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Development and reproductive biology of Dermaptera: a comparative study of thirteen species from eight families

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Abstract

We examine and describe the embryonic development of 13 species from eight families of Dermaptera, i.e., all families excluding Karschiellidae, Hemimeridae, and Arixeniidae: *Diplatys flavicollis* (Diplatyidae), *Cranopygia* sp., *Echinosoma* sp., and *Parapsalis infernalis* (Pygidicranidae), *Apachyus chartaceus* (Apachyidae), *Anisolabis maritima* and *Euborellia pallipes* (Anisolabididae), *Labidura riparia* (Labiduridae), *Forficula scudderi* and *Anechura harmandi* (Forficulidae), *Paralabella curvicauda* (Spongiphoridae), and *Proreus simulans* and chelisochid gen. sp. (Chelisochidae). We also provide new findings on the reproductive biology of the Pygidicranidae and the postembryonic development of the Apachyidae. Based on information from the present and previous studies, we reconstruct the developmental and reproductive-biological groundplan for Dermaptera and discuss phylogenetic issues related to this order. We confirmed that Dermaptera possesses the embryological features (related to mode of embryonic formation and manner of blastokinesis) that are regarded as autapomorphies of Polyneoptera. Eudermaptera is characterized by the extraordinarily great length of the embryo which attains its maximum length in anatrepsis period, the positioning of its posterior end at the egg's anterior ventral side, the type of egg tooth, and four larval instars. Anisolabididae, Labiduridae, and Eudermaptera share an elongation ratio of embryos in the anatrepsis period (ERE) of 160% or less and a larval instar number of five or less, whereas Protodermaptera is characterized by an ERE of 210% or more, a ratio of embryonic primordium relative to the egg's longitudinal circumference (IL) of 40% or less, and a larval instar number of six or more. Notably, the ERE, IL, and larval instar number of Apachyidae are within the ranges observed in Protodermaptera.

Keywords

1.   Introduction

Dermaptera (earwigs) is an order of hemimetabolous insects containing approximately 2,000 described species. They show remarkable uniformity, with several specialized features, such as short tegminous forewings, underneath which the fan-shaped hindwings are uniquely and compactly folded in winged forms, the presence of two penises, and cerci that are modified into the form of claspers.

Dermaptera is a member of Polyneoptera (cf. Kristensen 1991; Haas and Kukalová-Peck 2001; Klass 2009; Ishiwata et al. 2011; Yoshizawa 2011; Trautwein et al. 2012; Misof et al. 2014; Wipfler et al. 2019), whose monophyly has long been debated but is strongly supported in recent studies (cf. Ishiwata et al. 2011; Yoshizawa 2011; Misof et al. 2014; Mashimo et al. 2014; Wipfler et al. 2019). Despite the extensive research on Polyneoptera, the phylogenetic relationships among orders remain partly obscure. The affinity of Dermaptera has also long been debated, and almost all polyneopteran orders, or assemblages of some of these orders, have been proposed as the sister group of Dermaptera (cf. Neubert et al. 2017: table 1). Recent phylogenomic studies, however, may be well-disposed to the affinity of Dermaptera and Zoraptera (Misof et al. 2014; Wipfler et al. 2019), whose assemblage is named Haplocercata, and suggest that Haplocercata forms the sister group to the remaining polyneopterans.

Dermaptera is currently classified into 11 families: Karschiellidae, Diplatyidae, Pygidicranidae, Apachyidae, Anisolabididae, Labiduridae, Forficulidae, Spongiphoridae, Chelisochidae, Hemimeridae, and Arixeniidae. The relationships among dermapteran families have been variously discussed and reconstructed in morphological and/or phylogenomic studies (e.g., Haas 1995; Haas and Kukalová-Peck 2001; Haas and Klass 2003; Colgan et al. 2003; Kamimura 2004; Haas and Gorb 2004; Jarvis et al. 2005; Kocarek et al. 2013; Kamimura and Lee 2014a, b; Naegle et al. 2016), as summarized in the study by Wipfler et al. (2020). Dermaptera is generally addressed on the traditional framework of "Protodermaptera–Epidermaptera". Protodermaptera (= basal Dermaptera = Pygidicranidea) is a paraphyletic group that is characterized by primitive features such as the blattoid neck and two posterior-directed penises, representing basal lineages of Dermaptera. Protodermaptera includes Karschiellidae, Diplatyidae, and Pygidicranidae. Karschiellidae is considered to represent the basalmost clade in Protodermaptera, whereas both Diplatyidae and Pygidicranidae have been suggested to be non-monophyletic (cf. Haas 1995; Haas and Kukalová-Peck 2001; Colgan et al. 2003; Jarvis et al. 2005; Kocarek et al. 2013; Naegle et al. 2016). Epidermaptera (= higher Forficulina = Forficulidea), which represents the majority of Dermaptera, has been suggested to be monophyletic and is characterized by the presence of one anterior- and one posterior-directed penis. Epidermaptera includes Apachyidae, Anisolabididae, Labiduridae, Forficulidae, Spongiphoridae, Chelisochidae, Hemimeridae, and Arixeniidae, and morphological and molecular phylogenetic analyses (e.g., Haas and Kukalová-Peck 2001; Jarvis et al. 2005; Kocarek et al. 2013; Kamimura and Lee 2014a; Naegle et al. 2016) have assigned the basal(-most) position in Epidermaptera to Apachyidae. Within Epidermaptera, the most strongly supported clade is Eudermaptera, which is composed of Forficulidae, Spongiphoridae (partim), Chelisochidae, Hemimeridae, and Arixeniidae, which are characterized by the reduction of one penis (cf. Kamimura and Lee 2014b; Wipfler et al. 2020). In addition, morphological and phylogenomic

studies have cast doubt on the monophyly of the traditional families Labiduridae and Spongiphoridae (cf. Haas and Kukalová-Peck 2001; Jarvis et al. 2005; Kocarek et al. 2013; Kamimura and Lee 2014b; Naegle et al. 2016). Recently, after analyzing a transcriptomic dataset containing 3,247 nuclear single-copy genes for 16 dermapteran species representing all families except Karschiellidae and Arixeniidae, Wipfler et al. (2020) addressed the relationships among the major dermapteran lineages and provided the following significant phylogenetic results: 1) Apachyidae form the sister group to the remaining included Dermaptera, implying that Epidermaptera is not monophyletic; 2) Protodermaptera, which has been recognized as non-monophyletic, is revived as a monophyletic clade, subordinate in paraphyletic Epidermaptera; 3) Epidermaptera excluding Apachyidae is monophyletic; 4) the monophyly of Eudermaptera is corroborated.

Our knowledge of the embryology of Dermaptera is restricted to a few species. For Hemimeridae and Arixeniidae, despite the difficulty of collecting material, embryological studies were reported in earlier times, probably due to the interest in their special reproductive biology, i.e., on *Hemimerus talpoides* in Heymons (1912) and on *Arixenia jacobsoni* in Hagan (1951). A Polish research group conducted a series of embryological studies on *H. talpoides* and *Arixenia esau* (Tworzydlo et al. 2013a, b, 2019; Bilinski and Tworzydlo 2019; Bilinski et al. 2019) and suggested their affinity to Epidermaptera or Eudermaptera. However, regarding the other families, embryological information is only known for three species of Epidermaptera. For *Forficula auricularia* of Forficulidae, Heymons (1895) examined and described the whole embryonic development, Strindberg (1915) studied the development of the alimentary canal, and Chauvin et al. (1991) reported the egg structure. For *Labidura riparia* of Labiduridae, Bhatnagar and Singh (1965) briefly described embryogenesis, and Singh (1967) studied gonadal development. For *Anisolabis maritima* of Anisolabididae, Fuse and Ando (1983) described the changes in external features during embryogenesis, while Ando and Machida (1987) explained early development, germ type, and blastokinesis.

Thus, information regarding Protodermaptera and half of the families in Epidermaptera is lacking. To understand the embryonic development of Dermaptera and to reconstruct its groundplan, an investigation involving more families should be conducted. For example, an extensive embryo anlage is known to form in examined dermapterans (e.g., Heymons 1895; Fuse and Ando 1983), which appears to be similar to the case of long germ embryos. In fact, Fuse and Ando (1983) and Ando and Machida (1987) regarded Dermaptera as having the long germ type, referring to the correlation of long germ embryogenesis with polytrophic ovarioles (Krause 1939) and the fact that Dermaptera have meroistic polytrophic ovarioles (Yamauchi and Yoshitake 1982). However, to fully understand the germ type of Dermaptera, information covering more families is required. The micropyles in *F. auricularia* were investigated by Heymons (1895) and Chauvin et al. (1991). However, these studies identified different struc-

tures as the micropyles. By reconstructing the groundplan for egg structure through a comparative survey on more groups, we can determine which structure is the micropyle.

In light of this background, we conducted a comparative embryological study of Dermaptera. In the present study, we examined and described the eggs and embryonic development of 13 species from the following eight families, i.e., all dermapteran families excluding Karschiellidae, which is an extremely rare dermapteran group inhabiting ant hills in Central Africa, and epizoic Hemimeridae and Arixeniidae: Diplatyidae, Pygidicranidae, Apachyidae, Anisolabididae, Labiduridae, Forficulidae, Spongiphoridae, and Chelisochidae. In addition, we obtained several interesting findings on the reproductive bi-ology of Pygidicranidae and postembryonic development of Apachyidae. Compared with previous studies, the observations on the development and reproductive biology of Dermaptera were critically examined and carefully discussed, especially in terms of phylogenetic perspectives.

2. Materials and methods

2.1. Materials and rearing

Thirteen dermapteran species were collected and studied: *Diplatys flavicollis* Shiraki, 1907 (Diplatyidae) (Fig. 1A),

Figure 1. Dermapterans examined in the present study (all males). **A** *Diplatys flavicollis* Shiraki, 1907 (Diplatyidae) (reposted from Shimizu and Machida 2011b: fig. 1A). **B** *Cranopygia* sp. (Pygidicranidae). **C** *Echinosoma* sp. (Pygidicranidae). **D** *Parapsalis infernalis* (Burr, 1913) (Pygidicranidae). **E** *Apachyus chartaceus* (de Haan, 1842) (Apachyidae). **F** *Anisolabis maritima* (Bonelli, 1832) (Anisolabididae). **G** *Euborellia pallipes* (Dohrn, 1863) (Anisolabididae). **H** *Labidura riparia* Pallas, 1773 (Labiduridae). **I** *Forficula scudderi* Bormans, 1880 (Forficulidae). **J** *Anechura harmandi* (Burr, 1904) (Forficulidae). **K** *Paralabella curvicauda* (Motschlsky, 1863) (Spongiphoridae). **L** *Proreus simulans* (Stål, 1860) (Chelisochidae). **M** A chelisochid gen. sp. (Chelisochidae). – Scale bars: 5 mm.

Table 1. Information on the collection of examined Dermaptera.

Family	Subfamily	Species	Site and date
Diplatyidae	Diplatyinae	*Diplatys flavicollis*	Ishigaki Isl., Okinawa, Japan (Apr., Oct. 2007, Apr. 2008, Jun. 2010, 2011)
Pygidicranidae	Pygidicraninae	*Cranopygia* sp.	Ulu Gombak, Selangor, Malaysia (Apr. 2010, 2011)
Pygidicranidae	Echinosomatinae	*Echinosoma* sp.	Ulu Gombak, Selangor, Malaysia (Apr. 2010, 2011)
Pygidicranidae	Echinosomatinae	*Parapsalis infernalis*	Amami-O-Shima Isl., Kagoshima, Japan (Mar. 2010)
Apachyidae	Apachyinae	*Apachyus chartaceus*	Ulu Gombak, Selangor, Malaysia (Feb. 2009, Apr. 2010, 2011)
Anisolabididae	Anisolabidinae	*Anisolabis maritima*	Joetsu, Niigata, Japan (Sep. 2007–2009); Minamiminowa, Nagano, Japan (Sep. 2010, Jun. 2011)
Anisolabididae	Anisolabidinae	*Euborellia pallipes*	Tsukuba, Ibaraki, Japan (May 2010); Matsumoto, Nagano, Japan (Jul. 15, 2022)
Labiduridae	Labidurinae	*Labidura riparia*	Joetsu, Niigata, Japan (Sep. 2007–2009); Tsukuba, Ibaraki, Japan (Sep. 2010, Jun. 2012)
Forficulidae	Forficulinae	*Forficula scudderi*	Tsukuba, Ibaraki, Japan (Sep. 2010, Jun. 2012)
Forficulidae	Anechurinae	*Anechura harmandi*	Obuse, Nagano, Japan (Jun. 2010, Jul., Aug. 2011); Minamiminowa, Nagano, Japan (Aug. 2012)
Spongiphoridae	Labiinae	*Paralabella curvicauda*	Amami-O-Shima Isl., Kagoshima, Japan (Apr. 2007, 2008); Ishigaki Isl., Okinawa, Japan (Mar., Jul. 2010)
Chelisochidae	Chelisochinae	*Proreus simulans*	Amami-O-Shima Isl., Kagoshima, Japan (Apr. 2007, 2008); Ishigaki Isl., Okinawa, Japan (Mar., Jul. 2010)
Chelisochidae	Chelisochinae	gen. sp.	Tanah Rata, Pahang, Malaysia (Feb. 2009, Apr. 2011)

Cranopygia sp. (Pygidicranidae) (Fig. 1B), *Echinosoma* sp. (Pygidicranidae) (Fig. 1C), *Parapsalis infernalis* (Burr, 1913) (Pygidicranidae) (Fig. 1D), *Apachyus chartaceus* (de Haan, 1842) (Apachyidae) (Fig. 1E), *Anisolabis maritima* (Bonelli, 1832) (Anisolabididae) (Fig. 1F), *Euborellia pallipes* (Shiraki, 1905) (Anisolabididae) [with many synonyms, e.g., *E. annulata*, *E. plebeja*, and *E. stali*; see Kamimura et al. (2023)] (Fig. 1G), *Labidura riparia* (Pallas, 1773) (Labiduridae) (Fig. 1H), *Forficula scudderi* (Bormans, 1880) (Forficulidae) (Fig. 1I), *Anechura harmandi* (Burr, 1904) (Forficulidae) (Fig. 1J), *Paralabella curvicauda* (Motschlsky, 1863) (Spongiphoridae) (Fig. 1K), *Proreus simulans* (Stål, 1860) (Chelisochidae) (Fig. 1L), and a different chelisochid gen. sp. (Fig. 1M). The collection data are shown in Table 1.

The collected dermapterans were kept in cylindrical plastic cases (height 5 cm, diameter 8 cm) containing a layer of moistened soil. The cases were kept at 18–25°C for Japanese species and 25°C for Malaysian species, and the insects were fed on dried anchovies, dead *Drosophila*, or a compound feed composed of yeast extracts, chlorella extracts, carrot powder, goldfish food, and powdered dried silkworm pupae (commercially available fishing bait). Rearing methods for *D. flavicollis* and *A. chartaceus* have been described in detail in Shimizu and Machida (2011a, b).

2.2. Embryology

Fixation. Live eggs obtained were observed under a stereomicroscope (MZ 12, Leica, Heerbrugg, Switzerland) and photographed with a digital camera (E-8400, Nikon, Tokyo, Japan or E-620, Olympus, Tokyo, Japan). For fixation, eggs were cleaned with a soft brush in Ephrussi-Beadle solution (0.75% NaCl, 0.035% KCl, 0.021% CaCl$_2$), transferred to Carl's fixative (ethyl alcohol : formalin : acetic acid : distilled water = 15:6:2:30), punctuated with a fine needle, and left in the fixative for 1–3 h at room temperature (18–25°C). After this treatment, a small window was made on the eggshell with fine forceps, and the eggs were kept in the fixative for 2–3 days. Newly hatched first instar larvae were fixed in the same fixative for 1–3 h, and their body wall was perforated with a fine needle; subsequently, they were kept in the fixative for 2–3 days with a small window opened on their body wall. Fixed samples were transferred to and stored in 70% ethyl alcohol.

Light microscopy of embryos. The fixed eggs were stained with a DAPI (4′,6-diamidino-2-phenylindole dihydrochloride) solution (DAPI in 0.1 M HCl-sodium cacodylate buffer, pH 7.2, at 10 µg/ml) for 1 h to 1 week, observed with a fluorescence stereomicroscope (MZ FL III, Leica, Heerbrugg, Switzerland) under UV-excitation at 360 nm, and photographed with a digital camera (Nikon E-8400 or Olympus E-620).

Scanning electron microscopy of eggs and embryos. Some of the fixed eggs and the embryos that were dissected out of the fixed eggs with fine forceps, all of which had been stored in 70% ethyl alcohol, were hydrated through a graded ethyl alcohol series, postfixed with 1% OsO$_4$ for 1 h, dehydrated through a graded ethyl alcohol series, dried with a critical point dryer (Samdri®-PVT-3D, tousimis, Rockville, Maryland, USA), coated with gold with an ion sputter (JFC-1100, JEOL, Tokyo, Japan), and observed under a scanning electron microscope (SM-300, TOPCON, Tokyo, Japan).

Histology of embryos. Several fixed eggs and embryos were processed into 2-µm-thick methacrylate sections according to Machida et al. (1994). Sections were stained with Mayer acid hemalaun or 1% Delafield hematoxylin and 0.5% eosin G.

Orientation of eggs. The orientation of the egg, i.e., its anteroposterior and dorsoventral axes, was designated according to that of the embryo just before hatching, i.e., during the post-katatrepsis period.

Length and position of embryos. The length of the newly formed embryo (Stage 3) is designated as the "initial length (**IL**)". With the progressive development, the embryo elongates and attains its "maximum length in the anatrepsis period (**ML**)" (Stage 5). Both **IL** and **ML** are defined as the ratio between embryo length and the longitudinal circumference of the egg at the respective stage. The embryo's elongation in the anatrepsis period is defined by the "elongation ratio of embryo (**ERE**)", which is the **ML** divided by the **IL**. The "position of anterior end of the newly formed embryo (**PAEE**)" (Stage 3) is defined as the ratio between the distance from the embryo's anterior end to the egg's posterior pole and the egg length. The approximate "position of the posterior end of the embryo attaining its maximum length in the anatrepsis (**PPEE**)" (Stage 5) is also given in the description.

2.3.   Reproductive biology

The reproductive biology of some pygidicranid dermapterans, which has remained unknown or is only partially known, i.e., *Cranopygia* sp., *Echinosoma* sp., and *Parapsalis infernalis*, as well as that of apachyid *Apachyus chartaceus*, partially described in Shimizu and Machida (2011a), was recorded with a Nikon E-8400 or an Olympus E-620 digital camera. In addition, we succeeded in raising hatchlings of *A. chartaceus* to adults (for rearing technique see Shimizu and Machida 2011a). To record their postembryonic development, the specimens were anesthetized with diethyl ether vapor and photographed.

3.   Results

The egg structure and embryonic development of dermapterans were investigated, and we also report new findings on the reproductive biology of pygidicranids and the postembryonic development of *Apachyus chartaceus*. Regarding embryonic development, we first described that of *Diplatys flavicollis* in detail, with special reference to external morphology, dividing it into nine stages. Then we described the embryonic development of other dermapterans according to the staging defined for *D. flavicollis*, focusing on the differences from *D. flavicollis* and/or other species.

3.1.   *Diplatys flavicollis* (Diplatyidae)

3.1.1.   Eggs

We previously described the eggs of this species (Shimizu and Machida 2009; 2011b). They are ellipsoidal, approximately 1 mm long and 0.6 mm wide (freshly laid eggs), and yellowish ivory in color (Fig. 2A, B). The egg is covered with an adhesive substance, which is abundant at the posterior pole, where it forms a stalk ca. 250 μm long, used to attach the eggs to the nest wall (Fig. 2A, B) (Shimizu and Machida 2011b).

In the anterior pole of the egg, about 10 micropyles of 1–2 μm in diameter are arranged in a circle ca. 50 μm in diameter (Fig. 2C). The chorionic pore at the center of the circular arrangement of micropyles observed in some other dermapterans was not found.

3.1.2.   Embryonic development

At 25°C, the egg period is 18–19 days.

Stage 1. Fig. 6A. Egg cleavage is of the superficial type. Most cleavage nuclei arrive at the egg periphery by the seventh cleavage. These nuclei are uniformly distributed on the egg surface (Fig. 6A).

Stage 2. Fig. 6B. Cleavage nuclei in the egg periphery proliferate and form a unicellular layer, the blastoderm (Fig. 6B). Nuclei segregated from the blastoderm into the yolk as secondary yolk nuclei are uniformly distributed beneath the blastoderm (Fig. 6B, cf. Figs 6C, D, 7A, A').

Stage 3. Figs 6C–F, 7A, A', B–B", C–C'", D–D'", E, E'. The blastoderm differentiates into two areas with different cellular densities (Figs 6C, 7A, A'). The area with higher cellular density, where the lateral regions are more densely cellulated, is the embryonic area, which occupies 3/4 of the ventral side of the egg. The area with lower cellular density is the extraembryonic area, which represents the serosa, i.e., an embryonic membrane directly derived from the blastoderm. The paired lateral regions with a higher cellular density in the newly differentiated embryonic area, i.e., the lateral plates, are the precursor of ectoderm, and the median region between the paired lateral plates, i.e., the median plate, is the precursor of mesoderm (Fig. 7A'). Soon, the paired lateral plates start to migrate medially (Figs 6D, 7B, B', B"), and the sole-shaped embryo anlage appears: the wide anterior part is the protocephalon and the posterior narrower part is the protocorm (Figs 6E, 7C, C'–C'"). Figure 7E and E' show a transverse section of an embryo anlage of early-middle Stage 3, wherein paired thicker regions (lateral plates) and a thinner region (median plate) between them can be distinguished.

As a result of medial migration of the lateral plates, the median plate becomes narrower (Fig. 7B') to form the primitive groove (Fig. 7C'–C'"). The lateral plates further migrate medially and finally fuse with each other, with the primitive groove becoming obliterated, and the

embryo of ca. 700 µm length and 400 µm width completes (Fig. 7D, D'–D'''). The newly formed embryo (also called "embryonic primordium" in "4. Discussion") occupies ca. 35% of the egg's longitudinal circumference (IL = 35%) (Figs 6F, 7D). The embryo undergoes posterior concentration and migration during its formation. By passing the posterior pole of the egg, the posterior end of the newly formed embryo is situated at the dorsal side of the egg, and the anterior end descends until ca. 45% from the posterior pole of the egg relative to the egg length (PAEE = 45%) (Figs 6E, F, 7C, C'', C''', D, D'', D'''). As
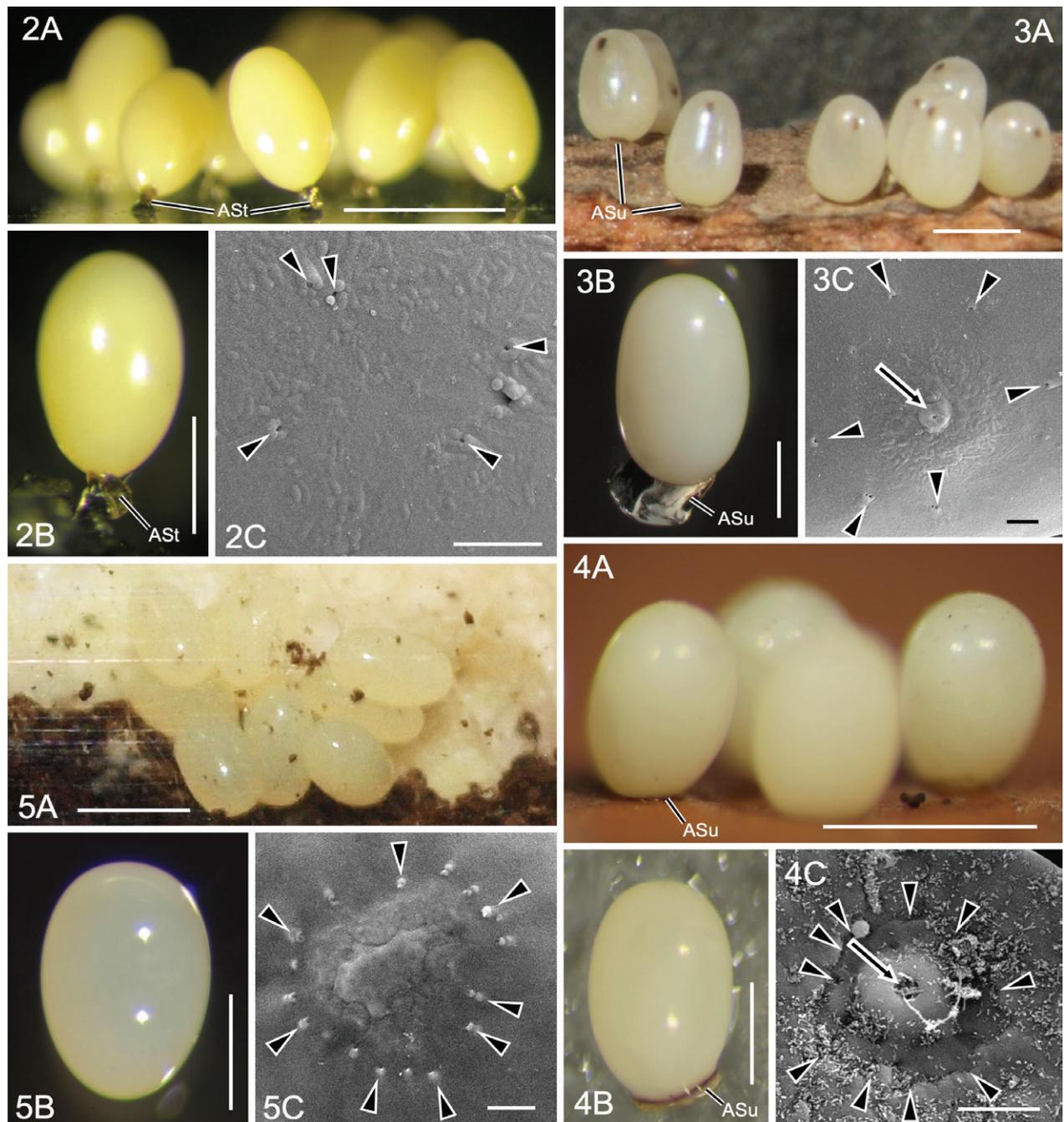
Figures 2–5. Eggs of the examined Protodermaptera. **2** *Diplatys flavicollis* (Diplatyidae). **2A** Egg clutch deposited on and attached to the substratum (glass plate) (reposted from Shimizu and Machida 2011b: fig. 5A). **2B** Enlarged image of an egg, anterior to the top (reposted from Shimizu and Machida 2011b: fig. 5B). **2C** Scanning electron micrograph (SEM) of the egg's anterior pole. **3** *Cranopygia* sp. **3A** Egg clutch stuck to the bark. **3B** Enlarged image of an egg with a stalk-shaped adhesive substance, anterior to the top. **3C** SEM of the anterior pole of the egg. Chorionic thickening with a central pore (arrow) at the center of the circular micropyle arrangement. **4** *Echinosoma* sp. **4A** Egg clutch stuck to the brick. **4B** Enlarged image of an egg, anterior to the top. **4C** SEM of the anterior pole of the egg. **5** *Parapsalis infernalis*. **5A** Egg cluch. **5B** Enlarged image of an egg, anterior to the top. **5C** SEM of the anterior pole of the egg. – Abbreviations: ASt – adhesive stalk; ASu – adhesive substance. – Symbols: arrow – chorionic pore at the center of the circular arrangement of micropyles; arrowhead – micropyle. – Scale bars: 2–5A – 1 mm; 2–5B – 500 µm; 2–5C – 20 µm.

a result, the newly formed embryo takes its position in the posterior half of the egg.

