clutches was 90 and 96, respectively (Fig. 8'). In the third case, a female and several late first instar larvae or newly molted second instar larvae were found in a hole in the ground beneath a rock.

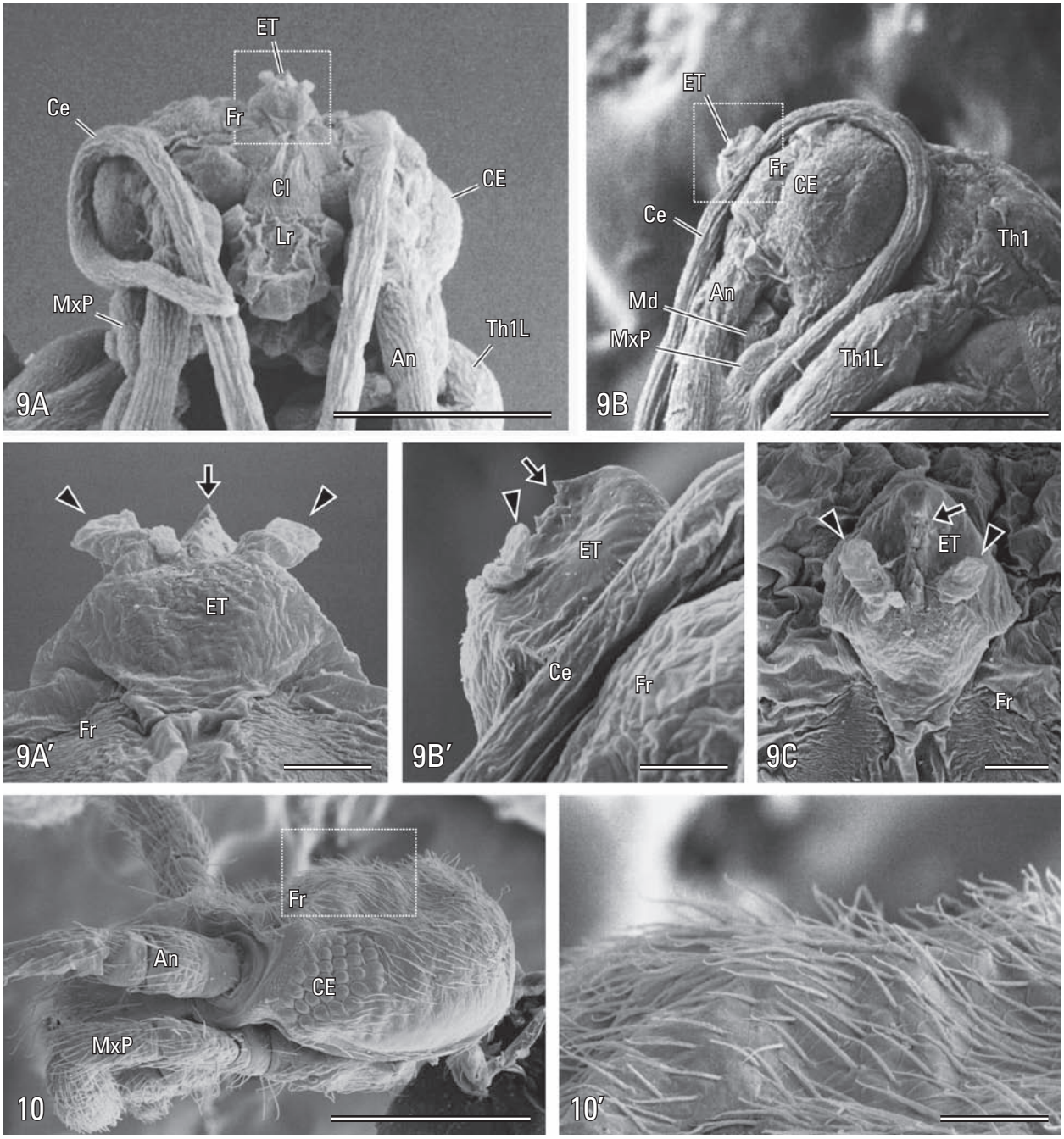
3.4. Postembryonic development

The exuviae are useful for judging whether molting occurred in a dermapteran and they have been utilized for this purpose (e.g., MATZKE & KLASS 2005). However, soon after molting, *Diplatys flavicollis* larvae eat their exuviae including the cercal parts, which are specialized into sclerotized forceps in other dermapteran larvae and usually left uneaten. Therefore, we had to look for other methods to count larval instars, and checked for changes in several qualitative and quantitative features for the captive-bred larvae every several days, focusing on the number of antennomeres. In

Figs. 6–8. Egg deposition, maternal brood care and egg clutch of *Diplatys flavicollis* (Shiraki, 1907). **6**: Female just giving birth to an egg (E). **6'**: Enlarged view of her rear end with the egg. **7**: Females caring for her eggs and offspring. 7A: Female attending the eggs (E). 7B: Female with her eggs (E) and first instar larvae (L). **8**: Egg clutch (EC) deposited on a rock, found in the field. **8'**: Enlarged view of the egg clutch. AS = adhesive stalk; Ab10 = 10th abdominal segment; E = egg; F = forceps. Scale bars = 6, 7A,B, 8, 8': 1 cm; 6': 1 mm.

