

Embryonic Development of Heel-walkers: Reference to Some Prerevolutionary Stages (Insecta: Mantophasmatodea)

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Abstract

The general features of eggs and some prerevolutionary stages of Mantophasmatodea were described, using *Karoophasma biedouwensis* and *Sclerophasma paresisensis* as materials. The eggs are deposited in the form of a hard pod, which contains 10 to 12 eggs. The egg is ellipsoidal, with a long diameter of 1.9–2.5 mm and short diameter of 1.0–1.2 mm. A ‘cap structure’ is distinguishable at the anterior egg pole. No structures relevant to micropyles could be discerned. The embryo is formed on the ventral side of the egg near the posterior pole. The embryo soon begins to invaginate into the yolk from its posterior end, and embryogenesis is of the short-germ-type. The invaginated embryo elongates, with its abdomen ahead, as the embryogenesis proceeds. The embryo takes its position at the egg surface, but in the final phase of diapause, it shifts deeper into the yolk. The blastokinesis (in prerevolutionary stages) of Mantophasmatodea resembles that of Grylloblattodea. The labrum is formed as a single swelling. The intercalary segment, although clearly defined, develops no appendicular structures. The first abdominal appendages develop into the pleuropodia. The 11th abdominal segment is clearly defined, and the cerci are formed as appendages of the segment. The corpora pedunculata are well developed. The embryo has precociously acquired the definitive body plan of a juvenile, in the diapause stage, and this precocity may be considered an embryological characteristic of Mantophasmatodea.

Introduction

Aiming at a comprehensive understanding of heel-walkers (gladiators) or a new insect order, Mantophasmatodea, described from the Afrotropics in May 2002 (Klass *et al.*, 2002), two international projects covering various disciplines have started (Adis *et al.*, 2002; Tojo and Machida, 2003; Machida and Tojo, 2003). Our team has set about an

embryological study, obtaining more than two hundred eggs of a South African *Karoophasma biedouwensis*, and several dozen eggs of a Namibian *Sclerophasma paretisensis* with the help of Dr. E. Marais [both species described in Klass *et al.* (2003)]. In this paper, we report the general features of these eggs and embryogenesis.

Although the eggs of *Karoophasma biedouwensis* usually develop normally in the laboratory in Cape Town, only one egg developed among those carried to the laboratory in Japan (Department of Systematic Zoology, Sugadaira Montane Research Center, University of Tsukuba) for detailed embryological analysis. Thus, information on the development of heel-walkers was obtained only from *Sclerophasma paretisensis* eggs, more than 50% of which were observed to develop. However, the eggs brought to Japan could not be developed beyond the diapause stage, never entering the katatrepsis stage: probably because some conditions needed for the release from dormancy could not be established. Thus, the description of mantophasmatodean embryogenesis herein concerns only the prerevolutionary stages. The general features of eggs are described, based on the eggs of *Karoophasma biedouwensis*: sand grains adhere too tightly to the eggs of *Sclerophasma paretisensis* to remove, and this makes the eggs utterly unsuitable for observations of structure; moreover, the opaque chorion of the species does not turn translucent on immersion in water, different from that of *Karoophasma biedouwensis*.