Stage 4. Figs 6G, 8A–A''', B, B'. The embryo starts elongating along the egg surface (Fig. 6G). In the following developmental steps up to katatrepsis, i.e., during the pre-katatrepsis period, the embryo keeps its cephalic end around the level of the egg's half length, and its posterior region ascends anteriorly on the dorsal surface of the egg (Fig. 6G–L). The embryo elongates, accompanied by segmentation, and the intercalary, mandibular, and maxillary segments differentiate in the anterior part of the protocorm (Fig. 8A–A'').

Simultaneous to the beginning of elongation, the embryo starts to sink beneath the serosa in association with the production of a second embryonic membrane, i.e., the amnion, and the amnioserosal fold starts to form (Fig. 8B, B'). This is the commencement of anatrepsis. The formation of the amnioserosal fold, which is faster toward the posterior, proceeds rapidly. Finally, the amnioserosal fold is closed at the anterior region of the embryo, i.e., around the gnathal region, and the amnioserosal fold completes.

Up to Stage 7, when katatrepsis occurs and the amnioserosal fold withdraws, the embryo undergoes development with its ventral side covered by the amnioserosal fold.

Stage 5. Figs 6H, I, 9A–A''', B–B'''', C–C''. With the embryo's progressive elongation, the segmentation, which started in the gnathal region in the previous stage, proceeds toward the posterior (Figs 6H, I, 9A, A', A''), and the appendages, which are lateroposteriorly-directed swellings, develop in the newly differentiated segments (Fig. 9B, B'–B''', C–C'').

Early in Stage 5, the embryo is segmented up to the thorax (Figs 6H, 9A–A'''), and antennal appendages arise in the posterior regions of the head lobe. Late in Stage 5, the posterior end of the embryo reaches the anterior pole of the egg (PPEE) (Figs 6I, 9B, B', B'''). The embryo acquires its maximum length in the anatrepsis period, covering ca. 80% of the egg's longitudinal circumference (ML = 80%; ERE = 230%) (Fig. 6I), and reaches its definitive position in the pre-katatrepsis period. This is the end of anatrepsis (for a definition of anatrepsis, see "4.3.3. Blastokinesis"). The segmentation proceeds up to
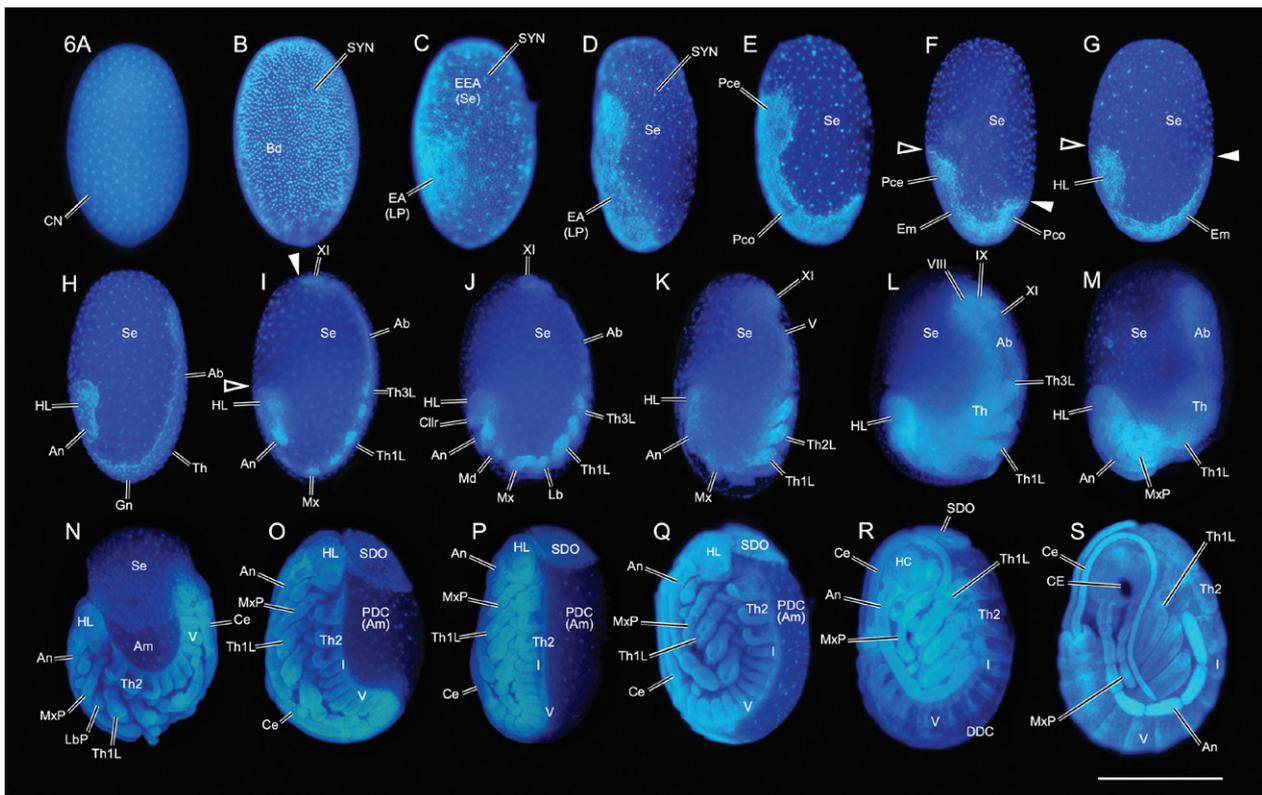

Figure 6. Embryonic development of *Diplatys flavicollis* (Diplatyidae), DAPI staining, UV-excitation, fluorescence microscopy. Lateral view, anterior to the top, ventral to the left. **A** Stage 1. **B** Stage 2. **C** Early Stage 3. **D** Early-middle Stage 3. **E** Middle-late Stage 3. **F** Late Stage 3. **G** Stage 4. **H** Early Stage 5. **I** Late Stage 5. **J** Early Stage 6. **K** Middle Stage 6. **L** Late Stage 6. **M** Early Stage 7. **N** Middle Stage 7. **O** Late Stage 7. **P** Early Stage 8. **Q** Middle Stage 8. **R** Late Stage 8. **S** Stage 9. – Abbreviations: Ab – abdominal region / abdomen; Am – amnion; An – antenna; Bd – blastoderm; CE – compound eye; Ce – cercus; Cllr – clypeolabrum; CN – cleavage nucleus; DDC – definitive dorsal closure; EA – embryonic area; EEA – extraembryonic area; Em – embryo; Gn – gnathal region; HC – head capsule; HL – head lobe; Lb – labium; LbP – labial palp; LP – lateral plate; Md – mandible; Mx – maxilla; MxP – maxillary palp; Pce – protocephalon; Pco – protocorm; PDC – provisional dorsal closure; SDO – secondary dorsal organ; Se – serosa; SYN – secondary yolk nucleus; Th – thoracic region / thorax; Th2 – 2nd thoracic segment; Th1L–3L – 1st to 3rd thoracic legs; I–XI – 1st to 11th abdominal segments. – Symbols: black arrowhead – anterior end of the embryo; white arrowhead – posterior end of the embryo. – Scale bar: 500 μm.

the middle region of the abdomen, but at its posterior end, the future 11th abdominal segment is precociously defined, with a pair of cercus anlagen distinguished as its segmen- tal appendages (Fig. 9B–B'''', C–C''). The segmental ap- pendages appear in the gnathal and thoracic regions (Figs 6I, 9B–B'''). The mandibular appendages are shorter than
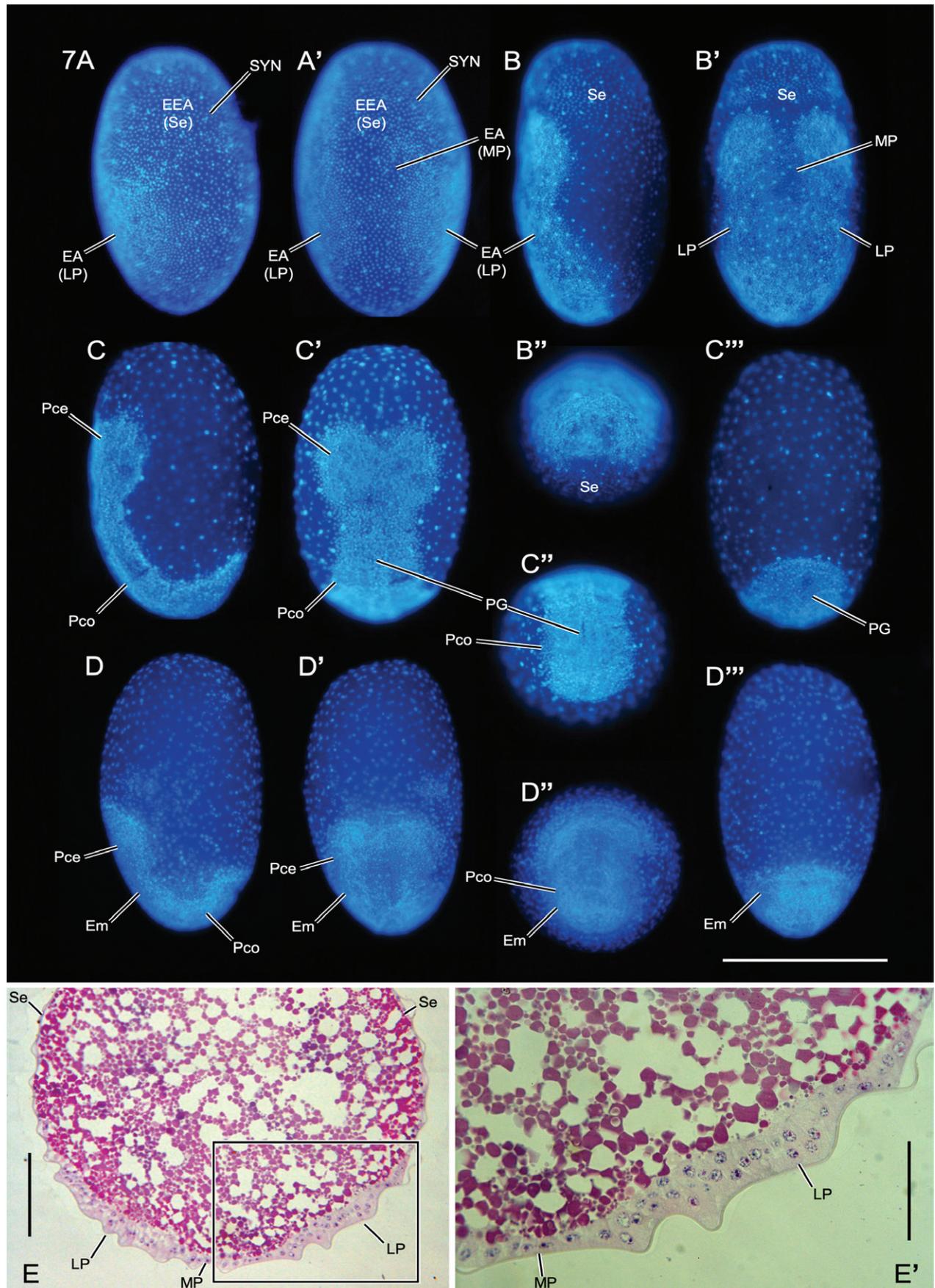
the others (Fig. 9B'', C). Appendages are not differentiated in the intercalary segment (Fig. 9B', C). The neural groove appears as a continuous median groove in the ventral surface of the embryo (Fig. 9C, C'). In the anterior extremity of the neural groove, the stomodaeum appears as a small depression (Fig. 9B', C).

Stage 6. Figs 6J–L, 10A–A''', B–B''', C–C''', D, D'. The embryo, which in the previous stage acquired its maximum length in the anatrepsis period on the egg surface (Fig. 6I), grows, with its abdomen gradually bent and immersed into the yolk (Figs 6J–L, 10A–C). The posterior region of the abdomen, not yet segmented in the previous stage (Fig. 9A''', B''', C''), is now segmented (Fig. 10A''', B''', C, D).

Early in Stage 6 the antennae have a medioposterior direction, while the other appendages aim lateroposteriorly (Fig. 10A'–A'''). The telopodites of the maxillary and labial appendages elongate and differentiate into the palps (Fig. 10A''). The medial region of the head lobe is swollen in front of the stomodaeum to become the clypeolabrum (Figs 6J, 10A–A''). The posterior part of the abdomen starts to bend ventrally (Fig. 10A, A''', arrowheads), and the proctodaeum appears as a small depression at the rear end of the embryo (Fig. 10A''').

In the middle of Stage 6, the appendages further develop, changing their direction from the original lateroposterior direction (Fig. 10A'–A''') to a medioposterior (Fig. 10B'–B''') direction. Late in Stage 6, with the progressive growth of the embryo, 11 abdominal segments are complete and the abdomen further elongates, curving between the 8th and 9th abdominal segments (Fig. 10C, D). Due to this ventral flexure of the abdomen, the caudal end points forward (Fig. 10C, C''', D). The appendages of the 11th abdominal segment, the cerci, elongate (Fig. 10C''', D). However, in the other abdominal segments, the appendages do not strongly develop (Fig. 10B'''). The pleuropodium, which is known to develop as the segmental appendage of the 1st abdominal segment in Ectognatha, does not develop, i.e., the area concerned remains level. The proctodaeum further elongates, as shown in Fig. 10C'''. The lateral galea and medial lacinia are differentiated as the endites of the maxilla (Fig. 10D, D'). An endite also develops on the labium but is single, without the glossa and paraglossa being differentiated (Fig. 10D'). The distal labrum and proximal clypeus are distinguished in the clypeolabrum (Fig. 10C', D, D').

In this stage, the embryo volume increases greatly. The embryo becomes indistinct in the lateral view, since it lodges deep in the yolk due to its substantial volume growth, although its cephalic and thoracic regions and the posterior abdomen remain on the egg surface (Figs 6L, 10C–C'''). The embryo undergoes development, maintaining this position and posture, until the withdrawal of the amnioserosal fold or katatrepsis in the next stage. Stage 6 represents intertrepsis (see Discussion "4.3.3. Blastokinesis").

Stage 7. Figs 6M–O, 11A–A'', B–B''', C–C''. Katatrepsis takes place. The amnioserosal fold first ruptures around the cephalic region of the embryo, initiating katatrepsis. The serosa begins to migrate and is concentrated toward the anterior pole of the egg, the amnion appears on the egg surface, and, after the amnion, the embryo appears on the egg surface (Figs 6M, 11A–A''). With the progressive serosa migration and concentration toward the anterior, the embryo moves along the egg surface with its head ahead, passing the egg's posterior pole, to the egg's ventral side (Figs 6N, 11B–B''). Finally, reversing its anteroposterior axis, the embryo positions itself on the ventral side of the egg, and katatrepsis completes (Figs 6O, 11C–C''). The serosa is condensed just dorsally to the embryo's head to form the secondary dorsal organ. The amnion spreads over the area previously occupied by the serosa to cover the dorsal yolk as a provisional dorsal closure.

The appendages acquire their basic articulation. For example, the antennae are articulated into eight antennomeres, as in the first instar larvae (Shimizu and Machida 2011b). A pair of spiracles appears in each segment from the second thoracic to 8th abdominal segments (Fig. 11B, B'', arrowheads). The 10th and 11th abdominal segments are no longer distinguishable, their external boundary being faded (Fig. 11B'', C, C''). The proctodaeum elongates (Fig. 11C'').

Stage 8. Figs 6P–R, 12A–A'', B–B''', C–C''. With its progressive growth, the embryo steadily enlarges and elongates (Fig. 6P, Q), finally taking a near-circumferential posture in which the cephalic and caudal ends can almost contact each other (Figs 6R, 12C, C'). The lateral wall of the embryo expands dorsally to form the definitive dorsal closure, replacing the amnion (Figs 6P, Q, 12A, A'', B, B''), and the dorsum of the embryo is completely covered by the definitive dorsal closure (Figs 6R, 12C, C''). The

Figure 7. Eggs of *Diplatys flavicollis* (Diplatyidae) in Stage 3. **A, A'** Egg in early Stage 3, DAPI staining, UV-excitation, fluorescence microscopy. **A** Lateral view, anterior to the top, ventral to the left. **A'** Ventral view, anterior to the top. **B–B''** Egg in early-middle Stage 3, DAPI staining, UV-excitation, fluorescence microscopy. **B** Lateral view, anterior to the top, ventral to the left. **B'** Ventral view, anterior to the top. **B''** Posterior view. **C–C'''** Egg in middle-late Stage 3, DAPI staining, UV-excitation, fluorescence microscopy. **C** Lateral view, anterior to the top, ventral to the left. **C'** Ventral view, anterior to the top. **C''** Posterior view. **C'''** Dorsal view, anterior to the top. **D–D'''** Egg in late Stage 3, DAPI staining, UV-excitation, fluorescence microscopy. **D** Lateral view, anterior to the top, ventral to the left. **D'** Ventral view, anterior to the top. **D''** Posterior view. **D'''** Dorsal view, anterior to the top. **E, E'** Transverse section of an egg in early-middle Stage 3, ventral to the bottom. **E'** Enlarged image of the boxed area in E. – Abbreviations: EA – embryonic area; EEA – extraembryonic area; Em – embryo; LP – lateral plate; MP – median plate; Pce – protocephalon; Pco – protocorm; PG – primitive groove; Se – serosa; SYN – secondary yolk nucleus. – Scale bars: A, A', B–B'', C–C''', D–D''' – 500 μm; E – 100 μm; E' – 50 μm.

secondary dorsal organ is still present, condensed in the anterior region of the thorax (Fig. 12C), but disappears by the end of this stage. Through the dorsal wall of the embryo, which eventually thickens, the newly developed dorsal blood vessel and the elongated proctodaeum are

clearly visible (Fig. 12C', C''). The definitive dorsal closure is finished in the gnathal region, and the head capsule is completed (Figs 6R, 12C).

The antennae and cerci elongate remarkably (Fig. 6P–R). A cuticular layer, the embryonic cuticle, is secret-
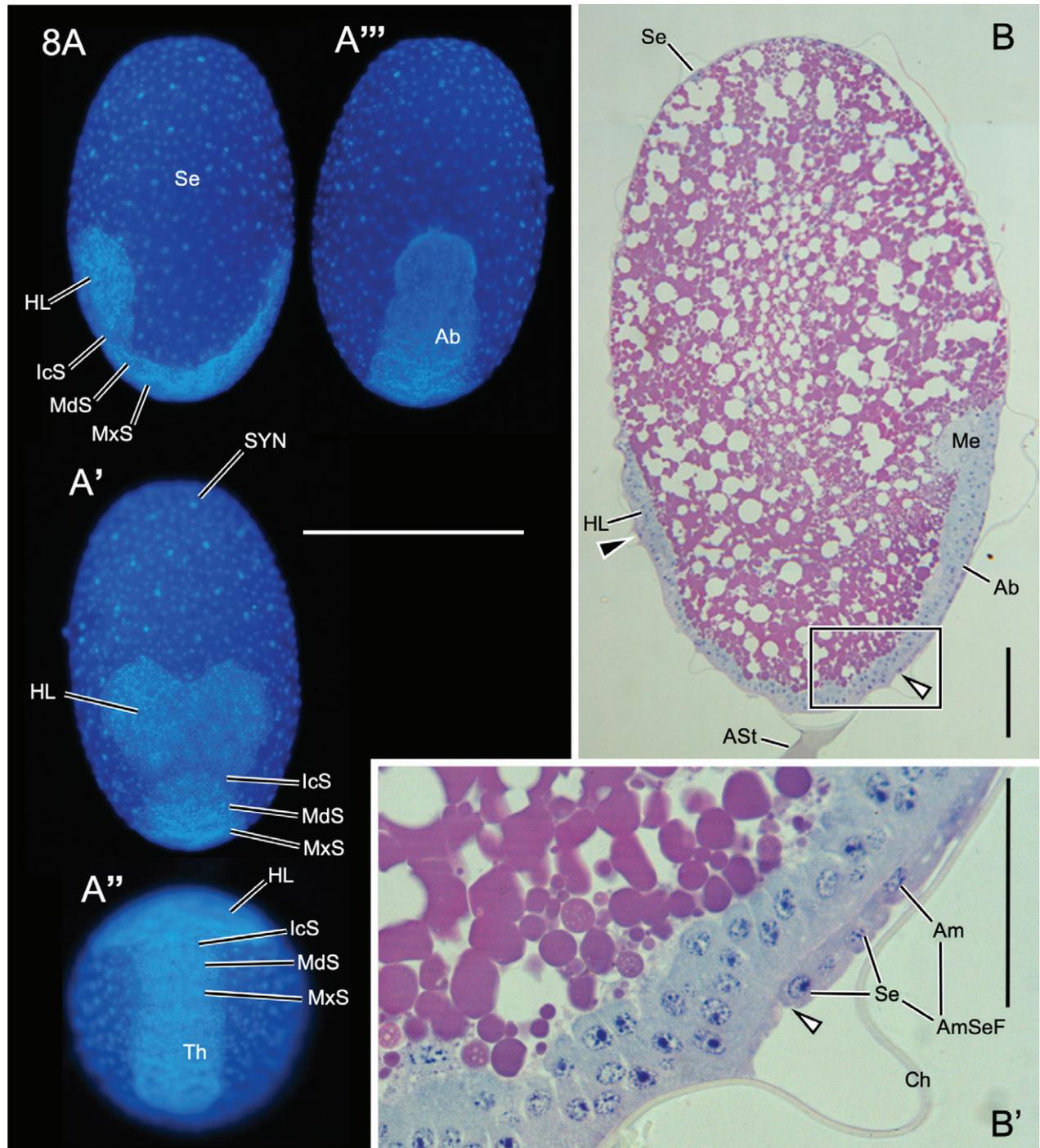

Figure 8. Eggs and embryo of *Diplatys flavicollis* (Diplatyidae) in Stage 4. **A–A'''** Egg, DAPI staining, UV-excitation, fluorescence microscopy. **A** Lateral view, anterior to the top, ventral to the left. **A'** Ventral view, anterior to the top. **A''** Posterior view. **A'''** Dorsal view, anterior to the top. **B**, **B'** Sagittal section of an egg, showing the formation of amnioserosal fold, anterior to the top, ventral to the left. The formation of the amnioserosal fold progresses toward the posterior. Black and white arrowheads represent the fronts of the anterior and posterior amnioserosal folds, respectively. **B'** Enlarged image of the boxed area in B. – Abbreviations: Ab – abdominal region; Am – amnion; AmSeF – amnioserosal fold; ASt – adhesive stalk; Ch – chorion; HL – head lobe; IcS – intercalary segment; MdS – mandibular segment; Me – mesoderm; MxS – maxillary segment; Se – serosa; SYN – secondary yolk nucleus; Th – thoracic region. – Symbols: black arrowhead – front of anterior amnioserosal fold in extension; white arrowhead – front of posterior amnioserosal fold. – Scale bars: A–A''' – 500 µm; B – 100 µm; B' – 50 µm.

ed on the embryo's surface, and the egg tooth is formed by the embryonic cuticle upon the frons. The egg tooth of *Diplatys flavicollis*, previously described by Shimizu and Machida (2009, 2011b), is a large knob-like structure furnished with a median denticulate ridge and a pair of horn-shaped, stout projections (cf. Fig. 14A, B).