Dermaptera, a regular increase in the number of antennomeres with each molt has been reported (GÜNTHER & HERTER 1974; MATZKE & KLASS 2005).

To clarify the postembryonic development of *Diplatys flavicollis*, we raised 45 captive-bred individuals from the first instar and preserved 25 specimens of



Figs. 9, 10. Scanning electron micrographs of the heads of the prelarva and first instar larva of *Diplatys flavicollis* (Shiraki, 1907). **9**: Prelarva. 9A: Frontal view of the head. 9A': Enlargement of the area surrounded by a square in 9A, showing details of the egg tooth. 9B: Lateral view of the head. 9B': Enlargement of the area surrounded by a square in 9B, showing details of the egg tooth. 9C: Enlarged dorsal view of the egg tooth. Arrows and arrowheads show the median denticulated ridge and paired horn-shaped, stout projections of the egg tooth, respectively. **10**: Lateral view of the head of the first instar larva. The area shown by a square corresponds to that bearing the egg tooth in the prelarva. **10'**: Enlargement of the area surrounded by a square in 10. An = antenna; Ce = cercus; CE = compound eye; Cl = clypeus; ET = egg tooth; Fr = frons; Lr = labrum; Md = mandible; MxP = maxillary palp; Th1 = prothorax; Th1L = prothoracic leg. Scale bars = 9A,B, 10: 200 μm; 9A',B',C, 10': 20 μm.

different instars (Table 1). We examined each specimen of the different instars and measured: (1) body length, (2) antennal lengths (right and left), (3) head length, (4) head width, (5) pronotum length and (6) width, (7) cercal lengths (right and left), (8) numbers of antennomeres (right and left), (9) numbers of ommatidia (right and left), and (10) numbers of cercomeres (right and left) (Table 1). We also described the changes in qualitative features such as the shape or development of the wing buds, stink glands and so on. We succeeded in raising three individuals up to the final larval instar (one male and two females) and two (one male and one female) up to adulthood (Table 1). We conclude that the larval instar number

Table 1. Measurements, ratios and counts in *Diplatys flavicollis* (Shiraki, 1907) specimens of different instars, taken from fixed specimens of a captive-bred population. "–" = the antenna of one side was missing.

Instar	Larva										Adult	
	I	II	III	IV	V	VI	VII	Final instar			IX	
								VIII		IX		
Specimens examined	5	4	3	2	2	2	2	1 (♂)	1 (♀)	1 (♀)	1 (♂)	1 (♀)
Body length [mm] (average)	2.7–3.0 (2.8)	3.2–3.9 (3.7)	4.0–4.4 (4.2)	5.0, 5.1 (5.1)	5.1, 5.6 (5.4)	6.0, 6.6 (6.4)	6.0, 8.9 (7.5)	8.6	10.1	10.9	9.7	10.1
Antennal length [mm] (average)	1.0–1.9 (1.8)	2.1–2.5 (2.3)	2.7–2.9 (2.8)	3.1–3.4 (3.2)	3.7–3.8 (3.8)	5.0–5.2 (5.1)	5.3–5.8 (5.6)	6.3, 6.3 (6.3)	7.6, — (7.6)	8.7, 8.7 (8.7)	7.8, 7.9 (7.9)	8.1, 8.4 (8.3)
Head length (HL) [mm] (average)	0.59–0.64 (0.62)	0.66–0.75 (0.72)	0.79–0.80 (0.79)	0.83, 0.90 (0.87)	0.98, 0.99 (0.99)	1.27, 1.28 (1.28)	1.25, 1.39 (1.32)	1.44	1.68	1.88	1.43	1.67
Head width (HW) [mm] (average)	0.68–0.71 (0.70)	0.76–0.83 (0.80)	0.90–0.91 (0.90)	0.98, 1.02 (1.00)	1.11, 1.13 (1.12)	1.39, 1.40 (1.40)	1.31, 1.54 (1.43)	1.61	1.88	2.03	1.60	1.76
HL/HW (average)	0.87–0.91 (0.89)	0.87–0.93 (0.90)	0.88 (0.88)	0.84, 0.88 (0.86)	0.88 (0.88)	0.91, 0.92 (0.92)	0.90, 0.95 (0.93)	0.90	0.89	0.93	0.89	0.95
Pronotum length (PL) [mm] (average)	0.40–0.43 (0.41)	0.45–0.55 (0.52)	0.58–0.61 (0.59)	0.68, 0.70 (0.69)	0.77, 0.80 (0.79)	1.00, 1.05 (1.03)	1.01, 1.18 (1.10)	1.17	1.43	1.58	1.15	1.35
Pronotum width (PW) [mm] (average)	0.51–0.53 (0.52)	0.58–0.66 (0.63)	0.70–0.71 (0.71)	0.81, 0.90 (0.86)	0.88, 0.91 (0.90)	1.14, 1.15 (1.15)	1.09, 1.29 (1.19)	1.25	1.55	1.78	1.17	1.38
PL/PW (average)	0.78–0.81 (0.79)	0.78–0.84 (0.82)	0.82–0.87 (0.84)	0.75, 0.86 (0.81)	0.88 (0.88)	0.88, 0.91 (0.90)	0.91, 0.93 (0.92)	0.93	0.93	0.89	0.98	0.98
Cercal length [mm] (average)	4.2–5.0 (4.6)	4.2–6.3 (5.6)	5.6–6.6 (6.2)	7.8–8.5 (8.2)	8.8–14.7 (11.9)	12.9–13.7 (13.2)	12.5–15.0 (13.7)	13.7, 14.3 (14.0)	17.4, 17.4 (17.4)	17.7, 18.2 (18.0)	1.4, 1.4 (1.4)	1.7, 1.7 (1.7)
No. of antennomeres	8	11	12, 13	14	15	16, 17	17	18, 18	19, —	20, 21	19, 19	19, 20
No. of ommatidia	38–42	58–66	85–97	112–141	133–145	192–227	266–288	369, 371	419, 430	479, 482	494, 499	449, 455
No. of cercomeres	28–34	32–42	16–29	29–36	30–32	37–44	33–41	31, 35	40, 41	33, 34	1, 1	1, 1