Stage 9. Figs 6S, 13A–C. The embryo acquires its definitive form (Figs 6S, 13A–C). Beneath the embryonic cuticle, the larval cuticle of the first instar is secreted, on which the setation is visible. The compound eyes form, which are pigmented dark brown. The appendages are fully developed and elongated. The cerci have elongated, and include approximately 30 cercomeres. One of
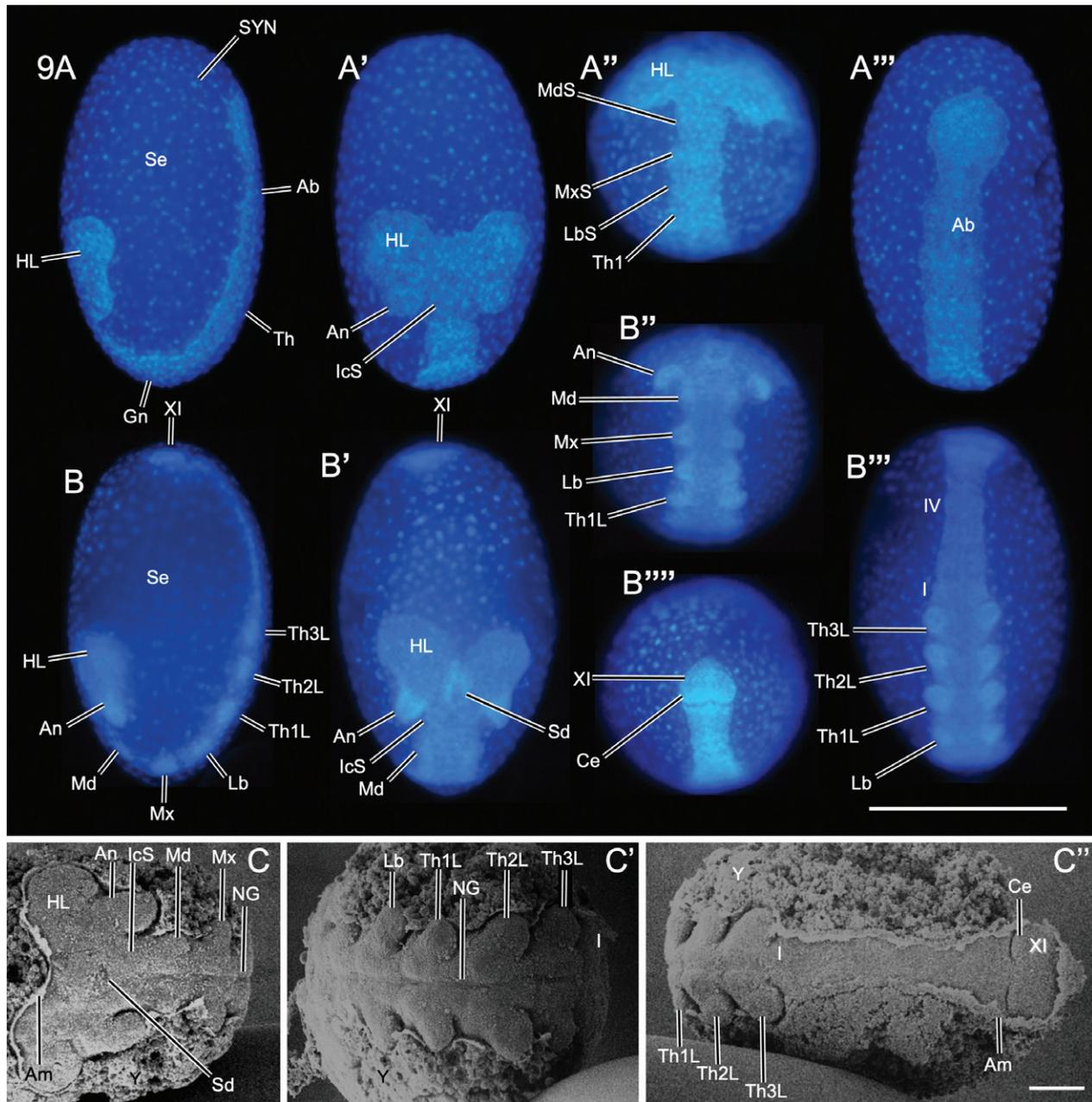
Figure 9. Eggs and embryo of *Diplatys flavicollis* (Diplatyidae) in Stage 5. **A–A'''** Egg in early Stage 5, DAPI staining, UV-excitation, fluorescence microscopy. **A** Lateral view, anterior to the top, ventral to the left. **A'** Ventral view, anterior to the top. **A''** Posterior view. **A'''** Dorsal view, anterior to the top. **B–B''''** Egg in late Stage 5, DAPI staining, UV-excitation, fluorescence microscopy. **B** Lateral view, anterior to the top, ventral to the left. **B'** Ventral view, anterior to the top. **B''** Posterior view. **B'''** Dorsal view, anterior to the top. **B''''** Anterior view. **C–C''** SEMs of an embryo in late Stage 5. The amnion was almost removed, its remnant visible along the margin of the embryo. **C** Cephalic region. **C'** Gnathal to thoracic regions. **C''** Thoracic to abdominal regions. – Abbreviations: Ab – abdominal region; Am – amnion; An – antenna; Ce – cercus; Gn – gnathal region; HL – head lobe; IcS – intercalary segment; Lb – labium; LbS – labial segment; Md – mandible; MdS – mandibular segment; Mx – maxilla; MxS – maxillary segment; NG – neural groove; Sd – stomodaeum; Se – serosa; SYN – secondary yolk nucleus; Th – thoracic region; Th1 – 1st thoracic segment; Th1L–3L – 1st to 3rd thoracic legs; Y – yolk; I–XI – 1st to 11th abdominal segments. – Scale bars: A–A''', B–B'''' – 500 µm; C–C'' – 100 µm.
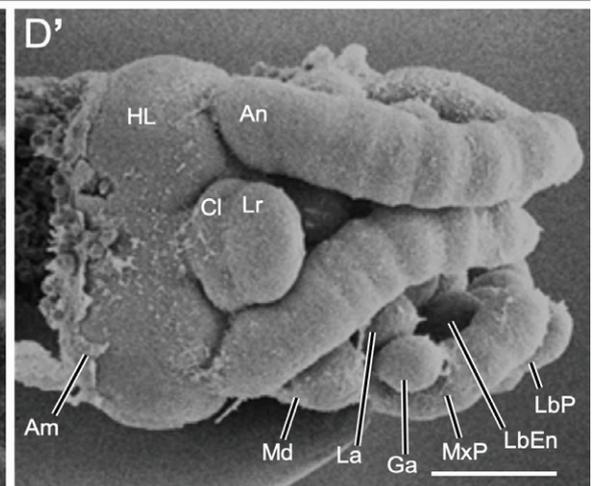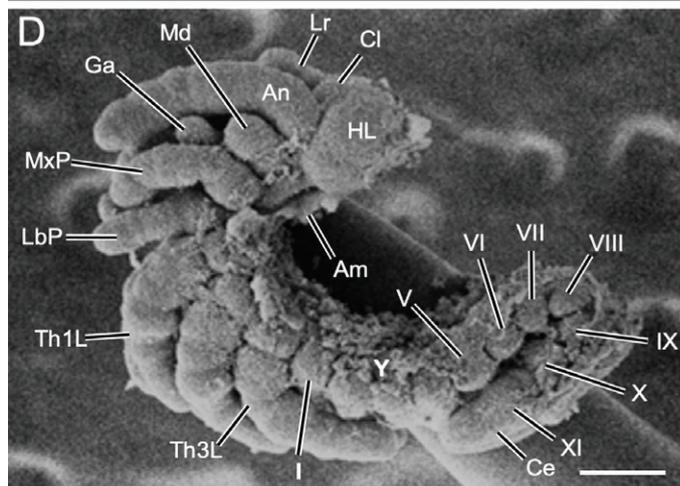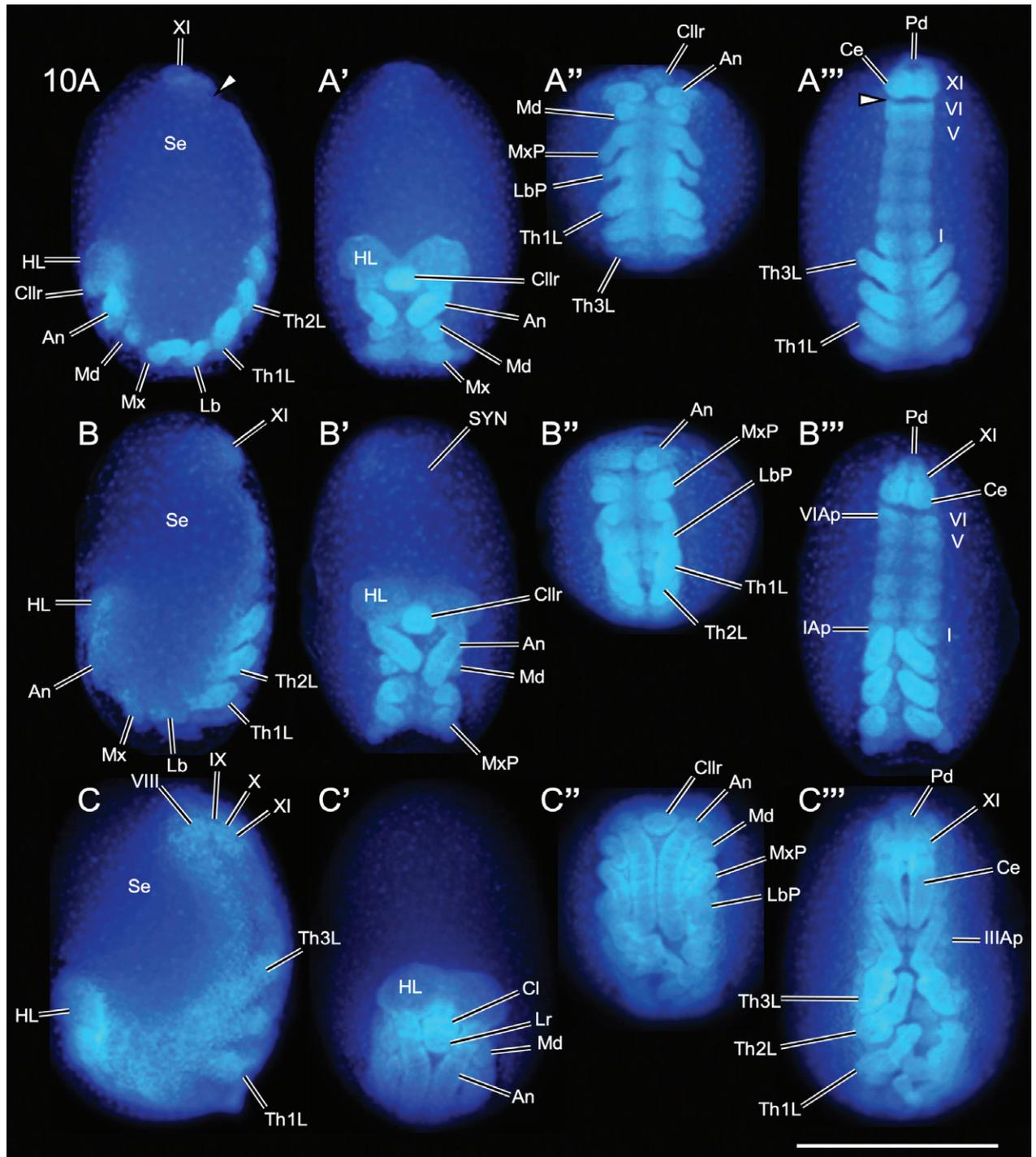
the most outstanding features of diplatyid dermapterans is this pair of annulated, long cerci, which do not transform into a pair of claspers until eclosion (Shimizu and Machida 2011b). In contrast, the cerci do not grow long nor annulate in the other dermapterans examined (Figs 20, 32, 43–47), and the larvae hatch out bearing a pair of prospective claspers.

The egg swells during development (Fig. 6A–S), and in the final Stage 9 it is approximately 1.3 times larger in diameter and more than twice in volume. The embryo breaks the chorion using the egg tooth, and the prelarva hatches out. Simultaneously, the prelarva sheds the embryonic cuticle, which is caught by the tear of the chorion, and becomes the first instar larva (Shimizu and Machida 2011b). Thus, the prelarval stage of an individual, characterised by bearing both the embryonic and the first-instar cuticles, and by being at least partly outside the egg, is limited to the process of hatching.

3.2.   *Cranopygia* sp. (Pygidicranidae)

3.2.1.   Reproductive biology

The females use narrow crevices in the substrate as nests, where they lay their eggs. We once encountered a female nesting in a crevice in the foot of a living tree in the Malaysian tropical rainforest, together with approximately 80 eggs (Fig. 18). Females deposit approximately 40–100 eggs in one round of egg-laying under rearing conditions. The eggs are laid on the nest wall and are attached by an adhesive substance, forming a clutch with some distance between eggs (Figs 3A, B, 18). The female attends the egg clutch and occasionally touches the eggs with her antennae and mouthparts, but maternal care is not intensive. The eggs are firmly stuck to the substratum and are never rearranged. Even if females leave the egg clutch, they soon return to their nest.

The female also takes care of the hatched first instar larvae, occasionally touching them with her antennae and mouthparts, and, when disturbed, counterattacks with her claspers. When nearing molting, the first instar larvae gradually expand their range outside the nest and disperse, and the second instar larvae part from their mother to become independent.

3.2.2.   Eggs

The eggs are ellipsoidal, approximately 1.3 mm long and 0.8 mm wide (freshly laid eggs). The eggs are ivory in color (Fig. 3A, B). An adhesive substance on the egg surface is heavily deposited at the posterior pole of the egg, forming either as an adhesive patch or a short, wide adhesive stalk (Fig. 3A, B). The chorion is transparent and has a smooth surface.

In the anterior pole of the egg, around 10 micropyles of 1–2 μm in diameter are arranged in a circle of ca. 120 μm in diameter (Fig. 3C). At the center of the micropylar arrangement is a chorionic knob of ca. 20 μm in diameter, at whose center there is a minute pore.

3.2.3.   Embryonic development

At 23–25°C, the egg period is about 14 days.

The embryonic development is outlined in Fig. 20. In Stage 3, a short embryo is formed (IL = 30%) in the posterior half of the egg, and its anterior end is positioned at the middle of the egg's posterior half (PAEE = 25%) (Fig. 20D). In Stage 4, the embryo starts to elongate with its abdomen ahead on the dorsal side of the egg (Fig. 20E). In Stage 5, the posterior end of the embryo attains the anterior pole of the egg (PPEE) (Fig. 20F, G), and the embryo acquires its maximum length (ML = 70%) (Fig. 20G). Thus, ERE is 230%.

The cerci do not grow long, showing a configuration of prospective one-segmented claspers throughout the development (Fig. 20I–O). The full-grown embryo has a knob-like egg tooth on the frons, with a posterior major process on its posterior end (Fig. 15A). The anterior facet of the posterior major process is finely denticulate (Fig. 15B).

3.3.   *Echinosoma* sp. (Pygidicranidae)

### 3.3.1.   Reproductive biology

The females use narrow crevices as nests where they lay their eggs. The females deposit approximately 20 eggs at a time under rearing conditions. The eggs are deposited in a group on the substratum and are attached by an ad-

Figure 10. Eggs and embryo of *Diplatys flavicollis* (Diplatyidae) in Stage 6. **A–A'''** Egg in early Stage 6, DAPI staining, UV-excitation, fluorescence microscopy. **A** Lateral view, anterior to the top, ventral to the left. **A'** Ventral view, anterior to the top. **A''** Posterior view. **A'''** Dorsal view, anterior to the top. **B–B'''** Egg in middle Stage 6, DAPI staining, UV-excitation, fluorescence microscopy. **B** Lateral view, anterior to the top, ventral to the left. **B'** Ventral view, anterior to the top. **B''** Posterior view. **B'''** Dorsal view, anterior to the top. **C–C'''** Egg in late Stage 6, DAPI staining, UV-excitation, fluorescence microscopy. **C** Lateral view, anterior to the top, ventral to the left. **C'** Ventral view, anterior to the top. **C''** Posterior view. **C'''** Dorsal view, anterior to the top. **D, D'** SEMs of an embryo in late Stage 6. Amnion almost removed. **D** Lateral view of the embryo. **D'** Frontal view of the same embryo as in D. – Abbreviations: Am – amnion; An – antenna; Ce – cercus; Cl – clypeus; Cllr – clypeolabrum; Ga – galea; HL – head lobe; La – lacinia; Lb – labium; LbEn – labial endite; LbP – labial palp; Lr – labrum; Md – mandible; Mx – maxilla; MxP – maxillary palp; Pd – proctodaeum; Se – serosa; SYN – secondary yolk nucleus; Th1L–3L – 1st to 3rd thoracic legs; Y – yolk; I–XI – 1st to 11th abdominal segments; I–XIAp – appendages of 1st to 11th abdominal segments. – Symbol: arrowhead – commencement of the ventral flexure of abdomen. – Scale bars: A–A''', B–B''', C–C''' – 500 μm; D, D' – 100 μm.
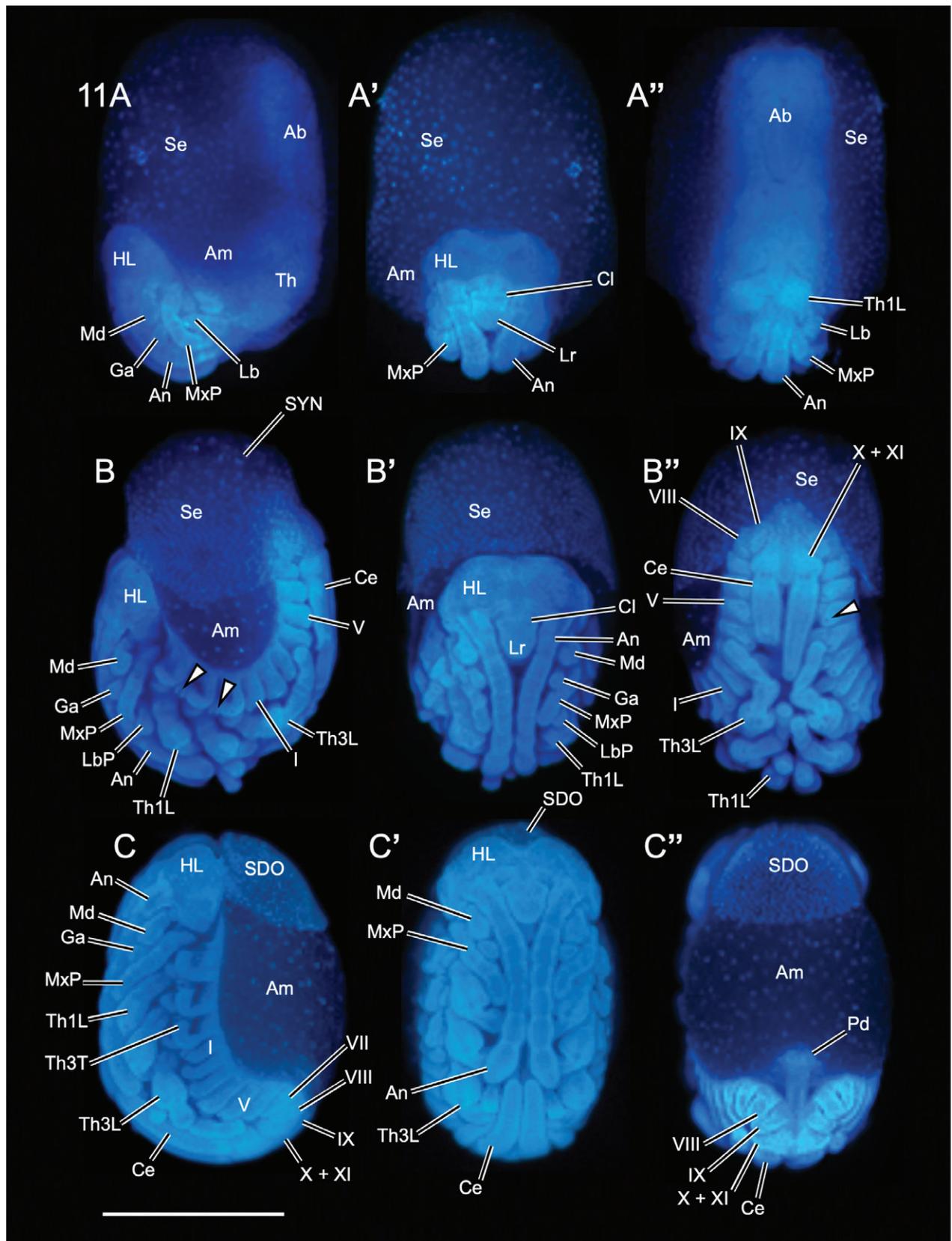
Figure 11. Eggs of *Diplatys flavicollis* (Diplatyidae) in Stage 7, DAPI staining, UV-excitation, fluorescence microscopy. **A–A"** Egg in early Stage 7. **A** Lateral view, anterior to the top, ventral to the left. **A'** Ventral view, anterior to the top. **A"** Dorsal view, anterior to the top. **B–B"** Egg in middle Stage 7. **B** Lateral view, anterior to the top, ventral to the left. **B'** Ventral view, anterior to the top. **B"** Dorsal view, anterior to the top. **C–C"** Egg in late Stage 7. **C** Lateral view, anterior to the top, ventral to the left. **C'** Ventral view, anterior to the top. **C"** Dorsal view, anterior to the top. – Abbreviations: Ab – abdomen; Am – amnion; An – antenna; Ce – cercus; Cl – clypeus; Ga – galea; HL – head lobe; Lb – labium; LbP – labial palp; Lr – labrum; Md – mandible; MxP – maxillary palp; Pd – proctodaeum; SDO – secondary dorsal organ; Se – serosa; SYN – secondary yolk nucleus; Th – thorax; Th1L, 3L – 1st and 3rd thoracic legs; Th3T – 3rd thoracic tergum; I–XI – 1st to 11th abdominal segments. – Symbol: arrowhead – spiracle. – Scale bar: 500 μm.
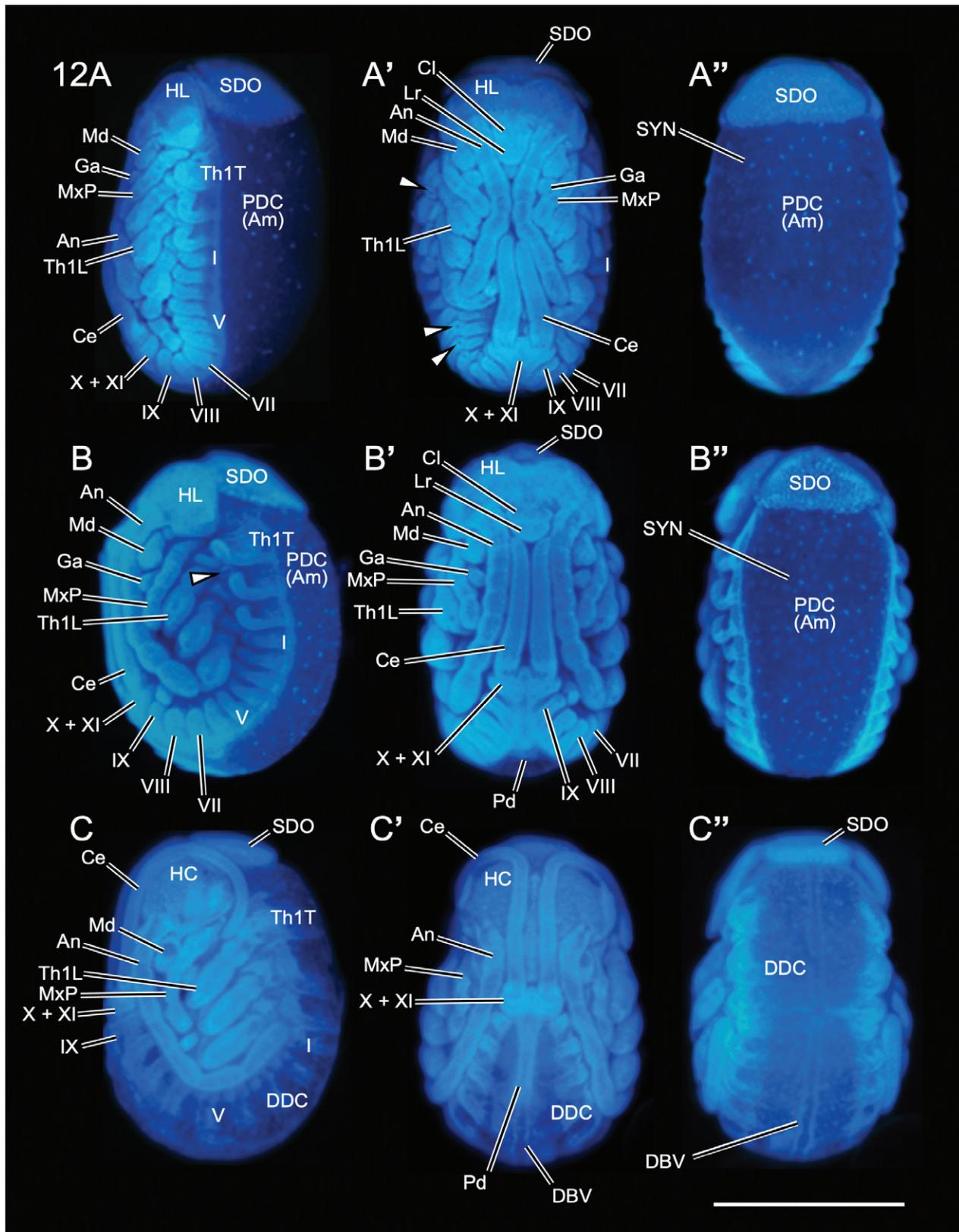
Figure 12. Eggs of *Diplatys flavicollis* (Diplatyidae) in Stage 8, DAPI staining, UV-excitation, fluorescence microscopy. **A–A"** Egg in early Stage 8. **A** Lateral view, anterior to the top, ventral to the left. **A'** Ventral view, anterior to the top. **A"** Dorsal view, anterior to the top. **B–B"** Egg in middle Stage 8. **B** Lateral view, anterior to the top, ventral to the left. **B'** Ventral view, anterior to the top. **B"** Dorsal view, anterior to the top. **C–C"** Egg in late Stage 8. **C** Lateral view, anterior to the top, ventral to the left. **C'** Ventral view, anterior to the top. **C"** Dorsal view, anterior to the top. – Abbreviations: Am – amnion; An – antenna; Ce – cercus; Cl – clypeus; DBV – dorsal blood vessel; DDC – definitive dorsal closure; Ga – galea; HC – head capsule; HL – head lobe; Lr – labrum; Md – mandible; MxP – maxillary palp; Pd – proctodaeum; PDC – provisional dorsal closure; SDO – secondary dorsal organ; SYN – secondary yolk nucleus; Th1L – 1st thoracic leg; Th1T – 1st thoracic tergum; I–XI – 1st to 11th abdominal segments. – Symbol: arrowhead – spiracle. – Scale bar: 500 μm.

hesive substance (Fig. 4A). The females attend the egg clutch. The mother occasionally touches the eggs with her antennae and mouthparts, but the maternal care is not intensive. The eggs are firmly stuck to the substratum and cannot be rearranged. Even if females leave the egg clutch being disturbed, they soon return to their nest.

We did not observe mothers taking care of the larvae. First instar larvae gradually expand their range outside
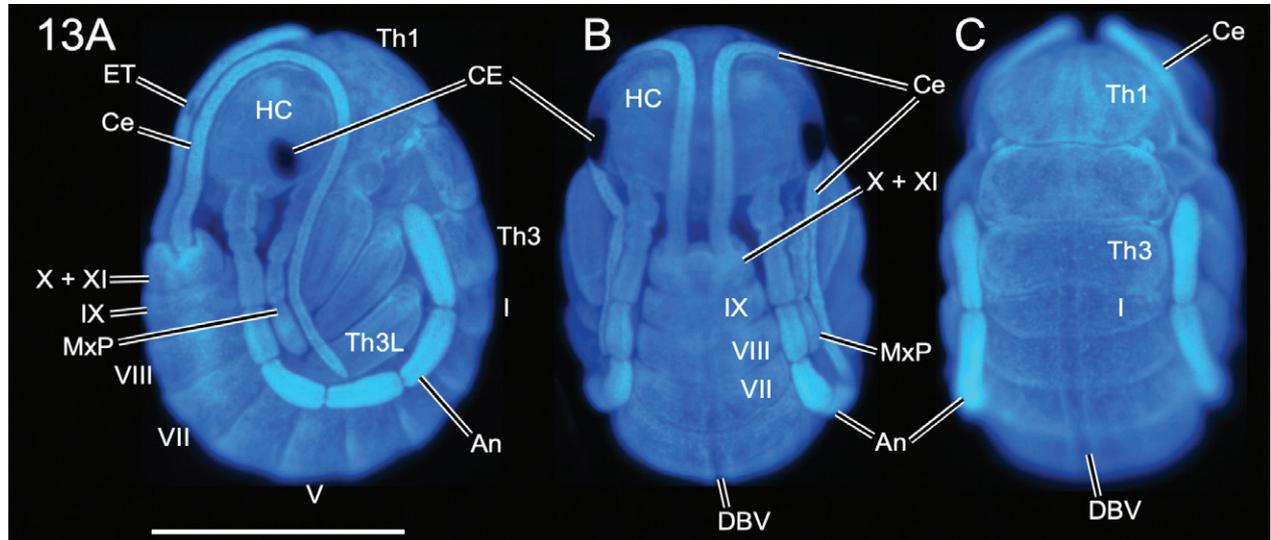
Figure 13. Egg of *Diplatys flavicollis* (Diplatyidae) in Stage 9, DAPI staining, UV-excitation, fluorescence microscopy. **A** Lateral view, anterior to the top, ventral to the left. **B** Ventral view, anterior to the top. **C** Dorsal view, anterior to the top. – Abbreviations: An – antenna; CE – compound eye; Ce – cercus; DBV – dorsal blood vessel; ET – egg tooth; HC – head capsule; MxP – maxillary palp; Th1, 3 – 1st and 3rd thoracic segments; Th3L – 3rd thoracic leg; I–XI – 1st to 11th abdominal segments. – Scale bar: 500 μm.
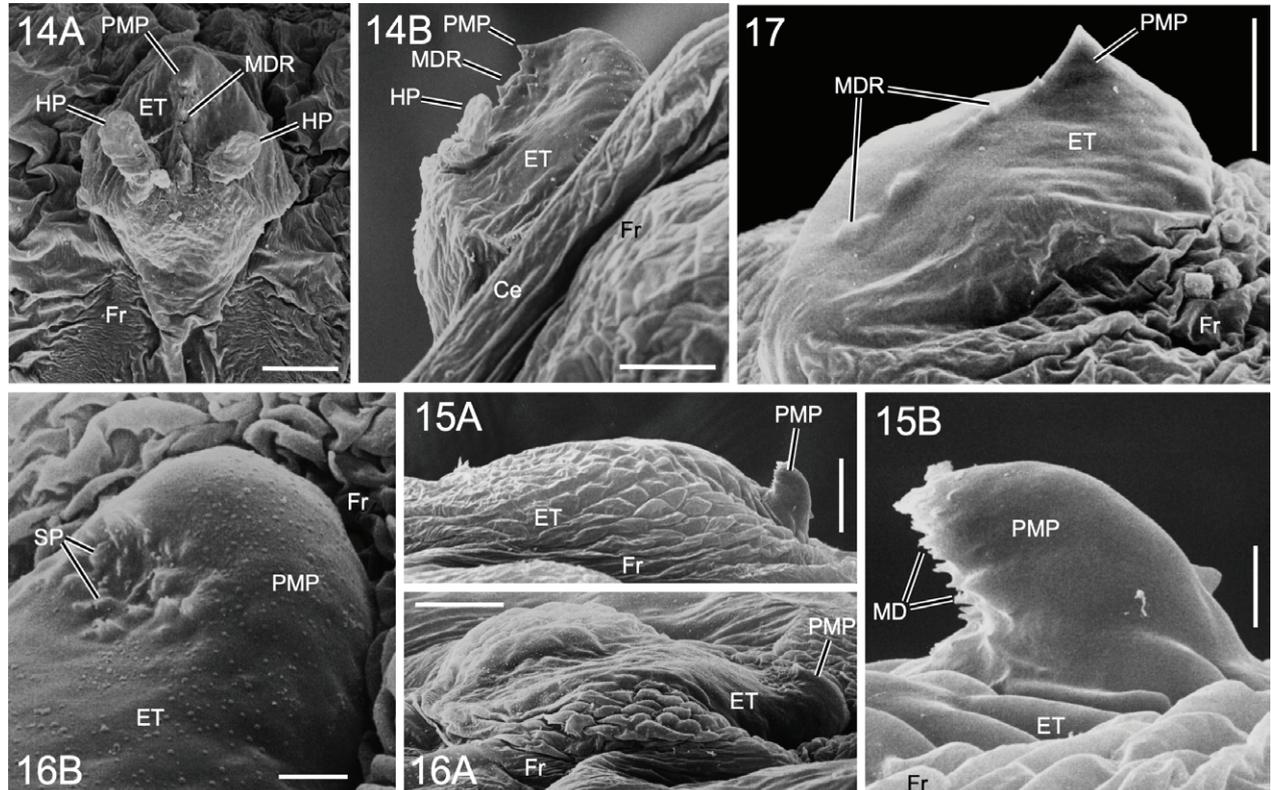
Figures 14–17. SEMs of the egg teeth of Protodermaptera. **14** *Diplatys flavicollis* (Diplatyidae) (reposted from Shimizu and Machida 2011b: fig. 9B', C). **14A** Frontal view, posterior to the top. **14B** Lateral view, posterior to the right. **15** *Cranopygia* sp. (Pygidicranidae). **15A** Lateral view, posterior to the right. **15B** Enlarged image. **16** *Echinosoma* sp. (Pygidicranidae). **16A** Lateral view, posterior to the right. **16B** Enlarged image. **17** *Parapsalis infernalis* (Pygidicranidae). Lateral view, posterior to the right. – Abbreviations: Ce – cercus; ET – egg tooth; Fr – frons; HP – horn-shaped projection; MD – minute denticle; MDR – median denticulate ridge; PMP – posterior major process; SP – small protuberance. – Scale bars: 14A, B, 15A, 16A, 17 – 20 μm; 15B, 16B – 5 μm.

the nest and disperse near molting. The second instar larvae completely part from their mother to become independent.

3.3.2. Eggs

The eggs are ellipsoidal, approximately 900 µm long and 600 µm wide (freshly laid eggs), and ivory in color (Fig. 4A, B). An adhesive substance covers the egg surface, being abundant around the posterior pole of the egg but not forming a distinct stalk (Fig. 4A, B). The chorion is transparent and has a smooth surface.

In the anterior pole of the egg, 20–25 micropyles of 1–2 µm in diameter are arranged in a circle of ca. 50 µm in diameter (Fig. 4C). A chorionic mound, at whose center there is a pore of ca. 5 µm in diameter, is at the center of the circular micropyle arrangement.

3.3.3. Embryonic development

We failed to follow the embryonic development. The egg tooth is a knob-like structure with a posterior major process, whose anterior facet bears small protuberances (Fig. 16A, B).

3.4. *Parapsalis infernalis* (Pygidicranidae)

3.4.1. Reproductive biology

The females use crevices as nests where they lay their eggs. The females deposit around 10 eggs at one time under rearing conditions (Fig. 19A, B). The eggs are not coated with a special secretion or adhesive substance and not attached to the substrate (Fig. 5A, B). The females attend the eggs (Fig. 19A, B). They take intensive care of the eggs, as reported in higher dermapterans, with behaviors such as cleaning by licking, rolling, and transport. Figure 19A and B show two consecutive frames that demonstrate egg rolling and rearranging by a female. When disturbed, the females leave the eggs but soon return to their nest. Excessive disturbance leads the mother to eat her eggs. If the mother dies, the eggs become moldy.

We did not observe mothers taking care of the larvae. First instar larvae gradually expand their range outside the nest and disperse near molting. The second instar larvae completely part from their mother to become independent.

3.4.2. Eggs

The eggs are ellipsoidal, ca. 1 mm in long and 0.75 mm wide (freshly laid eggs), and are ivory in color (Fig. 5A, B). The eggs lack any adhesive substance on their surface.

In the anterior pole of the egg, 15–20 micropyles of 1–2 µm in diameter are arranged in a circle of ca. 80 µm in diameter (Fig. 5C). The chorion in the circular arrangement of micropyles is slightly upheaved. There is no chorionic pore at the center of the micropylar arrangement.

3.4.3. Embryonic development

At 23–25°C, the egg period is about 10 days.

Due to the insufficient number of obtained eggs, we failed to follow embryogenesis, only observing the eggs at a few stages, as shown in Fig. 21A and B. In Stage 3 the embryo is formed (IL = 40%) in the posterior half of the egg, and its anterior end is near the equator of the egg (PAEE = 55%) (Fig. 21A). The embryo elongates with its abdomen ahead on the dorsal side of the egg and acquires its maximum length in the anatrepsis period (ML = 85%), with its posterior end nearly reaching the anterior egg pole (PPEE) in Stage 5 (Fig. 21B). Thus, ERE is 210%.

Figures 18, 19. Maternal brood care of Pygidicranidae. **18** *Cranopygia* sp. female and eggs deposited in a crevice in the foot of a living tree. **19** *Parapsalis infernalis* female attending her egg clutch. **19A** and **19B** are two consecutive frames showing the female rearranging her eggs. – Abbreviations: An – antenna; Ce – cercus; E – egg; F – female; H – head; Th3L – 3rd thoracic leg. – Scale bars: 18 – 2 cm; 19A, B – 2 mm.

The egg tooth is knob-like, with a median denticulate ridge and a posterior major process, of which the anterior facet is smooth (Fig. 17).

3.5. *Apachyus chartaceus* (Apachyidae)

3.5.1. Reproductive biology

Shimizu and Machida (2011a) previously reported the reproductive biology of this species. The present study corroborates their preliminary observations of its mating behavior. *Apachyus chartaceus* prefers and inhabits narrow spaces such as under bark, and specimens under rearing stayed in artificially created narrow spaces, such as between a box wall and a cylinder made of a non-woven fabric paper imitating bark (see Shimizu and Machida 2011a: figs 4, 5C). Mating takes place in these narrow spaces. Mating is of the end-to-end type, with the male and the female being dorsoventrally reversed; the male tightly holds his partner's postabdomen with his clasp-

ers in a symmetrical manner (see Shimizu and Machida 2011a: fig. 5A–C, C').

The females deposit 7–50 eggs at a time with some interspace onto the substratum (Fig. 22A). Previously, we reported one case where a female had a mass of several eggs on her anal process (Shimizu and Machida 2011a: fig. 6, 6'). This was not seen in the present study and may thus have been accidental.

Shimizu and Machida (2011a) did not observe any evidence of egg-caring behavior by mothers, but in the present study we encountered maternal care. The female attended the egg clutch (Fig. 22A), but did not engage in intensive egg-care behaviors such as cleaning by licking, as reported for higher dermapterans, but occasionally touched the eggs with her antennae and mouthparts. The eggs are firmly stuck to the substratum and are never rearranged. When disturbed, for example, by tweezers, the female counterattacks with her claspers. Excessive disturbance leads the mother to abandon her egg clutch or to eat her eggs. If the mother dies, the eggs become moldy.

The female also cares for the hatched larvae, although not intensively (Fig. 22B). She attends the first instar lar-
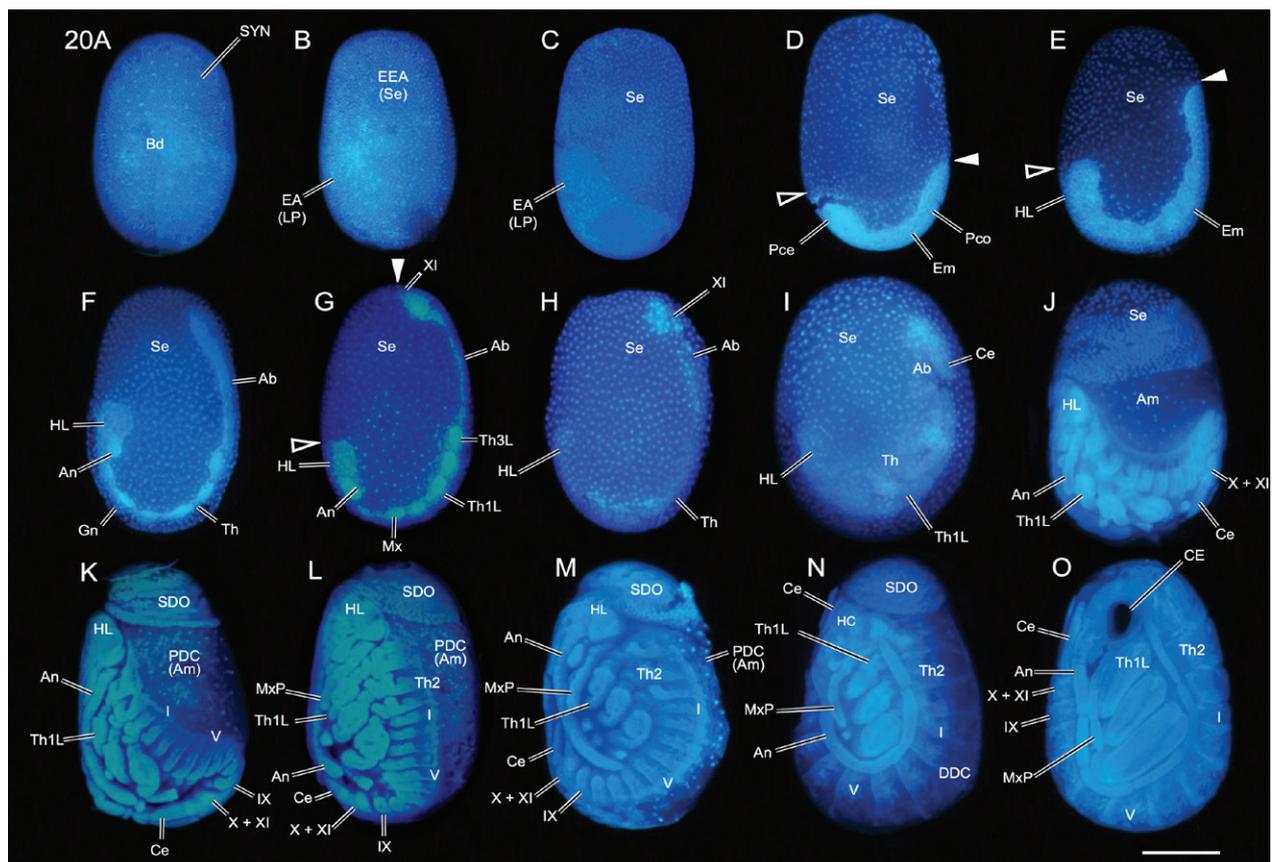
Figure 20. Embryonic development of *Cranopygia* sp. (Pygidicranidae), DAPI staining, UV-excitation, fluorescence microscopy. Lateral view, anterior to the top, ventral to the left. **A** Stage 2. **B** Early Stage 3. **C** Middle Stage 3. **D** Late Stage 3. **E** Stage 4. **F** Early Stage 5. **G** Late Stage 5. **H** Early Stage 6. **I** Late Stage 6. **J** Middle Stage 7. **K** Late Stage 7. **L** Early Stage 8. **M** Middle Stage 8. **N** Late Stage 8. **O** Stage 9. – Abbreviations: Ab – abdominal region / abdomen; Am – amnion; An – antenna; Bd – blastoderm; CE – compound eye; Ce – cercus; DDC – definitive dorsal closure; EA – embryonic area; EEA – extraembryonic area; Em – embryo; Gn – gnathal region; HC – head capsule; HL – head lobe; LP – lateral plate; Mx – maxilla; MxP – maxillary palp; Pce – protocephalon; Pco – protocorm; PDC – provisional dorsal closure; SDO – secondary dorsal organ; Se – serosa; SYN – secondary yolk nucleus; Th – thoracic region / thorax; Th2 – 2nd thoracic segment; Th1L, 3L – 1st and 3rd thoracic legs; I–XI – 1st to 11th abdominal segments. – Symbols: black arrowhead – anterior end of embryo; white arrowhead – posterior end of embryo. – Scale bar: 500 μm.
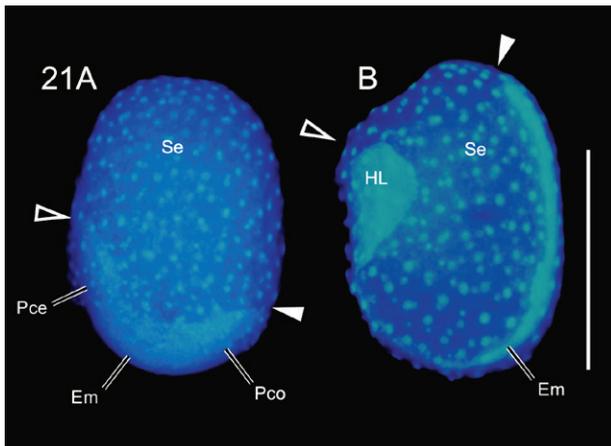
Figure 21. Eggs of *Parapsalis infernalis* (Pygidicranidae) in two developmental stages of the pre-katatrepsis period, DAPI staining, UV-excitation, fluorescence microscopy. Lateral view, anterior to the top, ventral to the left. **A** Egg in late Stage 3. **B** Egg in Stage 5. – Abbreviations: Em – embryo; HL – head lobe; Pce – protocephalon; Pco – protocorm; Se – serosa. – Symbols: black arrowhead – anterior end of embryo; white arrowhead – posterior end of embryo. – Scale bar: 500 μm.

vae and occasionally makes physical contact with the larvae with her antennae and mouthparts. When disturbed, she counterattacks with her claspers. The second instar larvae gradually expand their range outside the nest, finally parting from their mother, but usually together.

3.5.2. Eggs

The egg structure was previously described by Shimizu and Machida (2011a): the eggs are ellipsoidal, ca. 900 μm in long and 550 μm wide (freshly laid eggs). The eggs are whitish in color, with the anterior half slightly swollen, and covered with an adhesive substance, which is abundant in the posterior half, for attaching the egg to the substratum (Fig. 23A).

There is a circular, low chorionic elevation, 80–100 μm in diameter at the anterior pole of the egg (Fig. 23B). At the center of the chorionic elevation, there is a pore about 10 μm in diameter, which is spongy inside. Around the chorionic elevation, around 10 micropyles of 1–2 μm in diameter are arranged in a circle of ca. 150 μm (Fig. 23B) (Shimizu and Machida 2011a).

3.5.3. Embryonic development

At 23–25°C, the egg period is about 10 days.

The embryonic development is outlined in Fig. 32. In Stage 3, the embryo is formed (IL = 40%) on the ventral to the posterior side of the egg, and its anterior end is in the anterior half of the egg (PAEE = 70%) (Fig. 32D). In Stages 4 and 5, the embryo elongates along the egg surface (Fig. 32E–G). Late in Stage 5, the embryo, whose posterior end attains the anterior pole of the egg (PPEE), takes a characteristic U-shape, and acquires its maximum length in the anatrepsis period (ML = 90%) (Fig. 32G); thus, the ERE is 225%.

The cerci do not grow long, showing a configuration of prospective one-segmented claspers throughout the development (Fig. 32J–M). The full-grown embryo has a knob-like egg tooth on the frons, which is furnished with a posterior major process with small protuberances on its anterior facet (Fig. 33A, B).

3.5.4. Postembryonic development

We successfully followed the growth of two captive-bred individuals, one from the first to third instar (Fig. 42A–C, A', B') and another from the penultimate instar to adult (male) (Fig. 42D–F). The measurements and external features of each recognized larval instar are as follows:

First larval instar. Fig. 42A, A'. Body ca. 2.5 mm long, uniformly white, head 0.62 mm wide, 8 antennomeres, claspers rod-like, straight.

Second larval instar. Fig. 42B, B'. Body ca. 5 mm long, slightly brownish, head ca. 0.8 mm wide, 13 antennomeres, claspers rod-like, straight.

Third larval instar. Fig. 42C. Body ca. 9 mm long, light brown, habitus becoming dorsoventrally flattened, head ca. 1.0 mm wide, 25 antennomeres, claspers curving medially, anal process largely projecting backward.

Penultimate larval instar. Fig. 42D. Body ca. 16 mm long, brown, head ca. 1.7 mm wide, 25 (left) + 36 (right) antennomeres.

Final larval instar. Fig. 42E. Body ca. 22 mm long, darker, head ca. 2.1 mm wide, 31 (left) + 36 (right) antennomeres, hindwing buds, in which the venation is visible, developed.

Adult. Fig. 42F. Body ca. 25 mm long, abdomen orange, forewings or tegmina and hindwings dark brown, other parts yellowish, head ca. 2.5 mm wide, 23 (left) + 39 (right) antennomeres.

3.6. *Anisolabis maritima* and *Euborellia pallipes* (Anisolabididae)

3.6.1. Eggs

The eggs of *Anisolabis maritima* (Fig. 24A) and those of *Euborellia pallipes* (Fig. 25A) closely resemble each other. They are ellipsoidal, ca. 1.8 mm long and ca. 1.5 mm wide in *A. maritima*, and ca. 1 mm long and ca. 0.85 mm wide in *E. pallipes* (freshly laid eggs). The eggs are ivory in color, and there is no secretion on the smooth egg surface.