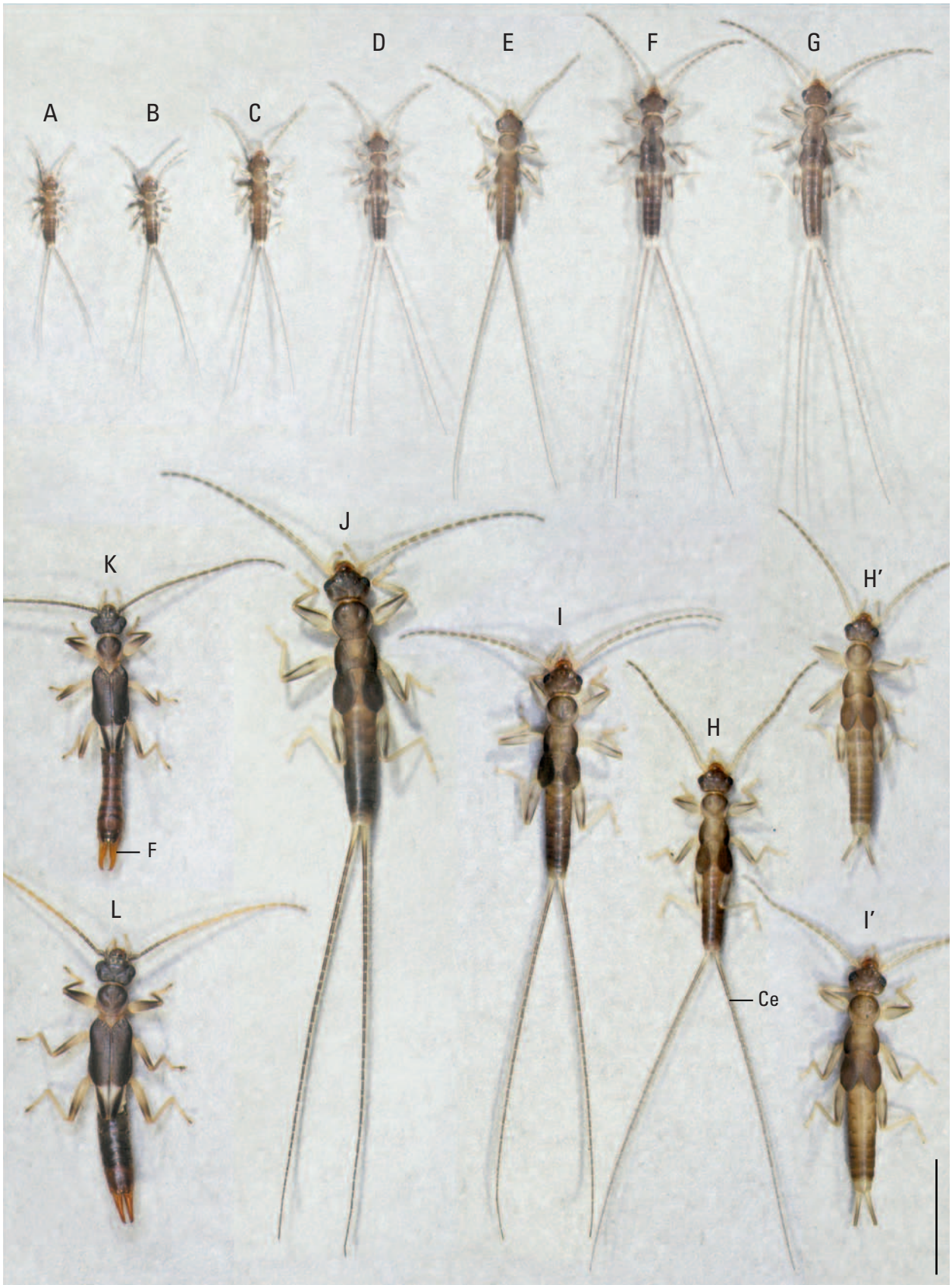
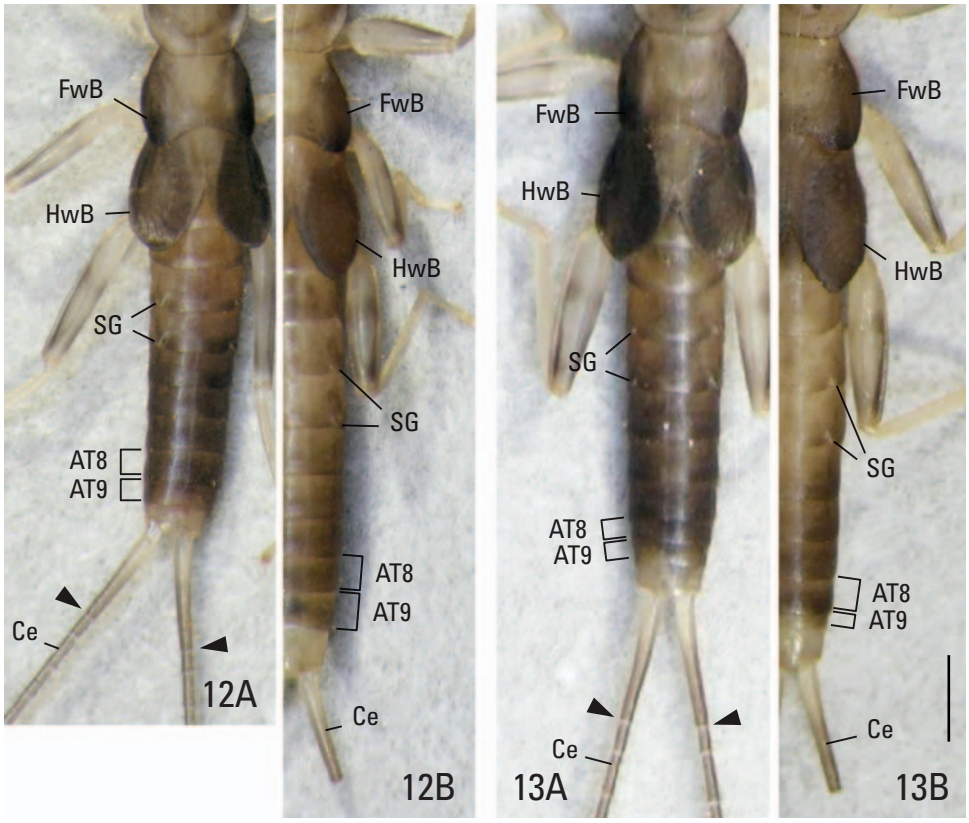