At the anterior pole of the eggs, in *A. maritima* around 10 and in *E. pallipes* 20 micropyles of 1–2 μm in diameter are arranged in a circle of ca. 40 μm diameter (Figs

Figure 22. Maternal brood care of *Apachyus chartaceus* (Apachyidae). **A** Female attending the eggs (E). **B** Female with first instar larvae (L). – Scale bar: 1 cm.
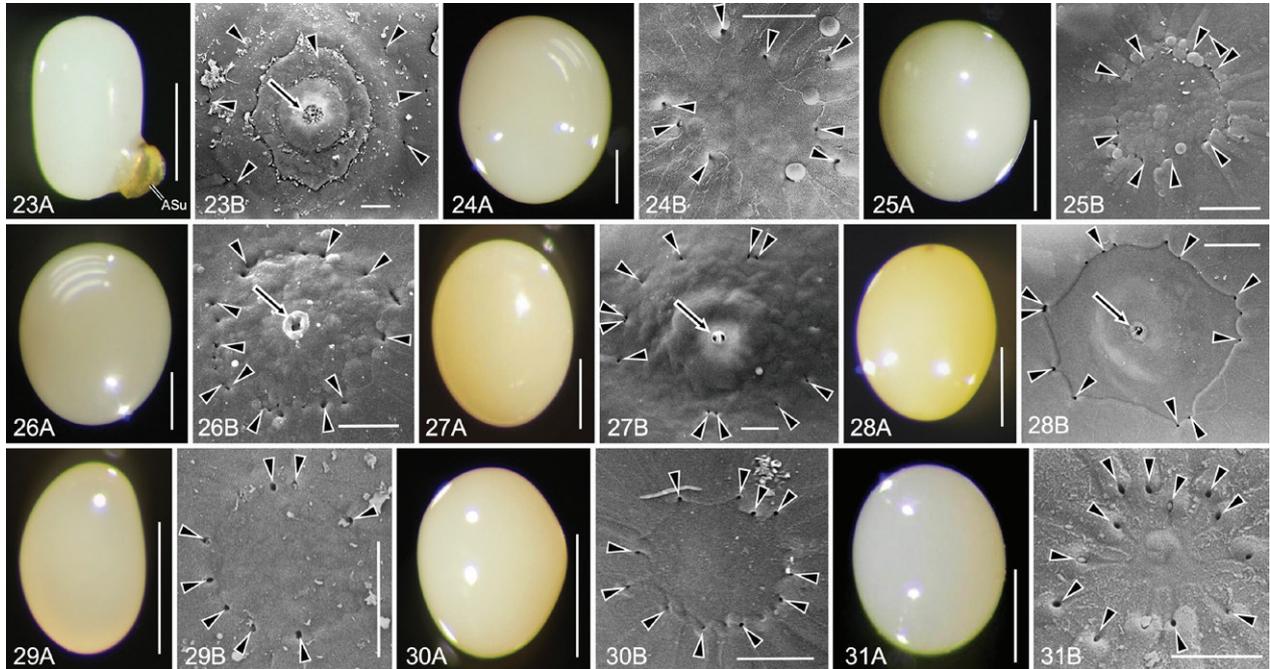
Figures 23–31. Eggs of the examined Epidermaptera. **23** *Apachyus chartaceus* (Apachyidae). **23A** Egg, anterior to the top. **23B** SEM of the anterior pole of the egg (reposted from Shimizu and Machida 2011a: fig. 8B). **24** *Anisolabis maritima* (Anisolabididae). **24A** Egg, anterior to the top. **24B** SEM of the anterior pole of the egg. **25** *Euborellia pallipes* (Anisolabididae). **25A** Egg, anterior to the top. **25B** SEM of the anterior pole of the egg. **26** *Labidura riparia* (Labiduridae). **26A** Egg, anterior to the top. **26B** SEM of the anterior pole of the egg. **27** *Forficula scudderi* (Forficulidae). **27A** Egg, anterior to the top. **27B** SEM of the anterior pole of the egg. **28** *Anechura harmandi* (Forficulidae). **28A** Egg, anterior to the top. **28B** SEM of the anterior pole of the egg. **29** *Paralabella curvicauda* (Spongiphoridae). **29A** Egg, anterior to the top. **29B** SEM of the anterior pole of the egg. **30** *Proreus simulans* (Chelisochidae). **30A** Egg, anterior to the top. **30B** SEM of the anterior pole of the egg. **31** A chelisochid gen. sp. (Chelisochidae). **31A** Egg, anterior to the top. **31B** SEM of the anterior pole of the egg. – Abbreviation: ASu – adhesive substance. – Symbols: arrow – chorionic pore at the center of the circular arrangement of micropyles; arrowhead – micropyle. – Scale bars: 23–31A – 500 μm; 23–28B – 20 μm; 29–31B – 10 μm.

24B, 25B). There is no chorionic pore at the center of the circular arrangement of micropyles.

3.6.2. Embryonic development

At 23–25°C, the egg period of *Anisolabis maritima* is about 14 days.

The embryonic development of *A. maritima* is outlined in Fig. 43. In Stage 3, the formed embryo is relatively large (IL = 50%), and its anterior end is in the anterior half of the egg (PAEE = 65%) (Fig. 43C). The embryo starts to elongate in Stage 4 (Fig. 43D). Late in Stage 5, the embryo acquires its maximum length in the anatrepsis period (ML = 70%) (Fig. 43F), and the ERE is 140%. The posterior end of the embryo comes close to the anterior pole of the egg, but does not attain there differently from other dermapterans (PPEE). The cerci do not grow long, showing a configuration of prospective one-segmented claspers throughout the development (Fig. 43I–M). The full-grown embryos of *A. maritima* and *E. pallipes* have knob-like egg tooth on the frons, which is equipped with a posterior major process with minute denticles on its anterior facet (Figs 34A, B, 35A, B).

3.7. *Labidura riparia* (Labiduridae)

3.7.1. Eggs

The eggs are ellipsoidal, with a long diameter of ca. 1.4 mm and a short diameter of ca. 1.2 mm (freshly laid eggs), and ivory in color (Fig. 26A). The egg membrane is transparent, and there is no secretion on the smooth egg surface.

At the anterior pole of the egg, around 25 micropyles of 1–2 μm diameters are arranged in a circle of ca. 50 μm in diameter (Fig. 26B). At the center of the micropylar arrangement is a chorionic pore that is a little larger than the micropyles and furnished with a fringe (Fig. 26B).

3.7.2. Embryonic development

At 23–25°C, the egg period is about 12 days.

The embryonic development is outlined in Fig. 44. In Stage 3, the formed embryo is relatively large (IL = 50%), and its anterior end is around the middle of the anterior half of the egg (PAEE = 75%) (Fig. 44C). In Stage 4, the embryo starts to elongate (Fig. 44D). Late in Stage 5, the posterior end of the embryo attains the anterior pole of the egg (PPEE), and the embryo acquires its maximum length in the anatrepsis period (ML = 75%). Thus, the ERE is 150%.

The cerci do not grow long, showing a configuration of prospective one-segmented claspers throughout the development (Fig. 44J–N). The full-grown embryo has a knob-like egg tooth on the frons (Fig. 36A, B), which is furnished with a posterior major process with minute denticles on its anterior facet.

3.8. *Forficula scudderi* and *Anechura harmandi* (Forficulidae)

3.8.1. Eggs

The eggs of *Forficula scudderi* and *Anechura harmandi*, which closely resemble each other, are ellipsoidal, ca. 1.3 mm long and ca. 1 mm wide, and ca. 1 mm long and ca. 0.8 mm wide, respectively (freshly laid eggs) (Figs 27A, 28A). The eggs of *Forficula scudderi* and *Anechura harmandi* are respectively ivory and a little yellowish in color, and there is no secretion on the smooth egg surface.

At the anterior pole of the egg, 10–15 micropyles of 1–2 μm in diameter are arranged in a circle of ca. 75 μm in diameter in both species (Figs 27B, 28B). The chorion surrounded by circular arrangement of micropyles is shallowly sunk but a little upheaved at its central region. At the center of the upheaved region, there is a pore of 3–5 μm in both species (Figs 27B, 28B).

3.8.2. Embryonic development

At 23–25°C, the egg period of *Forficula scudderi* is about 10 days.

The embryonic development of *F. scudderi* is outlined in Fig. 45. In Stage 3, the formed embryo is large (IL = 60%), and its anterior end is situated near to the anterior pole of the egg (PAEE = 85%) (Fig. 45D). In Stage 4, the embryo, where segmentation commences, starts to elongate (Fig. 45E). In Stage 5, the embryo further elongates along the egg surface with its posterior end ahead. Late in Stage 5, the posterior end of the embryo attains the egg's ventral side beyond the anterior pole of the egg (PPEE), and the embryo acquires its maximum length in the anatrepsis period (ML = 98%) (Fig. 45F). The anterior and posterior ends of the embryo come close, nearly contacting each other. ERE is 160%.

The cerci do not grow long, showing a configuration of prospective one-segmented claspers throughout the development (Fig. 45G–N). The full-grown embryos of *F. scudderi* and *A. harmandi* have knob-like egg tooh on the frons, with an anteriorly-pointed major process at its center (i.e., the central major process) (Figs 37, 38).

3.9. *Paralabella curvicauda* (Spongiphoridae)

3.9.1. Eggs

The eggs are ellipsoidal, ca. 670 μm long and ca. 450 μm wide (freshly laid eggs), and ivory in color (Fig. 29A). The egg membrane is transparent, and no secretion is found on the smooth egg surface.

At the anterior pole of the egg, around 10 micropyles of 0.5–1 μm in diameter are arranged in a circle of ca. 15 μm in diameter (Fig. 29B). There is no chorionic pore at the center of the micropylar arrangement.

3.9.2. Embryonic development

At 23–25°C, the egg period is about 8 days.

The embryonic development is outlined in Fig. 46. In Stage 3, the formed embryo is large (IL = 60%) and its anterior end is situated near to the anterior pole of the egg (PAEE = 90%) (Fig. 46C). The embryo elongates in the following two stages with its caudal end ahead (Fig. 46D–F). Late in Stage 5, the posterior end of the embryo attains the egg's ventral side beyond the anterior pole of the egg (PPEE) and acquires its maximum length in the anatrepsis period (ML = 95%) (Fig. 46F). The anterior and posterior ends of the embryo come close, nearly contacting each other. The ERE is 160%.

The cerci do not grow long, showing a configuration of prospective one-segmented claspers throughout the development (Fig. 46J–M). The full-grown embryo has a knob-like egg tooth on the frons, with an anteriorly-pointed, central major process (Fig. 39).
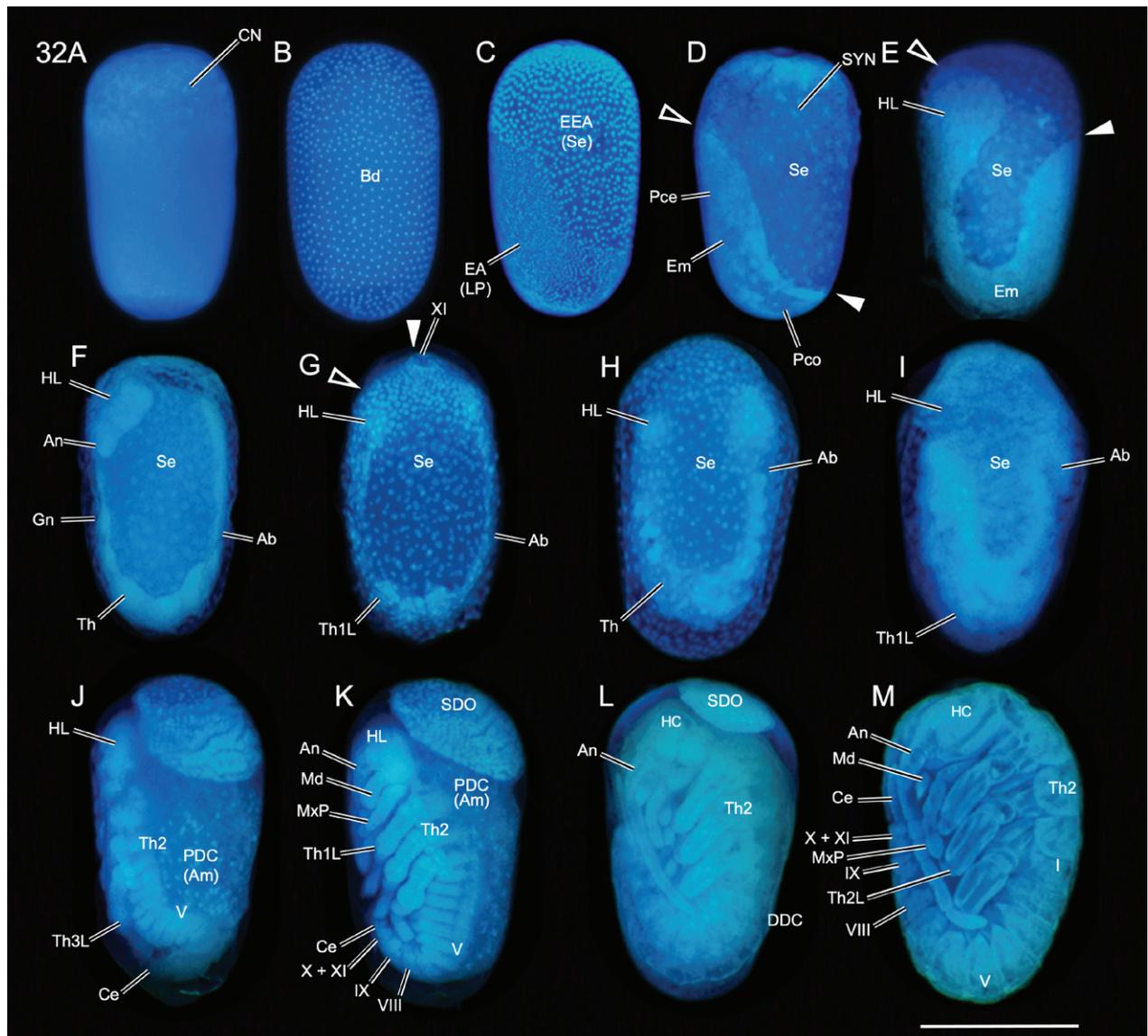
Figure 32. Embryonic development of *Apachyus chartaceus* (Apachyidae), DAPI staining, UV-excitation, fluorescence microscopy. Lateral view, anterior to the top, ventral to the left. **A** Stage 1. **B** Stage 2. **C** Middle Stage 3. **D** Late Stage 3. **E** Stage 4. **F** Early Stage 5. **G** Late Stage 5. **H** Middle Stage 6. **I** Early Stage 7. **J** Late Stage 7. **K** Early Stage 8. **L** Late Stage 8. **M** Stage 9. – Abbreviations: Ab – abdominal region / abdomen; Am – amnion; An – antenna; Bd – blastoderm; Ce – cercus; CN – cleavage nucleus; DDC – definitive dorsal closure; EA – embryonic area; EEA – extraembryonic area; Em – embryo; Gn – gnathal region; HC – head capsule; HL – head lobe; LP – lateral plate; Md – mandible; MxP – maxillary palp; Pce – protocephalon; Pco – protocorm; PDC – provisional dorsal closure; SDO – secondary dorsal organ; Se – serosa; SYN – secondary yolk nucleus; Th – thoracic region / thorax; Th2 – 2nd thoracic segment; Th1L–3L – 1st to 3rd thoracic legs; I–XI – 1st to 11th abdominal segments. – Symbols: black arrowhead – anterior end of embryo; white arrowhead – posterior end of embryo. – Scale bar: 500 µm.

3.10. *Proreus simulans* and a chelisochid gen. sp. (Chelisochidae)

3.10.1. Eggs

The eggs of *Proreus simulans* and a chelisochid gen. sp., resembling each other, are ellipsoidal, ca. 800 µm long and 600 µm wide, and ca.1 mm long and 0.85 mm wide, respectively (in freshly laid eggs) (Figs 30A, 31A). The eggs of *Proreus simulans* and a chelisochid gen. sp. are respectively ivory and whitish in color, and there is no secretion on the smooth egg surface.

At the anterior pole of the egg, around 15 micropyles of ca. 1 µm in diameter are arranged in a circle of ca. 20 µm in diameter in both species (Figs 30B, 31B). No chorionic pore is found at the center of the circular arrangement of micropyles in either of the two species.

3.10.2. Embryonic development

At 23–25°C, the egg period of *Proreus simulans* is about 10 days.

The embryonic development of *P. simulans* is outlined in Fig. 47. In Stage 3, the formed embryo is large (IL = 65%), and its anterior end is situated close to the anterior pole of the egg (PAEE = 95%) (Fig. 47C). The embryo starts to grow in Stage 4, and it rapidly and substantially elongates in Stage 5 with its posterior end ahead (Fig. 47D). Late in Stage 5, its posterior end passing the anterior pole of the egg, the embryo acquires its maximum length in the anatrepsis period (ML = 95%) (Fig. 47E). The anterior and posterior ends of the embryo come close, nearly contacting each other. The ERE is 145%.

The cerci do not grow long, showing a configuration of prospective one-segmented claspers throughout the development (Fig. 47G–M). The full-grown embryo of *P. simulans* has a knob-like egg tooth on the frons, with
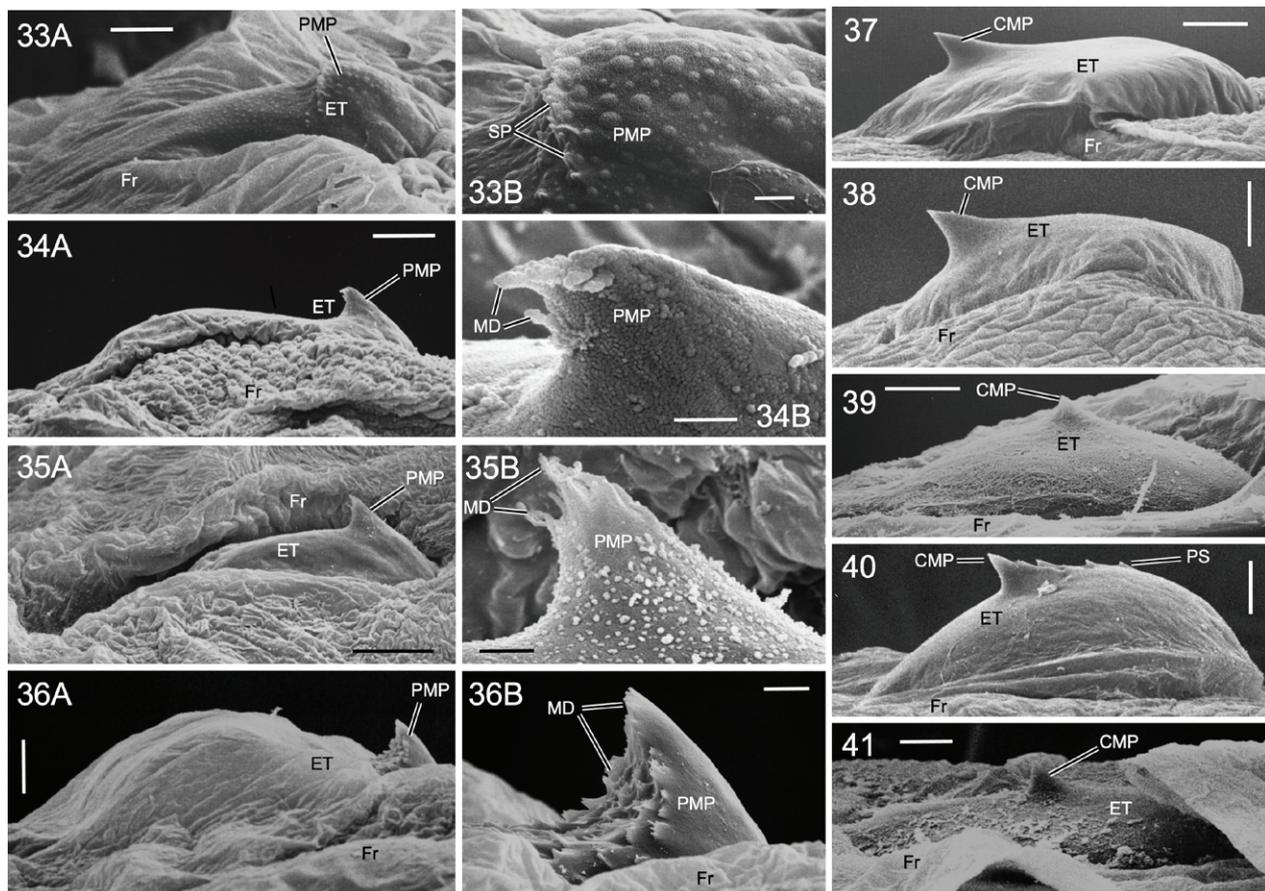
Figures 33–41. SEMs of the egg teeth of Epidermaptera. **33** *Apachyus chartaceus* (Apachyidae). **33A** Lateral view, posterior to the right. **33B** Enlarged image. **34** *Anisolabis maritima* (Anisolabididae). **34A** Lateral view, posterior to the right. **34B** Enlarged image. **35** *Euborellia pallipes* (Anisolabididae). **35A** Lateral view, posterior to the right. **35B** Enlarged image. **36** *Labidura riparia* (Labiduridae). **36A** Lateral view, posterior to the right. **36B** Enlarged image. **37** *Forficula scudderi* (Forficulidae). Lateral view, posterior to the right. **38** *Anechura harmandi* (Forficulidae). Lateral view, posterior to the right. **39** *Paralabella curvicauda* (Spongiphoridae). Lateral view, posterior to the right. **40** *Proreus simulans* (Chelisochidae). Lateral view, posterior to the right. **41** A chelisochid gen. sp. (Chelisochidae). Lateral view, posterior to the right. – Abbreviations: CMP – central major process; ET – egg tooth; Fr – frons; MD – minute denticle; PMP – posterior major process; PS – posterior serration; SP – small protuberance. – Scale bars: 33A, 39–41 – 10 µm; 34A, 35A, 36A, 37, 38 – 20 µm; 33B, 34B, 35B – 2 µm; 36B – 5 µm.

an anteriorly-pointed central major process and a posterior serration (Fig. 40). The egg tooth of the Malaysian chelisochid gen. sp. is similar to that of *P. simulans*, but without posterior serration (Fig. 41).

4.   Discussion

4.1.   Egg deposition and brood care

An adhesive substance is secreted over the egg surface, heavily deposited at the posterior pole of the egg in Diplatyidae, Pygidicranidae, and Apachyidae: Diplatyidae – *Diplatys greeni* Burr, 1904 (Green 1898), a Papua New Guinean gen. sp. (Matzke and Klass 2005), and *Diplatys flavicollis* (Shimizu and Machida 2009, 2011b); Pygidicranidae – *Tagalina papua* (de Bormans, 1903), *Tagalina burri* Hincks, 1955, *Paracranopygia siamensis* (Dohrn, 1863) (Matzke and Klass 2005), *Cranopygia* sp. (herein), and *Echinosoma* sp. (herein); and Apachyidae – *Apachyus chartaceus* (Shimizu and Machida 2011a; herein). In a Papua New Guinean diplatyid (Matzke and Klass 2005) and *D. flavicollis* (Fig. 2A, B; Shimizu and Machida 2009, 2011b), and occasionally in *Cranopygia* sp. (Fig. 3B), the adhesive substance is abundantly deposited in the form of a stalk (adhesive stalk) at the posterior pole of the egg. The situation in Karschiellidae is

unknown. Thus, in Protodermaptera and Apachyidae, the deposited eggs are attached to the substratum with the adhesive substance, and once it is dried and hardened, the eggs cannot be moved. In contrast, Epidermaptera have been known to lack this adhesive substance on the egg surface (Matzke and Klass 2005); the present study corroborates this, revealing that the adhesive substance on the egg is lacking in the Epidermaptera examined excluding Apachyidae. In these species, the eggs are simply deposited on the substratum and can be moved after deposition. These characters cannot be assessed, however, in the viviparous Hemimeridae and Arixeniidae due to their lack of deposited eggs.

Klass (2003) stated that most dicondylian insects with well-developed female external genitalia have ectodermal accessory glands ventrally in the 9th abdominal segment, which are most likely part of the groundplan of Dicondylia. Klass (2003) and Matzke and Klass (2005) suggested that the presence of an adhesive substance in Diplatyidae and Pygidicranidae is correlated with that of accessory glands in 9th abdominal segment. In the Apachyidae, Shimizu and Machida (2011a) revealed that the adhesive substance is on the egg surface, and Kaidel and Klass (2011) confirmed that accessory glands of 9th abdominal segment are present. In contrast, the accessory glands in 9th abdominal segment are known to be absent in the adults of Epidermaptera excluding Apachyidae (Giles 1961; Bhatnagar 1964; Schneider and Klass 2013). As Klass (2003) and Matzke and Klass (2005) suggested, the lack of these
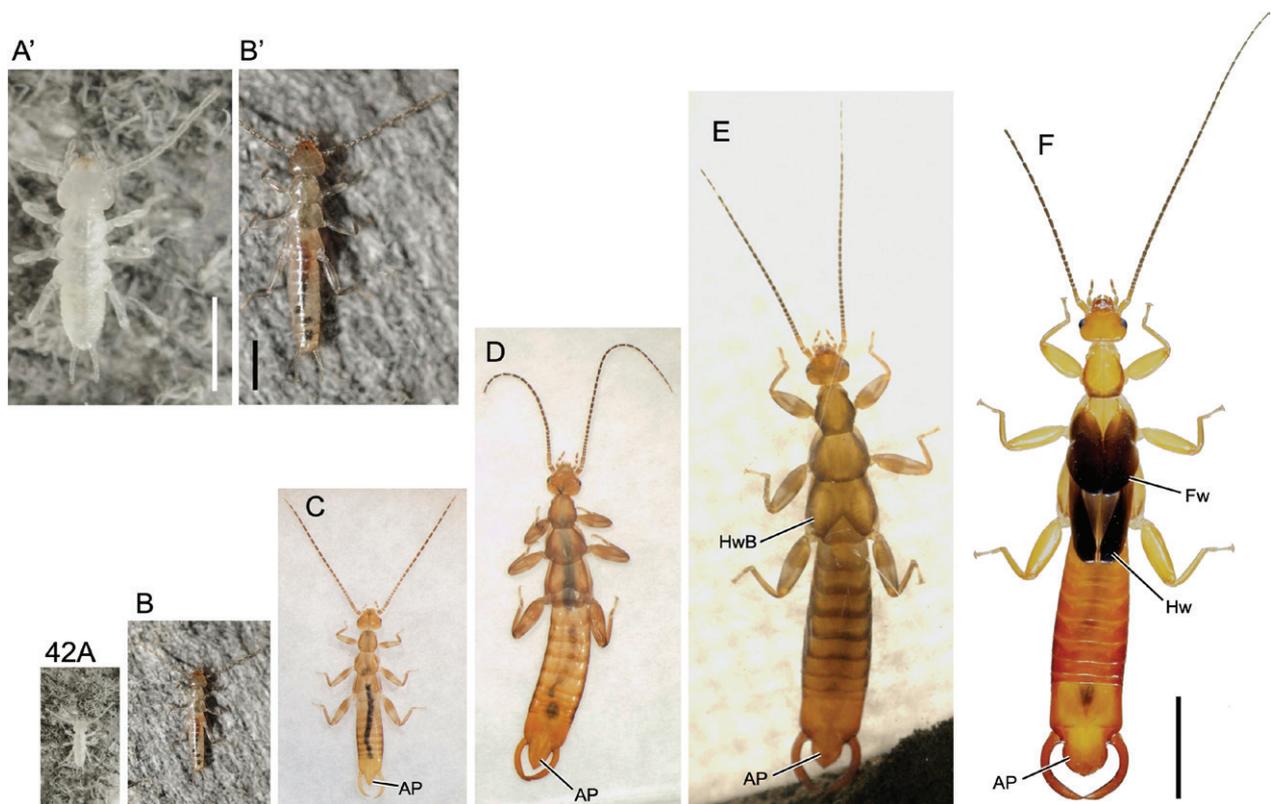
Figure 42. Larvae of recognized instars and adult of *Apachyus chartaceus* (Apachyidae). **A–C** Same individual. **A** First instar larva (**A'** enlarged image). **B** Second instar larva (**B'** enlarged image). **C** Third instar larva. **D–F** Same individual (male): **D** Penultimate instar larva; **E** Final instar larva; **F** Adult. – Abbreviations: AP – anal process; Fw – forewing or tegmen; Hw – hindwing or ala; HwB – hindwing bud. – Scale bars: A–F – 5 mm; A', B' – 1 mm.

accessory glands and the concomitant lack of adhesive substance on the egg surface may be a shared apomorphy of Epidermaptera (excluding Apachyidae).

The intensive and elaborate maternal care of eggs and young larvae is a well-known characteristic of Epidermaptera (excluding Apachyidae) and comprises attributes such as: 1) association with eggs, 2) cleaning and application of secretions to eggs by licking, 3) egg transport to favorable places, 4) defense of eggs, 5) association with the first instar larvae, 6) defense of the first instar larvae, 7) transportation of the first instar larvae, 8) help in hatching by feeding on egg shell, 9) frequent contact between the mother's and first instar larval mouthparts, and 10) providing food for the first instar larvae (sometimes represented by the mother's own dead body). Features 1–6 have been reported consistently in Epidermaptera, although data are available only for very few species (cf. Hinton 1981; Matzke and Klass 2005).

The maternal brood care of Protodermaptera (no data for Karschiellidae) and Apachyidae is less intensive, showing only some of the above-mentioned features, at most 1, 2, 4, 5, and 6: Diplatyidae – *D. greeni* (Green 1898), a Papua New Guinean gen. sp. (Matzke and Klass 2005), and *D. flavicollis* (Shimizu and Machida 2009, 2011b); Pygidicranidae – *T. papua* (Matzke and Klass 2005), *Cranopygia* sp. (herein), and *Echinosoma* sp. (herein); Apachyidae – *A. chartaceus* (Shimizu and Machida 2011a; herein). Diplatyidae and Pygidicranidae are well accepted to represent (along with Karschiellidae) basal groups of Dermaptera (Haas 1995; Haas and Kukalová-Peck 2001; Haas and Klass 2003). Whereas Apachyidae has been widely regarded as a basal branch of Epidermaptera, the latest phylogenomic study by Wipfler et al. (2020) yielded Apachyidae as the sister group of the remaing Dermaptera (Karschiellidae was not included in the analysis). Hence, the less intensive maternal brood care shown in Protodermaptera and Apachyidae, linked with the adhesive substance on the egg surface, may represent the ancestral condition, which was probably the groundplan for Dermaptera.
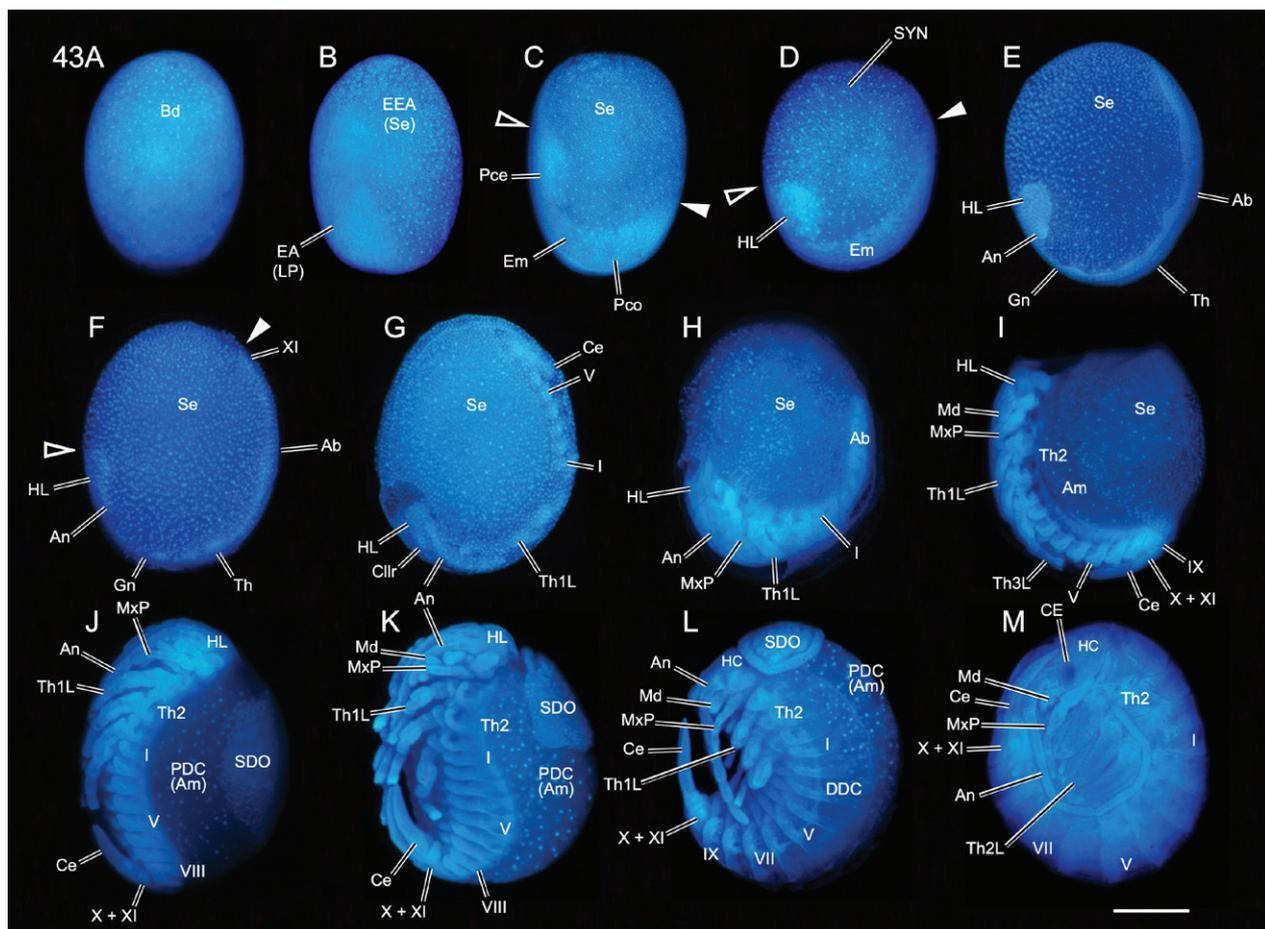
Figure 43. Embryonic development of *Anisolabis maritima* (Anisolabididae), DAPI staining, UV-excitation, fluorescence microscopy. Lateral view, anterior to the top, ventral to the left. **A** Stage 2. **B** Middle Stage 3. **C** Late Stage 3. **D** Stage 4. **E** Early Stage 5. **F** Late Stage 5. **G** Middle Stage 6. **H** Early Stage 7. **I** Middle Stage 7. **J** Late Stage 7. **K** Early Stage 8. **L** Middle Stage 8. **M** Stage 9. – Abbreviations: Ab – abdominal region / abdomen; Am – amnion; An – antenna; Bd – blastoderm; CE – compound eye; Ce – cercus; Cllr – clypeolabrum; DDC – definitive dorsal closure; EA – embryonic area; EEA – extraembryonic area; Em – embryo; Gn – gnathal region; HC – head capsule; HL – head lobe; LP – lateral plate; Md – mandible; MxP – maxillary palp; Pce – protocephalon; Pco – protocorm; PDC – provisional dorsal closure; SDO – secondary dorsal organ; Se – serosa; SYN – secondary yolk nucleus; Th – thoracic region / thorax; Th2 – 2nd thoracic segment; Th1L–3L – 1st to 3rd thoracic legs; I–XI – 1st to 11th abdominal segments. – Symbols: black arrowhead – anterior end of embryo; white arrowhead – posterior end of embryo. – Scale bar: 500 μm.

Table 2. Presence / absence of chorionic central pore at the egg's anterior pole in Demaptera.

Family	Species	Chorionic pore
Diplatyidae	*Diplatys flavicollis*	absent
Pygidicranidae	*Cranopygia* sp.	present
Pygidicranidae	*Echinosoma* sp.	present
Pygidicranidae	*Parapsalis infernalis*	absent
Apachyidae	*Apachyus chartaceus*	present
Anisolabididae	*Anisolabis maritima*	absent
Anisolabididae	*Euborellia pallipes*	absent
Labiduridae	*Labidura riparia*	present
Forficulidae	*Forficula scudderi*	present
Forficulidae	*Anechura harmandi*	present
Spongiphoridae	*Paralabella curvicauda*	absent
Chelisochidae	*Proreus simulans*	absent
Chelisochidae	gen. sp.	absent

Matzke and Klass (2005) assumed that the maternal care evolved within Dermaptera, and that the loss of accessory glands and egg attachment favored the intensification of brood care including transport of eggs to more favorable conditions. The present study revealed that the pygidicranid *Parapsalis infernalis*, to which Wipfler et al. (2020) assigned a basal position in Protodermaptera, shows egg deposition and brood care behaviors similar to those of higher dermapterans in: 1) the adhesive substance on the egg surface is lacking, 2) the eggs are not fixed to but simply deposited on the substratum, and 3) the mother provides intensive care to her eggs, including licking, rolling, and transport. Hence, the intensive maternal care well known in Dermaptera, associated with the lack of adhesive substance on the egg surface, may have been acquired independently in the lineage of *P. infernalis* and in Epidermaptera excluding Apachyidae, as
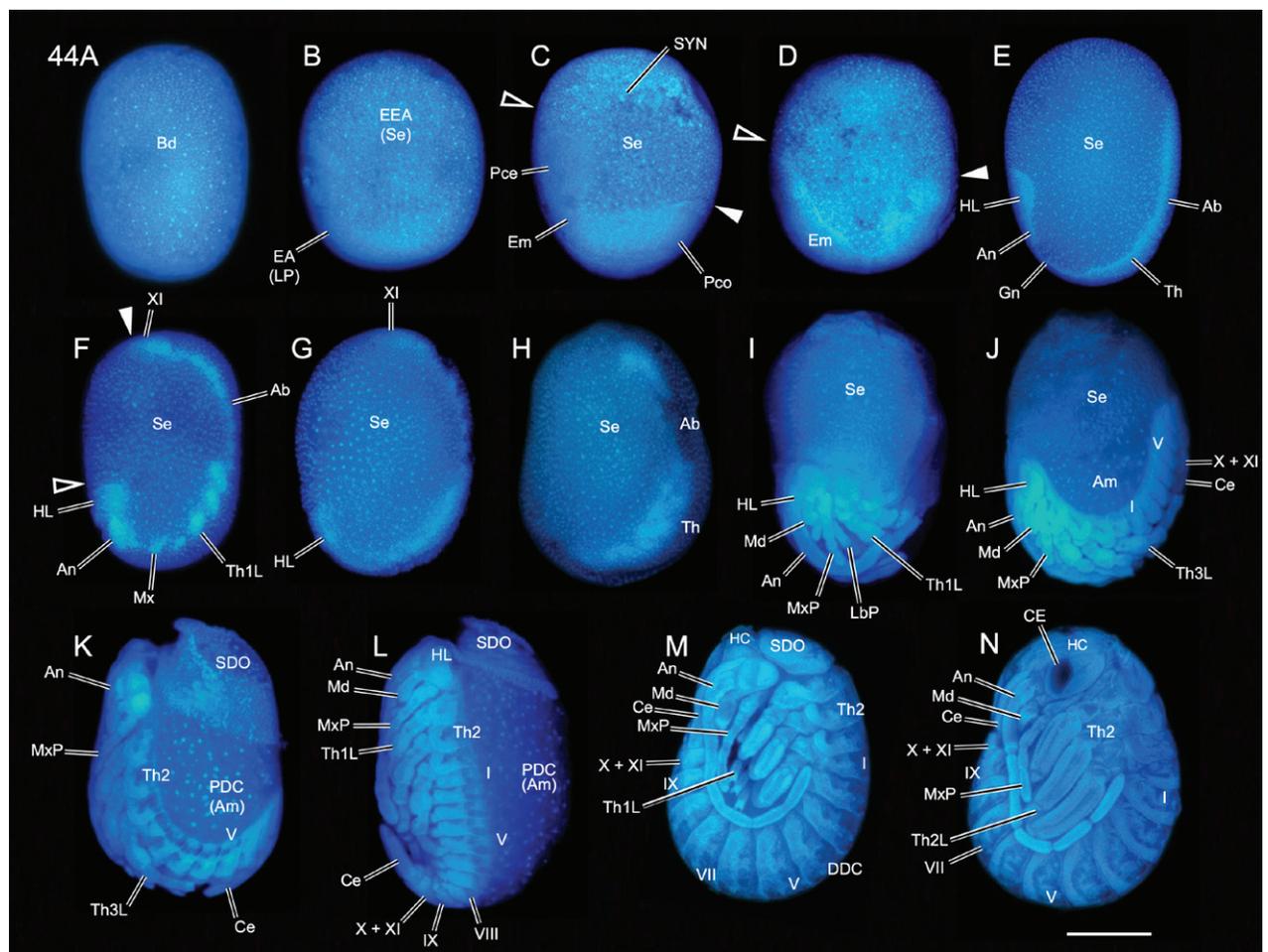
Figure 44. Embryonic development of *Labidura riparia* (Labiduridae), DAPI staining, UV-excitation, fluorescence microscopy. Lateral view, anterior to the top, ventral to the left. **A** Stage 2. **B** Early Stage 3. **C** Late Stage 3. **D** Stage 4. **E** Early Stage 5. **F** Late Stage 5. **G** Early Stage 6. **H** Late Stage 6. **I** Early Stage 7. **J** Middle Stage 7. **K** Late Stage 7. **L** Early Stage 8. **M** Late Stage 8. **N** Stage 9. – Abbreviations: Ab – abdominal region / abdomen; Am – amnion; An – antenna; Bd – blastoderm; CE – compound eye; Ce – cercus; DDC – definitive dorsal closure; EA – embryonic area; EEA – extraembryonic area; Em – embryo; Gn – gnathal region; HC – head capsule; HL – head lobe; LbP – labial palp; LP – lateral plate; Md – mandible; Mx – maxilla; MxP – maxillary palp; Pce – protocephalon; Pco – protocorm; PDC – provisional dorsal closure; SDO – secondary dorsal organ; Se – serosa; SYN – secondary yolk nucleus; Th – thoracic region / thorax; Th2 – 2nd thoracic segment; Th1L–3L – 1st to 3rd thoracic legs; I–XI – 1st to 11th abdominal segments. – Symbols: black arrowhead – anterior end of embryo; white arrowhead – posterior end of embryo. – Scale bar: 500 μm.

Wipfler et al. (2020) deduced from the lack of elaborate maternal care in Apachyidae.

4.2. Eggs

We (Shimizu and Machida 2011a, b; herein) examined the eggs of 13 species from eight families. The eggs of the examined dermapterans were found to share the following features: 1) prolate ellipsoidal shape, 2) whitish to yellowish color, 3) smooth surface, and 4) circular arrangement of micropyles, which are the entrance for sperm opened in the chorion, around the anterior pole of the eggs.

A chorionic pore was found at the center of the circular arrangement of micropyles in some dermapterans examined, i.e., *Cranopygia* sp. and *Echinosoma* sp. of Pygidicranidae, *Labidura riparia* of Labiduridae, *Apachyus chartaceus* of Apachyidae, and *Forficula scudderi* and *Anechura harmandi* of Forficulidae (Table 2). Chauvin et al. (1991) examined the egg structure of *Forficula auricu-laria* (Forficulidae) and described small pores circularly arranged around the anterior pole of the egg, which may be comparable to our micropyles, and a single pore at the center of the circular arrangement of small pores. They identified the central pore as the micropyle and the circularly arranged small pores as aeropyles. However, their identification requires re-examination because the central pore was, notably, found in only some examined dermapterans (Table 2), but the circularly arranged pores are universally found in the eggs of all dermapterans. Therefore, even if the central pore functions as a micropyle, as suggested by Chauvin et al., the micropyles are primarily represented by the circularly arranged pores, and the central pore would be the secondary one. The curious epizoic dermapterans, Hemimeridae and Arixeniidae, reproduce viviparously; consequently, their eggs lack the chorion and the micropyles (cf. Heymons 1912; Hagan 1951).

The circular arrangement of micropyles is common in Polyneoptera, i.e., reported for Grylloblattodea (Uchifune and Machida 2005), Mantophasmatodea (Uchifune et al.
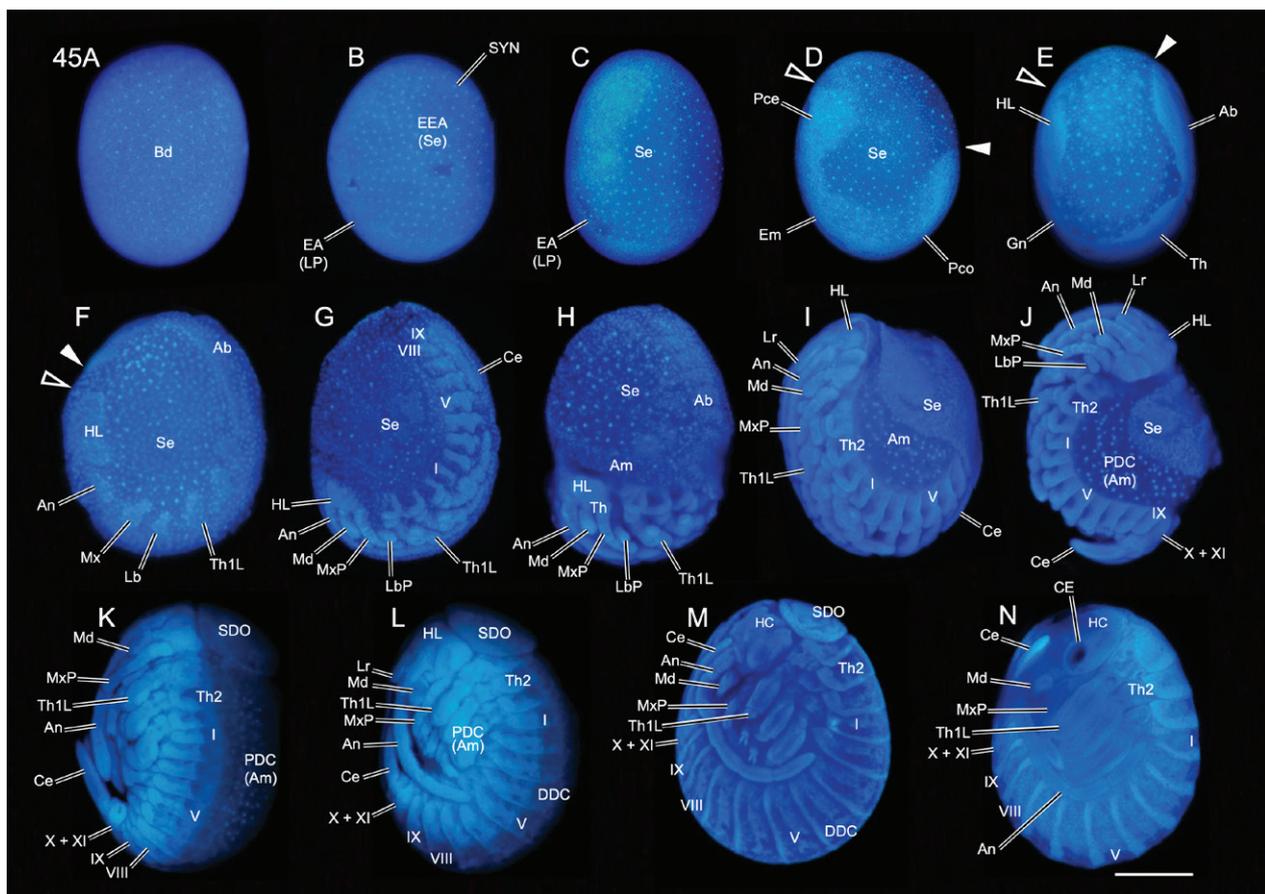
Figure 45. Embryonic development of *Forficula scudderi* (Forficulidae), DAPI staining, UV-excitation, fluorescence microscopy. Lateral view, anterior to the top, ventral to the left. **A** Stage 2. **B** Early Stage 3. **C** Middle Stage 3. **D** Late Stage 3. **E** Stage 4. **F** Late Stage 5. **G** Late Stage 6. **H** Early Stage 7. **I** Middle Stage 7. **J** Late Stage 7. **K** Early Stage 8. **L** Middle Stage 8. **M** Late Stage 8. **N** Stage 9. – Abbreviations: Ab – abdominal region / abdomen; Am – amnion; An – antenna; Bd – blastoderm; CE – compound eye; Ce – cercus; DDC – definitive dorsal closure; EA – embryonic area; EEA – extraembryonic area; Em – embryo; Gn – gnathal region; HC – head capsule; HL – head lobe; Lb – labium; LbP – labial palp; LP – lateral plate; Lr – labrum; Md – mandible; Mx – maxilla; MxP – maxillary palp; Pce – protocephalon; Pco – protocorm; PDC – provisional dorsal closure; SDO – secondary dorsal organ; Se – serosa; SYN – secondary yolk nucleus; Th – thoracic region / thorax; Th2 – 2nd thoracic segment; Th1L – 1st thoracic leg; I–XI – 1st to 11th abdominal segments. – Symbols: black arrowhead – anterior end of embryo; white arrowhead – posterior end of embryo. – Scale bar: 500 μm.

2006), Plecoptera (Mtow and Machida 2018a; Mtow et al. 2021), and the orthopteran Caelifera (cf. Mashimo et al. 2016). One or two micropyles on the ventral side of the egg are typical of Phasmatodea (Clark Sellick 1997, 1998; Jintsu et al. 2010), Embioptera (Jintsu and Machida 2009), and Zoraptera (Mashimo et al. 2014). Such a small number of micropyles might be explained by a strong reduction of circularly arranged micropyles. Blattodea (including Isoptera) and Mantodea share micropyles clustered in a restricted area on the ventral side of the egg, and this may be a groundplan feature of Dictyoptera (Fujita and Machida 2017; Fukui et al. 2018). The orthopteran Ensifera show a similar distribution of micropyles (Mashimo et al. 2016).

4.3. Embryonic development

In this section, we compare the embryonic development of the examined dermapterans, referring to previous research, to characterize the embryonic development of Dermaptera and discuss several comparative embryological issues related to Dermaptera.