Fig. 11. Larval instars and adults of *Diplatys flavicollis* (Shiraki, 1907). **A**: First instar larva. **B**: Second instar larva. **C**: Third instar larva. **D**: Fourth instar larva. **E**: Fifth instar larva. **F**: Sixth instar larva. **G**: Seventh instar larva. **H**: Eighth instar (final instar) larva, male. **H'**: Late eighth instar (final instar) larva, male: cerci eaten with only the basal part left. **I**: Eighth instar (final instar) larva, female. **I'**: Late eighth instar (final instar) larva, female: cerci eaten with only the basal part left. **J**: Ninth instar (final instar) larva, female. **K**: Adult, male. **L**: Adult, female. H, H' and K as well as I, I' and L are the same individuals. Ce = cercus; F = forceps. Scale bar = 5 mm (all figures are in the same magnification).



Figs. 12, 13. Thorax and abdomen of the eighth instar (final instar) larvae of *Diplatys flavicollis* (Shiraki, 1907). **12**: Male, the same individual as shown in Fig. 11H,H'. 12A: Early eighth instar larva. Arrowheads show the distal ends of the basalmost cercomeres. 12B: Late eighth instar larva, whose cerci have been eaten with only the basalmost cercomeres left, the same larva as shown in 12A. **13**: Female, the same individual shown in Fig. 11I,I'. 13A: Early eighth instar larva. Arrowheads show the ends of the basalmost cercomeres. 13B: Late eighth instar larva, whose cerci have been eaten with only the basalmost cercomeres left, the same larva as shown in 13A. AT8, 9 = eighth and ninth abdominal terga; Ce = cercus; FwB = forewing bud; HwB = hindwing bud; SG = stink gland. Scale bar = 1 mm (all figures are in the same magnification).

of *D. flavicollis* (after the prelarval stage) is eight or nine, the latter being based only on one case observed in a female (Table 1, Fig. 11). The larval period of *D. flavicollis* is about five months in total.