4.3.1. Formation of embryo

Mashimo et al. (2014) proposed two embryological autapomorphies for Polyneoptera, one concerning the elongation of the embryo (see "4.3.3. Blastokinesis"), and one concerning the formation of the embryo. In Polyneoptera, the embryo is formed by the fusion of paired regions with

Figure 46. Embryonic development of *Paralabella curvicauda* (Spongiphoridae), DAPI staining, UV-excitation, fluorescence microscopy. Lateral view, anterior to the top, ventral to the left. **A** Stage 2. **B** Middle Stage 3. **C** Late Stage 3. **D** Stage 4. **E** Middle Stage 5. **F** Late Stage 5. **G** Early Stage 6. **H** Late Stage 6. **I** Early Stage 7. **J** Middle Stage 7. **K** Late Stage 7. **L** Middle Stage 8. **M** Stage 9. – Abbreviations: Ab – abdominal region / abdomen; Am – amnion; An – antenna; Bd – blastoderm; Ce – cercus; DDC – definitive dorsal closure; EA – embryonic area; EEA – extraembryonic area; Em – embryo; Gn – gnathal region; HC – head capsule; HL – head lobe; Lb – labium; LbP – labial palp; LP – lateral plate; Lr – labrum; Md – mandible; Mx – maxilla; MxP – maxillary palp; Pce – protocephalon; Pco – protocorm; PDC – provisional dorsal closure; SDO – secondary dorsal organ; Se – serosa; SYN – secondary yolk nucleus; Th – thoracic region / thorax; Th2 – 2nd thoracic segment; Th1, 3L – 1st and 3rd thoracic legs; I–XI – 1st to 11th abdominal segments. – Symbols: black arrowhead – anterior end of embryo; white arrowhead – posterior end of embryo. – Scale bar: 500 μm.

Table 3. Length, elongation, and positioning of embryos in Dermaptera: length of embryonic primordium relative to the egg's longitudinal circumference (IL), maximum embryonic length in the anatrepsis period relative to the egg's longitudinal circumference (ML), embryonic elongation ratio in the anatrepsis period (ML/IL = ERE), position of the anterior end of the embryonic primordium = ratio of distance between its anterior end and the egg's posterior pole relative to egg length (PAEE), and position of the posterior end of the embryo when having attained its maximum length in the anatrepsis period (PPEE).

Family	Species	IL	ML	ERE	PAEE	PPEE
Diplatyidae	*Diplatys flavicollis*	35	80	230	45	at egg's anterior pole
Pygidicranidae	*Cranopygia* sp.	30	70	230	25	at egg's anterior pole
Pygidicranidae	*Parapsalis infernalis*	40	85	210	55	near egg's anterior pole, on egg's dorsal side
Apachyidae	*Apachyus chartaceus*	40	90	225	70	at egg's anterior pole
Anisolabididae	*Anisolabis maritima*	50	70	140	65	near egg's anterior pole, on egg's dorsal side
Labiduridae	*Labidura riparia*	50	75	150	75	at egg's anterior pole
Forficulidae	*Forficula scudderi*	60	98	160	85	passing egg's anterior pole, on egg's ventral side
Spongiphoridae	*Paralabella curvicauda*	60	95	160	90	passing egg's anterior pole, on egg's ventral side
Chelisochidae	*Proreus simulans*	65	95	145	95	passing egg's anterior pole, on egg's ventral side

higher cellular density differentiated in the blastoderm (e.g., Zoraptera: Mashimo et al. 2014; Orthoptera: Nakamura et al. 2010; Grylloblattodea: Uchifune and Machida 2005; Phasmatodea: Bedford 1970; Embioptera: Jintsu 2010; Blattodea: Fujita and Machida 2017). In contrast, in other hemimetabolans, i.e., Palaeoptera (e.g., Ephemeroptera: Tojo and Machida 1997; Odonata: Ando 1962) and Acercaria (e.g., Psocodea: Goss 1952; Thysanoptera: Heming 1979; Hemiptera: Muir and Kershaw 1912; Shinji 1919), the fusion process of the paired regions with higher cellular density is not conspicuous (except for some examples in Hemiptera: Seidel 1924; Butt 1949; Sander 1956), and the embryo is basically formed by a simple concentration and proliferation of blastoderm cells around the posterior pole of the egg, as known for the apterygote Ectognatha (e.g., Archaeognatha: Machida et al. 1990; Zygentoma: Masumoto and Machida 2006).

The present study revealed that dermapteran embryos are formed by the fusion of paired regions with higher cellular density differentiated in the blastoderm, as in other polyneopteran orders. The paired regions with a higher cellular density represent the lateral plates, which are the presumptive ectoderm, and the region in between with lower cellular density is the median plate, which is the presumptive mesoderm. The fusion of paired regions with higher cellular density leading to embryo formation in Polyneoptera may exist in the medial migration of lateral plates over the median plate leading to the differentiation of germ layers. Heymons (1895) made a similar description in *Forficula auricularia*.

In polyneopteran orders other than those above, i.e., Plecoptera and Mantodea, as well as in the blattodean subgroup Isoptera, the embryo formation by fusion of paired regions with higher cellular density has not been reported (no data for Mantophasmatodea; cf. Machida et al. 2004). In Plecoptera (Mtow and Machida 2018a, b) and Isoptera (Knower 1900; Mukerji 1970), this may be related to their unique early embryogenesis, where the embryo is formed as a small, ball-shaped embryo–amnion composite. In Mantodea, a small circular embryo has been reported to be formed by a simple concentration and proliferation of blastoderm cells (Hagan 1917;

Görg 1959; Fukui et al. 2018). Giardina (1897), however, described a U-shaped embryo anlage appearing first in a mantodean *Mantis religiosa*. This U-shape of the embryo might have some relation to the embryo formation by fusion of paired regions with higher cellular density. Critical examination is required to understand the embryo formation in Mantodea.

4.3.2. Germ type

Krause (1939) and his colleagues (e.g., Sander 1976) examined and compared the length of the embryonic primordium (called the "newly formed embryo" in "3. Results") relative to the egg size as well as the segmentation modes in different insect groups and distinguished three germ types: the short germ type, the semi-long germ type (intermediate germ type), and the long germ type (see also Schwalm 1988; Heming 2003). The short germ type is found in primitive insects such as apterygote Ectognatha (e.g., Archaeognatha: Nakagaki et al. 2015) and Palaeoptera (e.g., Ephemeroptera: Tojo and Machida 1997). A small, circular or heart-shaped embryonic primordium is practically represented by the protocephalon, which includes the growth zone in its posterior restricted region; the embryo grows accompanied by sequential production of segments to the anterior from the growth zone. The long germ type is predominantly found in most Holometabola (e.g., Diptera: Campos-Ortega and Hartenstein 1985). A long embryonic primordium proportioned to the definitive length, composed of the protocephalon and long protocorm, forms from the beginning; almost all segments simultaneously differentiate. The semi-long germ type, found in Polyneoptera [e.g., Orthoptera (*Acheta domesticus*): Sander 1976], Acercaria [e.g., Hemiptera (*Notonecta*): Krause 1939], and some holometabolans [e.g., Coleoptera (*Tenebrio molitor*): Ullman 1964], is an intermediate of the short and long germ types. The embryonic primordium is pear- or keyhole-shaped and composed of the protocephalon and the short protocorm with several predetermined segments at its anterior region and the growth zone at its posterior extremity. The embryo grows accompanied by sequential segment production

from the growth zone; newly formed segments are added posteriorly to segments already differentiated at the time of formation of the embryonic primordium.

The length of the embryonic primordium relative to the egg size tends to be short in the short germ type, very long in the long germ type, and intermediate in the semi-long germ type. Heymons (1895) described an extensive embryonic primordium in a forficulid, *Forficula auricularia*. This looks like the long germ; in particular, Ando and Machida (1987) categorized the germ type of Dermaptera as long. This might be suggestive of a closer relationship between Dermaptera and Holometabola, as suggested by the features concerning the ovariole type (cf. Büning 1994) (see "4.3.6. Other embryological features" and "4.3.7. Embryological groundplan of Dermaptera and its phylogenetic affiliation"). However, the present study revealed that the embryonic primordia of Epidermaptera are extensive, but those of Protodermaptera are relatively short, as mentioned in section "4.3.4. Positioning and length of the embryo" (IL, Table 3).

When discussing germ types, the segmentation mode is essential (cf. Sander 1976; Schwalm 1988; Heming 2003). The present study revealed that: 1) segments are formed sequentially from the anterior toward the posterior in Dermaptera (Figs 20, 32, 43–47), as demonstrated in *Diplatys flavicollis* (Figs 6–13), but 2) at least the posterior cephalic segments are predetermined in the protocorm (Figs 7, 8) (see also Heymons 1895; Bhatnagar and Singh 1965). Thus, the embryogenesis of Dermaptera can be categorized as semi-long germ. The embryonic primordium of Dermaptera is relatively extensive, as it includes several prospective segments. The semi-long germ type and the resultant, elongate embryonic primordium form the groundplan of Dermaptera.

Fujita and Machida (2017) mentioned that the embryogenesis in Polyneoptera is mainly of the short germ type. Namely, Plecoptera (e.g., Mtow and Machida 2018a), Orthoptera (partim) (e.g., Nelsen 1934), Grylloblattodea (Uchifune and Machida 2005), Mantophasmatodea (Machida et al. 2004), Phasmatodea (e.g., Bedford 1970), Mantodea (e.g., Fukui et al. 2018), "Blattaria (non-isopteran Blattodea) (partim)" (Fujita and Machida 2017), and Isoptera (e.g., Mukerji 1970) perform the embryogenesis of the short germ type. In contrast, the embryonic primordia of other polyneopterans, i.e., Zoraptera (Mashimo et al. 2014), Orthoptera (partim) (e.g., Sander 1976), Embioptera (e.g., Stefani 1959), and "Blattaria (partim)" (Wheeler 1889), are more extensive compared with those of the typical, short germ type, containing a region predetermined to develop into several cephalic segments. The embryogenesis of these polyneopterans, together with Dermaptera (herein), are therefore of the semi-long germ type.

Thus, the germ type of Polyneoptera may be short or semi-long. As primitive insects such as the apterygote Ectognatha and Palaeoptera show the short germ type, this may be regarded as plesiomorphic. The semi-long germ type in Dermaptera and Zoraptera, whose sister group relationship was strongly suggested in recent phylogenomic studies including large-scale transcriptome analyses

(Misof et al. 2014; Wipfler et al. 2019), might be taken as synapomorphic, but the question might be more complex, since the semi-long germ type is sporadically found in other polyneopterans.

4.3.3. Blastokinesis

Wheeler (1893) distinguished three phases in blastokinesis: "anatrepsis", "katatrepsis", and the intervening "diapause" ("intertrepsis" in the present study). Various researchers have previously discussed blastokinesis (Johannsen and Butt 1941; Schwalm 1988; Heming 2003). We (Fujita and Machida 2017; Mtow and Machida 2018a) defined the blastokinesis phases as follows. At earlier stages of development, in association with the formation of amnioserosal fold, insect embryos immerse in the yolk, in some groups shallowly and in others deeply. Then, the embryos elongate and reach their definitive position in the pre-katatrepsis period. The descending process of the embryo from the beginning of the amnioserosal fold formation up to this point is the "anatrepsis". Usually, in non-holometabolan Pterygota, the reversion of the embryo's anteroposterior axis is involved in anatrepsis. Thereafter, the embryos develop until katatrepsis, maintaining this positioning: this phase is the "intertrepsis (= diapause)". Then, the withdrawal of the amnioserosal fold leads to the embryo's reappearance on the egg surface; this ascending process is the "katatrepsis". Usually, in non-holometabolan Pterygota, drastic reversion of the embryo's axis is involved in katatrepsis.

In the present study, we examined the embryonic development in nine species of eight families of Dermaptera (Figs 6–13, 20, 21, 32, 43–47). The blastokinesis of Dermaptera can be summarized as follows, also referring to previous studies (Heymons 1895; Bhatnagar and Singh 1965; Fuse and Ando 1983). Anatrepsis is represented by Stages 4–5. In Stage 3, an embryo is newly formed on the egg surface from the ventral side to the posterior dorsal side of the egg, and the embryo, soon ventrally covered by the amnioserosal fold, starts to elongate in Stage 4. Then, in Stage 5, the embryo substantially elongates along the dorsal surface of the egg with its posterior end ahead, and the posterior end of the embryo is located around the anterior pole of the egg. As a result of anatrepsis, the anteroposterior axis of the embryo, initially coincident with the anteroposterior axis of the egg, is reversed, and the embryo finally acquires its definitive position in the pre-katatrepsis period. Intertrepsis is represented by Stage 6. Maintaining its position and orientation, the embryo largely grows. Katatrepsis occurs in Stage 7. The amnioserosal fold regresses, and the embryo re-appears on the egg surface. The embryo migrates with its head ahead, passing beyond the posterior pole of the egg, toward the ventral side of the egg; finally, the embryo reaches its position on the ventral side of the egg. As a result of katatrepsis, the anteroposterior axis of the embryo is reversed again, and the embryo recovers the original orientation.

Mashimo et al. (2014) proposed an autapomorphy for Polyneoptera concerning the anatrepsis mode. In Poly-

neoptera, the embryo is at an early stage covered by the amnioserosal fold; then, the embryo, which has shallowly immersed in the yolk beneath the amnioserosal fold, elongates along the egg surface to its maximum length in the anatrepsis period, in contrast to Palaeoptera and Acercaria, in which the full elongation of the embryo (in anatrepsis period) occurs (deeply) in the yolk, keeping step with the formation of the amnioserosal fold. The primary feature characterizing the anatrepsis of Polyneoptera is that the formation of amnioserosal fold is accomplished in earlier stages, because we know that the elongation of the embryo occurs deeply in the yolk in some Polyneoptera, e.g., Pteronarcyidae (Miller 1939) and Perlodidae (Mtow and Machida 2018a) of Plecoptera, Tettigoniidae (Wheeler 1893) and Gryllidae (Sander 1976) of Orthoptera; the embryo's elongation along the egg surface is recognized as a secondary feature of polyneopteran anatrepsis. May be said to be typical of Polyneoptera the anatrepsis of Dermaptera, where the embryo, fully covered

by the amnioserosal fold, undergoes full elongation along the egg surface.

The reversion of the embryo's axis is involved in blastokinesis in Palaeoptera, Acercaria, and Polyneoptera, with a few exceptions in Mantodea and blaberoid "Blattaria" (see Heming 2003; Fujita and Machida 2017); thus, this may be a groundplan feature of Neoptera. Blastokinesis involving the reversion of the embryo's axis is typical not only of Neoptera but also of Pterygota.

4.3.4. Positioning and length of the embryo

The embryonic primordia (newly formed embryos in "3. Results") of the Dermaptera examined occupy 30–65% of the egg's longitudinal circumference (Table 3). The protocephalon is located on the ventral side of the egg
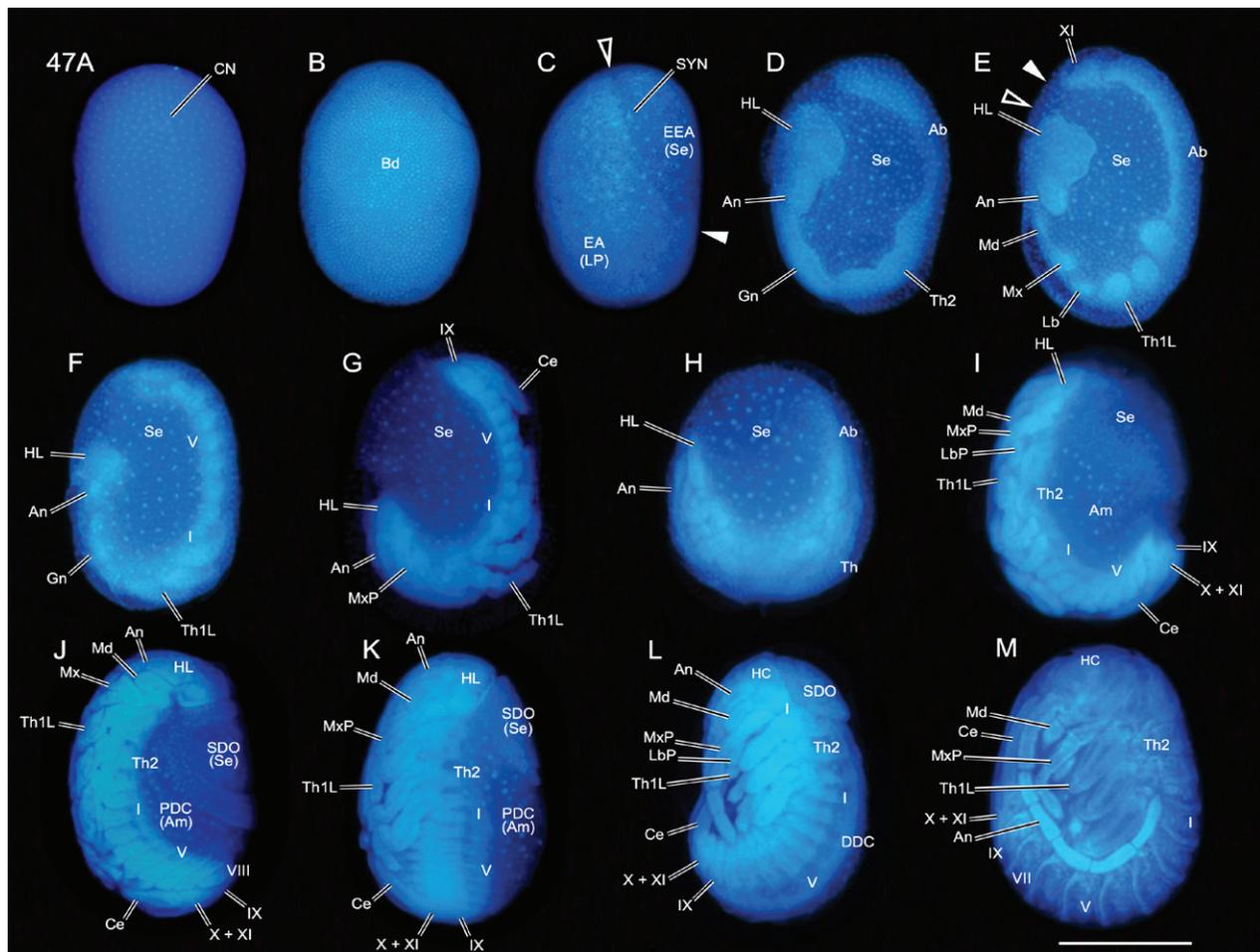
Figure 47. Embryonic development of *Proreus simulans* (Chelisochidae), DAPI staining, UV-excitation, fluorescence microscopy. Lateral view, anterior to the top, ventral to the left. **A** Stage 1. **B** Stage 2. **C** Stage 3. **D** Early Stage 5. **E** Late Stage 5. **F** Early Stage 6. **G** Late Stage 6. **H** Early Stage 7. **I** Middle Stage 7. **J** Late Stage 7. **K** Early Stage 8. **L** Late Stage 8. **M** Stage 9. – Abbreviations: Ab – abdominal region / abdomen; Am – amnion; An – antenna; Bd – blastoderm; Ce – cercus; CN – cleavage nucleus; DDC – definitive dorsal closure; EA – embryonic area; EEA – extraembryonic area; Gn – gnathal region; HC – head capsule; HL – head lobe; Lb – labium; LbP – labial palp; LP – lateral plate; Md – mandible; Mx – maxilla; MxP – maxillary palp; PDC – provisional dorsal closure; SDO – secondary dorsal organ; Se – serosa; SYN – secondary yolk nucleus; Th – thoracic region / thorax; Th2 – 2nd thoracic segment; Th1 – 1st thoracic leg; I–XI – 1st to 11th abdominal segments. – Symbols: black arrowhead – anterior end of embryo; white arrowhead – posterior end of embryo. – Scale bar: 500 μm.

and the posterior end of the embryo is on the dorsal side of the egg (Figs 6F, 20D, 21A, 32D, 43C, 44C, 45D, 46C, 47C). The present study revealed that the embryonic primordia of Protodermaptera are basically short, whereas those of Epidermaptera except for Apachyidae are extensive (IL, Table 3): i.e., in Diplatyidae, and *Cranopygia* sp. and *Parapsalis infernalis* of Pygidicranidae IL = 30–40% (Figs 6F, 20D, 21A), whereas in Epidermaptera, i.e., Anisolabidae, Labiduridae, Forficulidae, Spongiphoridae, and Chelisochidae IL more than 50% (Figs 43C, 44C, 45D, 46C, 47C). Thus, the less extensive embryonic primordium may be a groundplan feature in Dermaptera, whereas the extensive one may be a derived feature. Interestingly, the embryonic primordium of *Apachyus chartaceus* of Apachyidae, to which the latest phylogenomic study (with unclear status of Karschiellidae; Wipfler et al. 2020) assigned the basalmost position in Dermaptera, is as short as those of Protodermaptera, with an IL of 40% (Fig. 32D; IL, Table 3).

The difference in IL between basal and derived dermapterans tends to parallel the difference in the position of the embryonic primordium formation. The positions of the anterior end of the embryonic primordium (PAEE) in the Dermaptera examined are compared in Table 3. Roughly, the embryonic primordia are posteriorly formed in the posterior half of the egg in Protodermaptera (Diplatyidae and Pygidicranidae), i.e., PAEE is 25–55% (Figs 6F, 20D, 21A), whereas the embryonic primordia are more anteriorly formed in Epidermaptera, and its anterior end is located in the anterior half of the egg (PAEE 65–95%) (Figs 32D, 43C, 44C, 45D, 46C, 47C). The embryonic primordia of Eudermaptera (Forficulidae, Spongiphoridae, and Chelisochidae) largely occupy the ventral side of the egg, and the PAEE is fairly large, i.e., 85–95% (Figs 45D, 46C, 47C). This may be a notable characteristic of Eudermaptera.

With the progressive development, the embryo substantially elongates along the egg surface, with its posterior end ahead. Finally, the posterior end of the embryo reaches the area of or around the anterior pole of the egg (PPEE, Table 3) (Figs 6I, 20G, 21B, 32G, 43F, 44F, 45F, 46F, 47E), and acquires the maximum length in the anatrepsis period, occupying 70–98% of the egg's longitudinal circumference (ML, Table 3). The substantial elongation of the embryo during anatrepsis is one of the notable groundplan features of Dermaptera. Such an elongated embryo in the anatrepsis period is rare in non-holometabolan insects, with few examples, such as in *Gryllotalpa vulgaris* (Orthoptera, Ensifera, Gryllotalpidae) (Heymons 1895). Particularly in Eudermaptera, the embryo elongates extensively, and its posterior end passes beyond the egg's anterior pole, finally reaching the egg's ventral side (Figs 45F, 46F, 47E; PPEE, Table 3). This may be one of the groundplan features of Eudermaptera. Interestingly, the embryos of Hemimeridae and Arixeniidae develop long, their posterior end passing beyond the anterior pole of the egg as in Eudermaptera (Hemimeridae: Heymons 1912: fig. 12; Arixeniidae: Hagan 1951: fig. 95).

The Dermaptera examined can be clearly classified into two groups in terms of the elongation ratio of em-

Table 4. Types of egg tooth in Dermaptera: type A – egg tooth furnished with a median denticulated ridge and a pair of horn-shaped, stout projections; type B – egg tooth having a posterior major process with denticles or protuberances on its anterior facet; type C – egg tooth with denticulation along its median line and a posterior major process; type D – egg tooth with an anteriorly-pointed, central major process.

Family	Species	Egg tooth type
Diplatyidae	*Diplatys flavicollis*	type A
Pygidicranidae	*Cranopygia* sp.	type B
Pygidicranidae	*Echinosoma* sp.	type B
Pygidicranidae	*Parapsalis infernalis*	type C
Apachyidae	*Apachyus chartaceus*	type B
Anisolabididae	*Anisolabis maritima*	type B
Anisolabididae	*Euborellia pallipes*	type B
Labiduridae	*Labidura riparia*	type B
Forficulidae	*Forficula scudderi*	type D
Forficulidae	*Anechura harmandi*	type D
Spongiphoridae	*Paralabella curvicauda*	type D
Chelisochidae	*Proreus simulans*	type D
Chelisochidae	gen. sp.	type D

bryos in the anatrepsis period, i.e., ML/IL (ERE, Table 3). ERE is > 210% in Protodermaptera, i.e., Diplatyidae and Pygidicranidae, and notably in Apachyidae (225%), while ERE is < 160%, in Epidermaptera (excluding Apachyidae), i.e., Anisolabididae, Labiduridae, and Eudermaptera (Forficulidae, Spongiphoridae, and Chelisochidae).

4.3.5. Egg tooth

The egg tooth or egg burster is a cuticular hatching device on the cuticle of the prelarva (pronymph, prolarva) or of the first instar larva. Emden (1946) and Kobayashi and Suzuki (2016) reviewed the egg teeth in insects. The most common egg teeth are frontal egg teeth on the cranium. This type of egg teeth is known in Zygentoma (apterous Dicondylia) and most Pterygota, but has not been reported in Entognatha and Archaeognatha (Heymons 1895, 1897; Jura 1972; Machida 1981; Heming 2003; Kobayashi and Suzuki 2016). Thus, the egg tooth may be an apomorphic groundplan feature of Dicondylia. In Zygentoma and some Holometabola, the egg tooth is found on the first instar larval cuticle and is accordingly retained during the first instar larval stage, whereas the egg tooth in Pterygota, except for some Holometabola, is formed by the embryonic cuticle (prelarval cuticle), and discarded at hatching with molting of the embryonic cuticle (Emden 1946; Konopová and Zrzavý 2005).