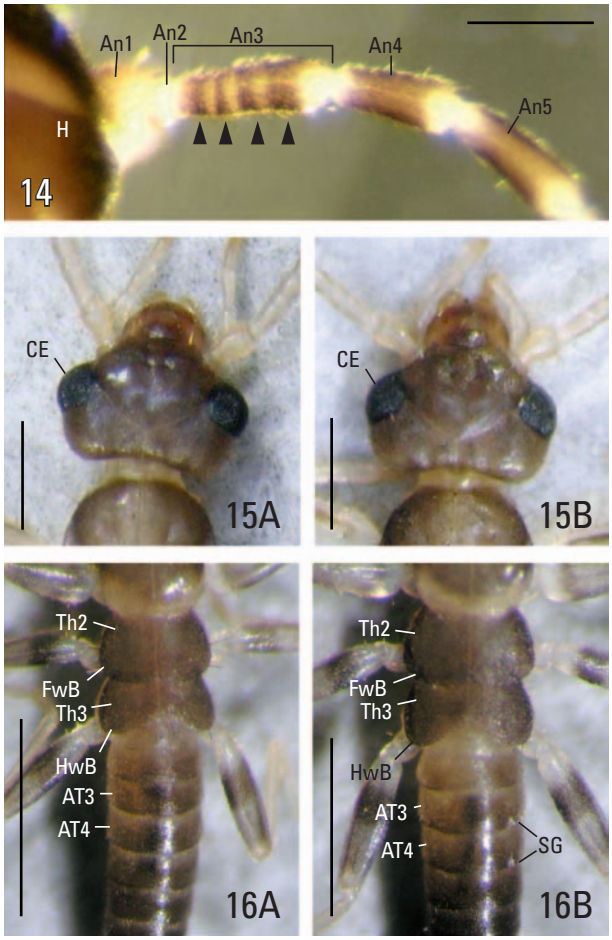
1. Body coloration. The body of the larvae is uniformly brownish (Figs. 1C, 11A–J,H',I'). In adults, the head, forewings and squamae are dark brown, the abdomen and forceps are reddish brown, and the pronotum has a pattern of dark brown and ivory colors, which varies between individuals (Figs. 1A,B, 3, 4, 6, 11K,L).

2. Body length. It increases 3.5-fold from 2.8 mm in average in the first instar larvae to ca. 10 mm in the adults (Table 1). The final instar larvae of the males show a conspicuous elongation of the body, which is due to a large extension of the abdomen (Fig. 12A,B), compared to those of the females, in which the ninth abdominal segment is shortened (Fig. 13A,B).

In the captive-bred population we found one female who underwent one more molting after the eighth instar (Fig. 11J). This female was notably larger than ordinary larvae of the eighth instar (Fig. 11H,I,H',I').

3. Head. The head increases in size with development, but its length-width ratio is nearly constant at around 0.9 (Table 1).

4. Antennae. The number of antennomeres increases with each molt (Table 1). No overlap in the number of antennomeres between instars was observed except for the sixth and seventh instars and for the final larval instar and adults (Table 1). The first instar larvae have eight antennomeres. With the first molt, three antennomeres are added, and with each subsequent molt, the antennomeres increase in number by one or two. The number of antennomeres in adults is around 20. In the final larval instar, the number was 18 or 19, and in one example where an additional molting occurred, it was 20 and 21 (Table 1). The new antennomeres are produced in the third antennomere (= first flagellomere) named the "meriston". Fig. 14 shows the basal part of the antenna of a first instar larva, and in the meriston four annuli are observed.



Figs. 14–16. Some morphological features of *Diplatys flavicollis* (Shiraki, 1907) larvae. **14**: Proximal part of the right antenna of first instar just before molting. Arrowheads show the antennomeres prepared for the second instar inside the third antennomere (meriston). **15**: Head of eighth instar (final instar) male (15A) and female (15B). **16**: Thorax and abdomen of the first (16A) and second (16B) instar. An1–5 = first to fifth antennomeres; AT3, 4 = third and fourth abdominal terga; CE = compound eye; FwB = forewing bud; H = head; HwB = hindwing bud; SG = stink gland; Th2, 3 = meso- and metathorax. Scale bars = 14: 500 µm; 15A,B, 16A,B: 1 mm.

5. Compound eyes. The ommatidia constantly increase in number from about 40 in the first instar to nearly 500 in adults (Table 1). Between- and within-individual variances in the ommatidial numbers become larger with successive moltings (Table 1). In adults, the compound eyes are more protruding and rounded in males than in females. The same was found in final instar larvae whose sex was determined (Fig. 15A,B).

6. Pronotum. The length-width ratio of the pronotum is ca. 0.8 in the first instar larvae, and it gradually approaches 1 (Table 1).

7. Wing buds and wings. The wing buds or the anlagen of the fore- and hindwings are the "posterolateral corners" of the meso- and metanotum, respectively. While the forewing buds are difficult to recognize in early instars (Figs. 1C, 16A,B), they gradually increase in size and distinctness (Fig. 11A–J,H',I'). The venation of the hindwings appears in the sixth instar larvae.

8. Stink glands. *D. flavicollis* has a pair of stink glands each at their posterior margins of the third and fourth abdominal terga. They are clearly found in the second instar larvae (Fig. 16B) but are at least externally difficult to discern in the first instar (Fig. 16A).

9. Cerci. In *D. flavicollis*, the cerci are filamentous throughout the larval period, and become a pair of forceps in the adults. The number of cercomeres in the larvae is 30–40; it varies between individuals (Table 1) but there is no regular variation of cercomere number between different instars. However, individual "variation" may be because the larval filamentous cerci of *D. flavicollis* are very delicate and break easily. When sucked by an aspirator and struck to its wall, the cerci are sometimes broken partially, and in extreme cases, they are shed off from the bases. At the molting, shorter cerci are regenerated, and with subsequent moltings, they reach their original length.

Nearing the eclosion, the final instar larvae eat their own cerci leaving only the fairly long basalmost cercomere. Fig. 17A, B and C are successive scenes of a female's self-feeding of cerci: (A) she is eating her right cercus; (B) the right cercus is almost eaten; (C) she has eaten both cerci. Fig. 12A and B show the posterior body of the same male before and after the cerci-eating, respectively, and likewise, Fig. 13A and B show that of the same female before and after the cerci-eating. The arrowheads in the figures show the distal ends of the basalmost cercomeres, and it is evident that the cerci have been totally eaten leaving the basalmost cercomeres. The individuals go through eclosion and become adults in which the cerci have changed into a pair of forceps (Fig. 18).

4. Discussion

4.1. Egg deposition

Diplatys flavicollis deposits eggs with an adhesive stalk at the posterior pole, which attaches to the substratum. Although Green (1898) mentioned the attachment of *Diplatys greeni* (Burr, 1898) eggs without any reference to an adhesive stalk, an adhesive

stalk was reported for a Papua New Guinean diplatyid gen. sp. by MATZKE & KLASS (2005). For another basal dermapteran family, Pygidicranidae, adhesive substances have been reported to occur on the eggs of *Tagalina papua*, *Tagalina burri* Hincks, 1955, and *Paracranopygia siamensis* (Dohrn, 1863) (MATZKE & KLASS 2005), but they are simply massive, not stalk-shaped. The adhesive stalk may be a characteristic of Diplatyidae. Very recently, we (SHIMIZU & MACHIDA 2011) reported that the apachyid dermapteran *Apachyus chartaceus* (de Haan, 1842) lays eggs with an adhesive substance on their posterior half. Once the adhesive substance has dried and hardened, the eggs cannot be moved (MATZKE & KLASS 2005; SHIMIZU & MACHIDA 2009, 2011, herein). Then the mothers can no longer rearrange their eggs, different from the higher dermapterans, which often rearrange and sometimes transport their eggs to more favorable places, i.e. eggs are subject to intensive maternal care.

Adhesive substance on the eggs thus occurs in all Diplatyidae and Pygidicranidae so far examined in this regard (data are lacking for Karschiellidae), and in Apachyidae, which likely represents (one of) the basalmost clade(s) of the higher Forficulina (cf. HAAS & KLASS 2003; KLASS 2003). On the other hand, this feature was observed to be absent is all other higher Dermaptera with brood care studied (surveyed in MATZKE & KLASS 2005). Thus, the possession of an adhesive which attaches eggs to the substratum may be regarded as an ancestral feature in Dermaptera as MATZKE & KLASS (2005) and SHIMIZU & MACHIDA (2009, 2011) suggested. KLASS (2003) and MATZKE & KLASS (2005) suggested the presence of adhesive substance to be correlated with the presence of accessory glands of abdominal segment IX, which are present in many dicondylian Insecta with well-developed female external genitalia (not yet examined for Apachyidae). The lack of these glands and the adhesive substance might be a shared apomorphy of higher Forficulina excluding Apachyidae. It is noteworthy, however, that in Diplatyidae the degree of development of the accessory glands varies strongly: they are well developed in *Haplodiplatys orientalis* Steinmann, 1974 but vestigial in *Diplatys macrocephalus* Palisot de Beauvois, 1805 (KLASS 2003: "ag" in figs. 38, 43). A study of a broader range of Diplatyidae with regard to egg attachment would thus be of interest.