The present study showed that all dermapterans examined have an egg tooth on the frons, formed by the prelarval cuticle, and that the egg tooth is discarded at hatching, as in other pterygotes, except for some holometabolans (see also Shimizu and Machida 2011b). The egg teeth of Dermaptera are knob-like and categorized into four types, A–D (Table 4). Type A is found in *Diplatys flavicollis* (Diplatyidae). The egg tooth of this type is the

most complex, being a knob-like structure furnished with a median denticulated ridge and a pair of horn-shaped, stout projections (Fig. 14A, B). The egg teeth of B–D types are simple knob-like structures equipped with a single major process. Type B is found in *Cranopygia* sp. and *Echinosoma* sp. (Pygidicranidae), *Apachyus chartaceus* (Apachyidae), *Anisolabis maritima* and *Euborellia pallipes* (Anisolabididae), and *Labidura riparia* (Labiduridae). In this type, the egg tooth has a major process in its posterior region (posterior major process), of which the anterior facet has denticles or protuberances (Figs 15A, B, 16A, B, 33A, B, 34A, B, 35A, B, 36A, B). Type C is found in *Parapsalis infernalis* (Pygidicranidae). The egg tooth has denticulation along its median line and a major process in its posterior region, of which the anterior facet is smooth without either denticles or protuberances (Fig. 17). Type D is found in *Forficula scudderi* and *Anechura harmandi* (Forficulidae), *Paralabella curvicauda* (Spongiphoridae), and *Proreus simulans* and a Malaysian gen. sp. (Chelisochidae). The egg tooth has an anteriorly-pointed, major process in its central region (central major process) (Figs 37–41).

The phylogenetic mapping of these four types may be premature, but the following may be likely: 1) the structurally most complex type A, only found in Diplatyidae, represents its autapomorphy; 2) types B–D have a common feature in the simple knob-like structure equipped with a single major process; 3) among types B–D, type B is the most widely distributed in Dermaptera, both in Protodermaptera (Pygidicranidae) and Epidermaptera (Apachyidae, Anisolabididae, and Labiduridae) and may be the plesiomorphic type of egg tooth in Dermaptera; 4) type B is transformed into types C and D in *P. infernalis* of Pygidicranidae and in Eudermaptera, respectively, accompanied by the following: in type C, the denticles or protuberances in the anterior facet of the posterior major process in type B are lost and a denticulated median ridge is newly acquired and, in type D, the major process is anteriorly translocated and the denticles or protuberances as found in the anterior facet of posterior major process in type B are lost; 5) type D may be a shared apomorphy of Forficulidae, Spongiphoridae, and Chelisochidae (i.e., an autapomorphy of Eudermaptera).

Interestingly, a strong egg tooth is formed on the frons of Hemimeridae, whose egg lacks the chorion (Heymons 1912: fig. 18). It has a large, anteriorly-pointed process, similar to the egg tooth of Eudermaptera, which is a knob-like structure furnished with a large anteriorly inclined acute process (Figs 37–41). The resemblance of egg teeth between Eudermaptera and Hemimeridae may be backed with phylogeny. Heymons (1912) suggested that the embryo uses the egg tooth to irritate the mother's tissues, whereby her musculature is stimulated into peristaltic contractions that expel the offspring (cf. Hagan 1951). However, it may be more likely that the egg tooth in the Hemimeridae does not have any function but is simply a remnant of the egg tooth that their ancestors possessed as an egg burster.

4.3.6. Other embryological features

The eggs of apterygote and hemimetabolous insects tend to have a thin periplasm, whereas those of Holometabola have a thick periplasm (Anderson 1972a, b; Heming 2003). The tendency in periplasm thickness seems to parallel the differences in ovariole type. Most apterygote and hemimetabolous insects have panoistic ovarioles, whereas most Holometabola have meroistic ovarioles (Büning 1994). Among Polyneoptera, Dermaptera is known to have an exceptionally thick periplasm (Heymons 1895; Ando and Machida 1987), and it is worth noting that Dermaptera have polytrophic meroistic ovarioles (Yamaguchi and Yoshitake 1982) in contrast to other Polyneoptera having the panoistic ovarioles (Büning 1994). However, data on Dermaptera are very sparse and limited to a small part of Epidermaptera with regard to these characters.

In Dermaptera, the abdominal segmental appendages are not strongly developed, except the last pair on the 11th segment (herein; Heymons 1895; Fuse and Ando 1983). In the apterygote Ectognatha (Woodland 1957; Machida 1981) and most Pterygota (see Johannsen and Butt 1941; Schwalm 1988; Heming 2003), the appendages of the 1st abdominal segment develop into remarkable glandular embryonic organs called pleuropodia. Since pleuropodia are not known in other arthropods and entognathan hexapods (Jura 1972; Anderson 1972a, b, 1973), they may be an apomorphic groundplan feature of Ectognatha. Regarding Polyneoptera, pleuropodia develop in all orders other than Dermaptera: i.e., Zoraptera (Mashimo et al. 2014), Plecoptera (Kishimoto and Ando 1985), Orthoptera (Pétavy 1985), Grylloblattodea (Uchifune and Machida 2005), Mantophasmatodea (Machida et al. 2004), Phasmatodea (Louvet 1976), Embioptera (Ando and Haga 1974), Mantodea (Görg 1959), and Blattodea (Fujita and Machida 2017; Striebel 1960 for Isoptera). The present study confirmed the lack of pleuropodia in Dermaptera (Heymons 1895; Bhatnagar and Singh 1965; Fuse and Ando 1983) based on a broader taxon sampling. The lack of pleuropodia is likely an autapomorphy of Dermaptera.

Dermaptera develop appendages of the 11th abdominal segment into the cerci (herein; Heymons 1895; Bhatnagar and Singh 1965; Fuse and Ando 1983). The cerci form as multi-segmented appendages in the last abdominal segment in Diplura (10th abdominal segment: Ikeda and Machida 1998; Sekiya and Machida 2009) and Ectognatha (11th abdominal segment: Heymons 1897; Johannsen and Butt 1941; Machida 1981), but no appendicular structures develop in the last abdominal segment in Ellipura (= Protura + Collembola) (Jura 1972). The cerci may be thus a groundplan feature, possibly an autapomorphy, of Cercophora (= Diplura + Ectognatha) (cf. Klass 2009). The cerci are multi-segmented and filamentous in lower forms such as rhabduran Diplura and all Archaeognatha, Zygentoma, and Ephemeroptera (cf. Beutel et al. 2014). Hence, cerci with such traits can be regarded as a groundplan of Cercophora.

In Dermaptera, the cerci are modified and transformed into a pair of one-segmented claspers; this is one of the characteristic autapomorphic features of Dermaptera.

The present study confirmed a lack of subdivision into cercomeres and some clasper-shape throughout embryonic development in Pygidicranidae (Fig. 20) and all six families of Epidermaptera (Figs 32, 43–47), as previously reported for higher dermapterans (Heymons 1895; Bhatnagar and Singh 1965; Fuse and Ando 1983). However, in Diplatyidae, the cerci are divided into many cercomeres and become fairly long in the embryonic period (Figs 6–13). Such multi-segmented, prolonged cerci are maintained during the postembryonic period (Shimizu and Machida 2011b), as in early cercophoran lineages (e.g., Machida 1981; Tojo and Machida 1997; Masumoto and Machida 2006), and the transformation of the filamentous cerci into claspers occurs at the final molting to adult (Shimizu and Machida 2011b). This may be true of Karschiellidae, although their embryonic development has not been well clarified and only a final stage of postembryonic development is known (see Matsuda 1976). The multi-segmented, elongate cerci shown in the embryonic and postembryonic periods of Diplatyidae (and possibly Karschiellidae) may represent a plesiomorphic state, whereas the cerci that show a configuration of prospective one-segmented claspers from the beginning of embryonic development in Pygidicranidae and Epidermaptera represent the derived state. The cerci of Hemimeridae and Arixeniidae are thread-like, but non-segmented not only in the postembryonic period (Klass 2001; Haas and Klass 2003; see Popham 1985) but also in the embryonic period (Heymons 1912; Bilinski and Tworzydlo 2019; Bilinski et al. 2019). Their cerci may be comparable to the claspers of higher dermapterans.

Wipfler et al. (2020) concluded that Apachyidae represents the basalmost lineage of Dermaptera (Karschiellidae was not included in the analysis), and that Diplatyidae, which has multi-segmented, elongate cerci in the embryonic and larval periods, is nested in the Pygidicranidae. According to this, the transformation of cerci into the configuration of prospective one-segmented claspers from the beginning of their development is regarded as having occurred in parallel several times, at least in each of the Apachyidae, in some lineages of Pygidicranidae, and in Epidermaptera. Or, more parsimoniously, the presence of multi-segmented, elongate cerci in Diplatyidae is a character reversal.

4.3.7. Embryological groundplan of Dermaptera and its phylogenetic affiliation

We have discussed the embryological features of Dermaptera. In this section, we list its embryological groundplan features.

Egg. 1) The egg has a prolate-ellipsoidal shape, with a smooth surface. 2) The micropyles are circularly arranged, at the anterior pole of the egg, as usual in Polyneoptera. 3) The adhesive substance is applied to the egg surface in basal forms, i.e., Diplatyidae, most Pygidicranidae, and Apachyidae; this may be the groundplan for Dermaptera. The lack of the adhesive substance in pygidicranid

Parapsalis infernalis and in Epidermaptera (excluding Apachyidae) is an apomorphy, and an autapomorphy of the latter taxon.

Periplasm. 1) The periplasm is exceptionally thick compared to other Polyneoptera; this may be an autapomorphy of Dermaptera.

Formation of embryo. 1) The embryo is formed by the fusion of the paired regions with higher cellular density differentiated in the blastoderm, i.e., by the medial migration of lateral plates over the median plate. This type of embryo formation is an autapomorphy of Polyneoptera.

Germ type. 1) The germ type is semi-long; this is one of the common types in Polyneoptera.

Blastokinesis. 1) The embryonic primordium (newly formed embryo) is extensive, and its anterior and posterior ends are on the ventral and dorsal sides, respectively. 2) The embryo is first covered by the amnioserosal fold; then it elongates along the egg surface to its maximum length in the anatrepsis period. This type of superficial elongation of the embryo, which is ventrally covered by the amnioserosal fold from the early stage, is an autapomorphy of Polyneoptera. 3) The posterior end of the embryo reaches the area of or around the anterior pole of the egg, and as a result of anatrepsis, the anteroposterior axis of the embryo is reversed. 4) The embryo undergoes katatrepsis, and its anteroposterior axis is reversed again. 5) Blastokinesis involving reversions of the embryo's anteroposterior axis is common not only in Polyneoptera but also in Pterygota.

Positioning and length of the embryo. 1) The embryonic primordium (newly formed embryo), whose anterior and posterior ends are on the ventral and dorsal sides of the egg, respectively, is extensive, occupying 30%–65% of the egg's longitudinal circumference (IL). 2) The embryo substantially elongates on the egg's dorsal surface with its posterior end ahead, keeping its cephalic region at the egg's ventral side; finally, its posterior end reaches the area of or around the egg's anterior pole. Thus, the embryo occupies most of the egg's longitudinal circumference (ML 70%–98%). Both features 1) and 2) are notable groundplan features of Dermaptera.

Appendages. 1) There is no pleuropodium; its absence is an autapomorphy of Dermaptera. 2) The cerci are transformed into a pair of one-segmented claspers; this is an autapomorphy of Dermaptera. In the Diplatyidae of Protodermaptera, the multi-segmented cerci develop long in the embryonic period, are maintained in postembryonic periods, and transform into a pair of claspers at final molting to adult. This may also be true of Karschiellidae. The multi-segmented, elongate cerci in the embryonic and postembryonic periods may be plesiomorphic, but it is also probable that multi-segmented, elongate cerci as found in the diplatyid embryos and larvae are of a character reversal as mentioned in "4.3.6. Other embryological

features". The cerci showing a configuration of prospective one-segmented claspers from the beginning of embryonic development in Pygidicranidae and Epidermaptera are apomorphic.

Egg tooth. 1) The egg tooth is formed on the frons as a knob-like structure derived from the prelarval cuticle and is discarded during hatching. An egg tooth of this type is typical at least in the hemimetabolous Pterygota.

Phylogenetic position of Dermaptera. The monophyly of Polyneoptera under inclusion of Dermaptera is strongly supported by recent studies (cf. Misof et al. 2014; Wipfler et al. 2019). The present study confirmed this, as Dermaptera possesses two features related to embryonic formation and anatrepsis that we previously proposed to be autapomorphies of Polyneoptera (Mashimo et al. 2014).

The exact position of Dermaptera in Polyneoptera has been disputed, but phylogenomic studies suggest a close affinity to Zoraptera (Terry and Whiting 2005; Misof et al. 2014; Wipfler et al. 2019). Among the embryological features listed above, some are supposed to be autapomorphic to Dermaptera, like the thick periplasm, lack of pleuropodia, and clasper-like cerci. Other characteristics shared by Dermaptera and other polyneopteran orders are autapomorphies of Polyneoptera (see above), or symplesiomorphies for polyneopterans, such as the egg tooth of embryonic cuticular origin. Dermaptera share the circular arrangement of micropyles with Polyneoptera excluding Dictyoptera and ensiferan Orthoptera, the semi-long germ type with Zoraptera, some Orthoptera, some Blattodea, and Embioptera, and blastokinesis involving reversions of the embryo's longitudinal axis with Polyneoptera excluding Mantodea and blaberoid Blattodea. However, the sharing of these embryological features by Dermaptera and other polyneopteran orders are insufficient to deepen the discussion on the affinity of Dermaptera.

4.4. Postembryonic development

Matzke and Klass (2005) reviewed the number of larval instars of Dermaptera, referring to various sources and adding their observations on two species of Pygidicranidae. At that time, information on Karschiellidae, Diplatyidae, and Apachyidae was not available. Thereafter, we (Shimizu and Machida 2011b) studied in detail the postembryonic development of Diplatyidae using *Diplatys flavicollis*. Finally, in the present study, we succeeded in following the postembryonic development of *Apachyus chartaceus* of Apachyidae.

4.4.1. Number of larval instars in *Apachyus chartaceus*

We successfully followed the postembryonic development of two captive-bred individuals of *Apachyus chartaceus*, and at least five larval instars were recognized: the first three, i.e., the first to third larval instars (Fig.

Table 5. Number of larval instars in Dermaptera: as reviewed by Matzke and Klass (2005) (simplified), and based on our studies on Diplatyidae and Apachyidae (Shimizu and Machida 2011b, herein). See the text. ND – no data.

Family	Number of larval instars
Karschiellidae	ND
Diplatyidae	8–9
Pygidicranidae	6–7
Apachyidae	6
Anisolabididae	5
Labiduridae	5
Forficulidae	4
Spongiphoridae	4
Chelisochidae	4
Hemimeridae	4
Arixeniidae	4

42A–C), and last two, i.e., the penultimate and final larval instars (Fig. 42D, E).

The head width of adjacent instars (see "3.5. *Apachyus chartaceus* (Apachyidae)", "3.5.4. Postembryonic development") linearly increased in size among the first three larval instars and between the penultimate and final larval instars: the head width increased 1.29 times from the first to second instar, from the second to third instar 1.25 times, and from the penultimate to final instar 1.24 times. Accordingly, the head width increases approximately by 1.25 to 1.3 times with each molting. Regarding the penultimate and third larval instars, the head width of the former is 1.7 times larger than that of the latter. Note that the square root of 1.7 is approximately 1.3. This suggests that one more instar should exist between the third and the penultimate larval instars. Thus, *A. chartaceus* probably has six larval instars, placing a "fourth" one between the third and penultimate instars.

4.4.2. Number of larval instars in Dermaptera

Table 5 shows a simplified summary of Matzke and Klass' (2005) review on the number of dermapteran larval instars, with our data on Diplatyidae (Shimizu and Machida 2011b) and Apachyidae (herein) added. The intragroup or intraspecific variation in the number of larval instars has often been reported. The most remarkable case may be *Euborellia cincticollis*, for which Knabke and Grigarick (1971) reported a wide variation of five to eight larval instars. In Epidermaptera, however, Eudermaptera (= Chelisochidae + Forficulidae + Spongiphoridae) has four larval instars, and Anisolabididae and Labiduridae, which may be less derived families in Epidermaptera, generally have five larval instars. Epizoic Hemimeridae and Arixeniidae, whose subordinate positions in Eudermaptera may be currently certified (e.g., Jarvis et al. 2005; Kocarek et al. 2013; Naegle et al. 2016; Wipfler et al. 2020), are supposed to have four (or three for the former) larval instars (see Matzke and Klass 2005).

Herter (1964, 1965) reported five larval instars in some species of Forficulidae. As Matzke and Klass (2005) deduced, it is highly probable that Herter included the prelarva (= pronymph, prolarva), overcounting the number of instars. The prelarva is not a hatched larva but the definitive, full-grown embryo, covered by the embryonic cuticle with an egg tooth on its frontal region. Herter stated that his "first instar" had a very short duration. This is just a trait of prelarva. As we previously described (Shimizu and Machida 2011b, herein), the prelarva is ephemeral, and its cuticle is shed at hatching. Thus, one should be cautious not to include the prelarval stage when counting the larval instars, not only in Dermaptera but also in other hemimetabolous insects.

For Protodermaptera, Matzke and Klass (2005) first reported the number of larval instars in the Pygidicranidae as six or seven in two *Tagalina* species. Shimizu and Machida (2011b) examined the postembryonic development of Diplatyidae using *Diplatys flavicollis* and determined eight or nine larval instars. Thus, as Matzke and Klass (2005) suggested, the number of larval instars may be smaller in derived families and larger in basal ones: the number of larval instars is basically five or less in Epidermaptera, with four in Eudermaptera, whereas six to nine larval instars occur in Protodermaptera (Table 5). Apachyidae has been dealt with as a primitive member of Epidermaptera in terms of the reproductive system and wing and leg structures (Haas 1995; Haas and Kukalová-Peck 2001; Haas and Klass 2003; Haas and Gorb

2004), but Wipfler et al. (2020) revealed that Apachyidae represents the basalmost position in Dermaptera (Karschiellidae was not included in the analysis). The present study revealed that the number of larval instars of Apachyidae is six, which falls within the range of the instar number of Protodermaptera.

5. Conclusion

We investigated the embryonic development of all dermapteran families excluding Karschiellidae and the epizoic Hemimeridae and Arixeniidae, and discussed the phylogenetic issues concerning Dermaptera. We confirmed that Dermaptera possesses the embryological features (related to the mode of embryonic formation and manner of blastokinesis) that are regarded as autapomorphies of Polyneoptera, corroborating that Dermaptera is a member of Polyneoptera. However, we could not provide embryological evidence enlightening the relationships of Dermaptera to other polyneopteran orders. Embryological studies on Dermaptera, surveying various developmental aspects in detail covering more lineages, are warranted for a better basis allowing Polyneoptera-wide embryological comparisons.

The developmental and reproductive biological features among Dermaptera were compared and evaluated,
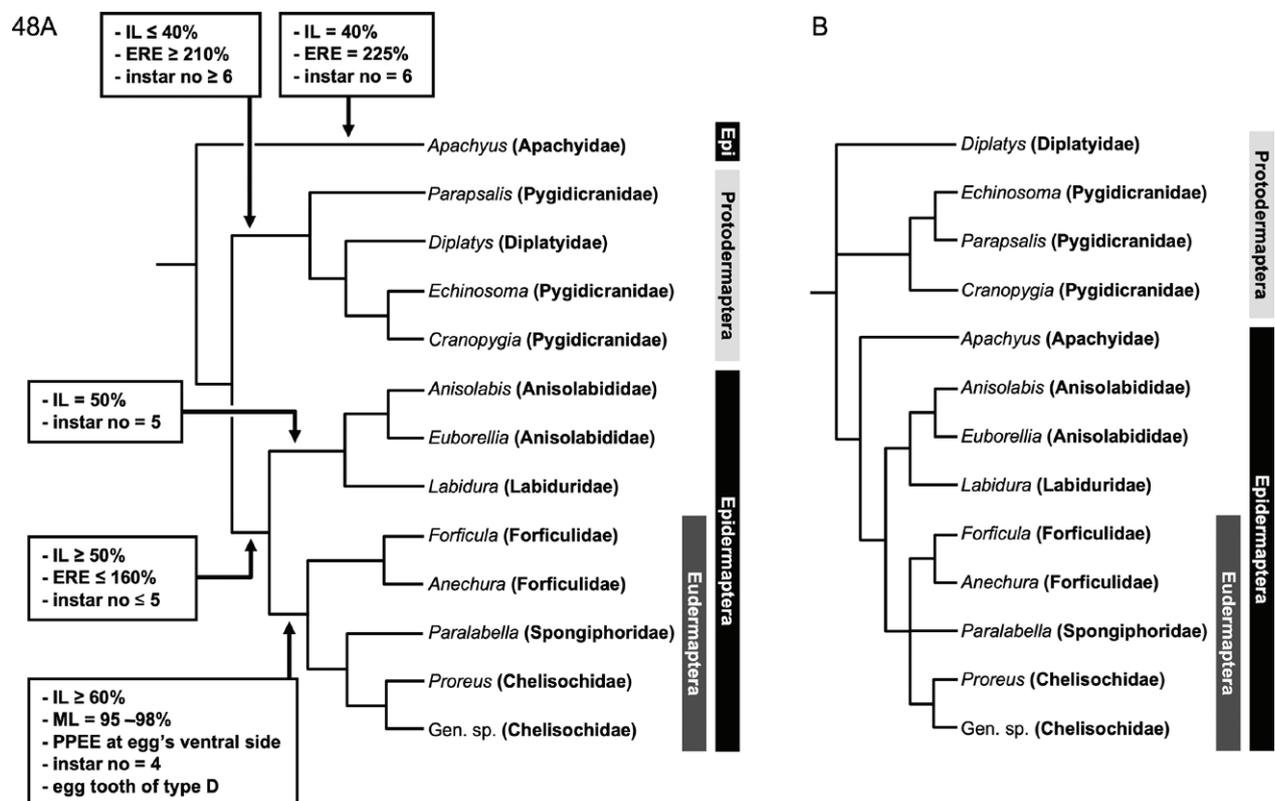
Figure 48. Dermapteran phylogeny inferred from the latest phylogenomic study by Wipfler et al. (2020) (**A**) and conventional tree (**B**), on which the dermapterans examined in the present study are given: *Paralabella* is placed in the position of *Labia* belonging to the same subfamily Labiinae. Significant features characterizing Eudermaptera, Protodermaptera, and others are shown in **A**. See the text.

referring to Wipfler et al. (2020). Figure 48A shows the proposed phylogenetic tree, on which the dermapterans examined in the present study are given: *Paralabella curvicauda* is placed in the position of *Labia minor*, which was analyzed by Wipfler et al., belonging to the same subfamily Labiinae. A conventional phylogenetic tree of Dermaptera, which is a modification of fig. 2 in Wipfler et al. (2020), is also shown for reference (Fig. 48B). The present study revealed that Eudermaptera is characterized by a large ML, a PPEE at the anterior ventral side of the egg (Table 3), an egg tooth of type D (Table 4), and four larval instars (Table 5) (Fig. 48A), and its monophyly is also supported from its embryological features. Anisolabididae, Labiduridae, and Eudermaptera share a low ERE (160% or less) (Table 3) and larval instars of five or less (Table 5), and Anisolabididae and Labiduridae have in common an IL of 50% and five larval instars (Fig. 48A). Protodermaptera is also well characterized by its embryological features: an ERE of 210% or more and an IL of 40% or less (Table 3), and larval instars of six or more (Table 5) (Fig. 48A). Notably, the ERE, IL, and number of larval instars in Apachyidae are categorized in the range of Protodermaptera (Fig. 48A). Although Apachyidae has often been affiliated with Epidermaptera (Fig. 48B), the latest phylogenomics study by Wipfler et al. (2020) places it at the basalmost position of Dermaptera (Karschiellidae was not included in the analysis) (Fig. 48A), and our present study may be consistent with the latter. Thus, the information on the developmental and reproductive studies from 13 species of eight families can be consistently understood in line with the latest phylogenomics of Dermaptera. However, as addressed above in "4.1. Egg deposition and brood care" and "4.3.6. Other embryological features", in the phylogeny of Dermaptera may be supposed the multiple acquisition of the elaborate maternal brood care, which is associated with lack of adhesive substance on the egg surface, and the multiple occurrence of transformation of cerci into the configuration of prospective one-segmented clasper from the beginning of their development. For better understanding of phylogenetic issues concerning the developmental and reproductive biology among Dermaptera, more basal representatives should be included, the highest priority being Karschiellidae, and Haplodiplatyinae of Diplatyidae and apparently heterogeneous Pygidicranidae as well. Regarding Eudermaptera, especially the families of which monophyly is dubious, e.g., Labiduridae and Spongiphoridae, should be critically examined, introducing more genera into analysis.

6.   Acknowledgments

7.   References

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