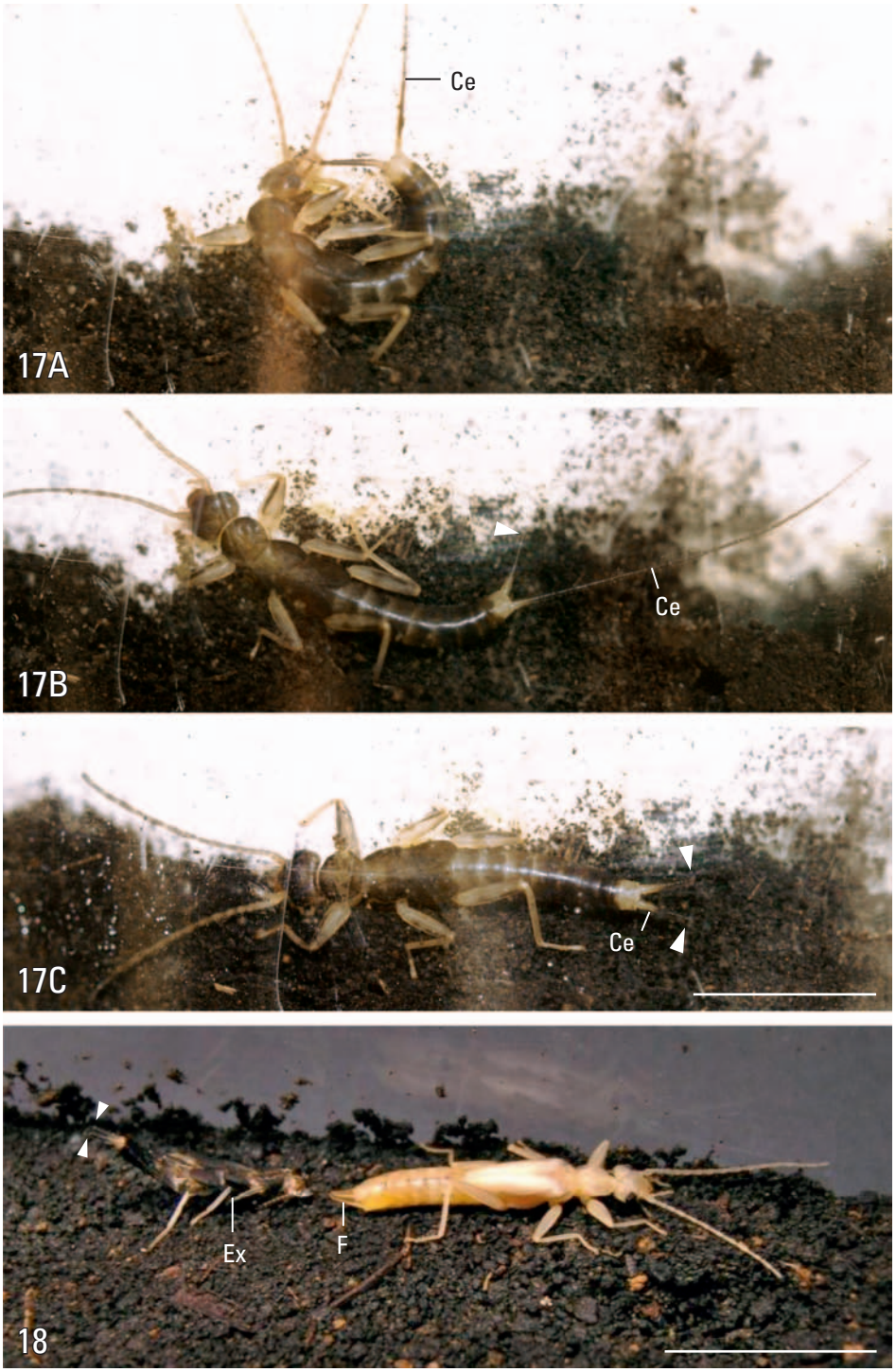
4.2. Maternal brood care

The intensive and elaborate maternal brood care of eggs and young larvae is a well known characteristic of the higher Forficulina (except for Apachyidae, in which the maternal care of eggs has not yet been observed: SHIMIZU & MACHIDA 2011). MATZKE & KLASS (2005) listed the following attributes of brood care: (1) association with her eggs, (2) cleaning of and application of secretions to eggs by licking, (3) transport of eggs to favorable places, (4) defense of eggs, (5) association with first instar larvae, (6) defense of first instar larvae, (7) transportation of first instar larvae, (8) help in hatching by feeding on egg shell, (9) frequent contact between mother's and first instar larval mouthparts, (10) providing food for first instar larvae (sometimes represented by the mother's own dead body); and (11) young larvae occasionally sit on the mother's back. While features (1)–(6) have been found quite consistently in studies on higher Forficulina, features (7)–(11) have been reported more sporadically.

MATZKE & KLASS (2005) provided detailed information on the reproductive biology of Pygidicranidae, based on their study of *Tagalina papua*. According to them, Pygidicranidae show features (1), (4), (5), (6) (i.e. association with and defense of eggs and young larvae) but not (2), (3), (7), (8), (9), (10), (11): the *T. papua* mother merely touches the eggs with her mouthparts, but never licks them or applies secretions. The maternal brood care in Pygidicranidae may be much less intensive and elaborate than in the higher Forficulina.

Concerning maternal brood care in Diplatyidae, GREEN (1898) reported features (1) and (2) for *Diplatys greeni*, and MATZKE & KLASS (2005) found features (1) and (5) in a Papua New Guinean diplatyid gen. sp. The present study revealed in *Diplatys flavicollis* the features (1), (3), (4), (5), and (6). This means, the mother not only remains with the eggs and young larvae but also defends them. The lacking observation of defence in the study of MATZKE & KLASS (2005) could well be an effect of captivity. GREEN (1898) did not report a relationship between mother and young larvae, but it cannot be excluded that the observations were simply stopped before the first larvae hatched. In addition, the *D. flavicollis* mother arranges her eggs, but only shortly after oviposition before the adhesive stalks have firmly attached the eggs to the substratum. This initial arrangement rarely observed in *D. flavicollis* is not strictly comparable to feature (3) in the higher Forficulina, where eggs can be rearranged at any time until hatching.

Maternal brood care may thus differ in some features among species of Diplatyidae, but they are similar in not showing features (7)–(11) and the maternal brood care observed in these diplatyids (and pygidicranids) is less intensive and elaborate than in the higher Forficulina. Diplatyidae and Pygidicranidae are well accepted to represent (along with Karschiellidae) the basal clades of Forficulina (HAAS 1995; HAAS &



Figs. 17, 18. Self-feeding of cerci and eclosion of *Diplatys flavicollis* (Shiraki, 1907). **17**: Successive scenes of a female's self-feeding of cerci (see text). Arrowheads show the distal ends of cerci. **18**: Eclosion, female. Arrowheads show the distal ends of cerci. Ce = cercus; Ex = exuvia; F = forceps. Scale bars = 5 mm.

Kukalová-Peck 2001; Haas & Klass 2003), and their less intensive and elaborate maternal brood care may represent the ancestral condition. Matzke & Klass (2005) assumed that transport and cleaning of eggs have evolved within Dermaptera, and the attachment of the eggs was given up and the accessory glands reduced in favor of an intensified care including transport of eggs to more favorable conditions.

4.3. Postembryonic development

Matzke & Klass (2005) summarized the number of larval instars of Forficulina hitherto investigated. In the higher Forficulina, although there are intraspecific variations, Anisolabididae and Labiduridae have generally five larval instars, while the more advanced

groups of the higher Forficulina (Eudermaptera including Chelisochidae, Forficulidae and Spongiphoridae) have only four larval instars. Arixeniina and Hemimerina are supposed to have four larval instars either. MATZKE & KLASS (2005) first clarified in detail the postembryonic development of Pygidicranidae. They revealed that the number of larval instars in Pygidicranidae is six and rarely seven, and suggested that the larger number is plesiomorphic in Dermaptera, taking the currently proposed phylogenetic hypotheses for Dermaptera into consideration (cf. HAAS & KUKALOVÁ-PECK 2001; KLASS 2003). In this respect, the present results on the postembryonic development of *Diplatys flavicollis* are noteworthy. The present study revealed that Diplatyidae have eight and occasionally nine larval instars, the maximum number reported for Dermaptera. It should be noted, however, that eight larval instars have previously been observed as a rare case in *Euborellia cincticollis* (Gerstaecker, 1883) (Anisolabididae; KNABKE & GRIGARICK 1971, see also KLASS & MATZKE 2005: table 4), where the number of larval instars usually ranges from 5 to 7.

GÜNTHER & HERTER (1974) reviewed the changes of antennomeres during postembryonic development in Dermaptera including Arixeniina and Hemimerina. Adding to this the data of MATZKE & KLASS (2005) for Pygidicranidae and the present results for Diplatyidae, we know that the first instar larvae of Dermaptera have eight antennomeres (no information on postembryonic development available for Karschiellidae and Apachyidae). Most likely this is a first-instar groundplan feature of Dermaptera. GILES (1953) reported that the antennomeres are newly produced within the third annulus of antenna, i.e., the first annulus of flagellum (meriston) in *Anisolabis littorea* (White, 1846). In the present study, we found the same condition for *Diplatys flavicollis*. This kind of production of antennomeres is typical in Polyneoptera (cf. HOCKMAN et al. 2009).

The forceps are the most outstanding characteristic of the forficuline earwigs. They are derivatives of cerci, which are multisegmented in many other Polyneoptera as well as Zygentoma and Archaeognatha. Some extinct, primitive representatives of Dermaptera, such as Jurassic Protodiplatyidae, possessed multisegmented filamentous cerci as adults, as shown by their co-occurrence with wings in the same specimen (e.g. GRIMALDI & ENGEL 2005: fig. 7.47). GRIMALDI & ENGEL (2005) thus rightfully regarded multisegmented cerci as plesiomorphic for Dermaptera. Among extant dermapterans only larvae of Karschellidae and Diplatyidae are known to have multisegmented filamentous cerci, which become forceps only with the last molt (VERHOEFF 1902; GRIMALDI & ENGEL 2005). *Karschiella neavei* Burr, 1909, however, has one-segmented cerci also in the larval stage (HINCKS 1959). GREEN (1898) found the forceps prepared inside the cerci cut in short in *Diplatys gerstaeckeri* (Dohrn, 1863), and he supposed that the cerci were shortened by self-feeding. In the present study, we verified GREEN's prediction (Fig. 17A–C). Some kind of cell death (apoptosis) may have occurred prior to the self-feeding.

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