Materials and Methods

Karoophasma biedouwensis females were captured in September, 2002, in Namaqualand (Western Cape Province, South Africa), and deposited their eggs in the form of pods into sand in a laboratory in Cape Town. Several females of a Namibian heel-walker, *Sclerophasma paretisensis* from Paretisberg, Otjiwarango District, Namibia, were kindly provided by Dr. E. Marais, and successfully laid eggs in a laboratory in Pretoria. *Karoophasma biedouwensis* eggs were isolated from the egg pod, by soaking in water. The isolated eggs were cleaned with a small brush and observed with a light microscope and scanning electron microscope: SEM specimens were processed using standard methods, and observed under an SEM TOPCON SM-300. *Sclerophasma paretisensis* embryos were dissected out of the eggs, fixed with Karnovsky's fixative and postfixed in Bouin's fixative, according to Machida (2000). The fixed embryos stored in 70% ethyl alcohol were hydrated through a graded series, stained a couple of weeks in DAPI solution (4',6-diamidino-2-phenylindole dihydrochloride, diluted about 10 $\mu\text{g/l}$ with PBS), and observed under a Laica MZ FL III fluorescence stereomicroscope with UV excitation. Some embryos of *Sclerophasma paretisensis* were processed into 2 μm -thick methacrylate sections in accordance with Machida *et al.* (1994), and stained with haematoxylin, eosin and fast green FCF. *Sclerophasma paretisensis* eggs in which the serosal cuticle had been secreted could, although not easily, be manually dechorionated. Such eggs were fixed with Karnovsky's fixative in accordance with Machida *et al.* (1994), and stained in DAPI if necessary.

Results and Discussion

Eggs

Both *Karoophasma biedouwensis* and *Sclerophasma paretisensis* laid their eggs as pods (Tojo *et al.*, 2004). The pod, tightly formed with a cementing material and sand grains, is composed of 10 to 12 eggs (Fig. 1A). In *Karoophasma biedouwensis*, each egg is easily isolated from the pod by immersion in water, but it is almost impossible to isolate the eggs of *Sclerophasma paretisensis* from the pod due to its solidity. The egg shape and size of the two species are almost the same, ellipsoidal with 1.9–2.5 mm long and 1.0–1.2 mm short diameters (Fig. 1B). The chorion of *Karoophasma biedouwensis* is opaque when dried, but turns translucent in water. Tsutsumi *et al.* (2004) revealed that the chorion of *Karoophasma biedouwensis* eggs is composed of three layers, *i. e.*, the outermost, thinnest, surface layer (less than 1 μm in thickness), a thick exochorion (7–11 μm) and an endochorion (2–4 μm). Under the SEM, the surface layer of the chorion appears rough in structure, with a faint honeycomb pattern of hexagons *ca.* 10 μm in diameter in places (Fig. 1D, E). The exochorion is an outer thick, complex sublayer composed of numerous vertical columns, which sometimes fuse with each other (Fig. 1D, E). The endochorion is solid and uniform in structure (Fig. 1E). We could not detect any structures relevant to micropyles, even by SEM, on the outer and inner surfaces of the chorion. Near the anterior egg pole is found a circular line, which anteriorly demarcates a 'cap structure' (Fig. 1B, C). The observations mentioned above fundamentally coincide with those on *Mantophasma zephyra* eggs made by Klass *et al.* (2002) and Zompro *et al.* (2002).

Tsutsumi *et al.* (2004) showed that the circular line around the anterior egg pole in *Karoophasma biedouwensis* is

merely a thickening of the chorion and that the 'cap structure,' in which the two-layered organization of the chorion, *i. e.*, the exo- and endochorion, is obliterated, is structurally continuous with the chorion of the main body of the egg. Opercula for hatching have been reported in the eggs of many insect groups, for example for orthopteroid orders, in Phasmatodea (Leuzinger *et al.*, 1926; Hinton, 1981) and Embioptera (Kershaw, 1914), and for paraneopterans, in Hemiptera (Hinton, 1981). In these examples, the operculum is an elaborated and well-defined hatching lid. The 'cap structure' in *Karoophasma biedouwensis* eggs seemingly resembles these opercula, but the correlation may lack a sufficient basis, because the former is fairly simple and continuous in structure with the main body of the chorion (cf. Tsutsumi *et al.*, 2004).

In most of the *Karoophasma biedouwensis* eggs observed, yolk globules were localized to a specific area, while the rest of the egg was occupied by a structure-less, hyaline substance (Fig. 1B). However, how to understand the heterogeneous composition of the egg content shown in *Karoophasma biedouwensis*, requires circumspection, because such conditions have not been detected in *Sclerophasma paresisensis* eggs and even in an egg of *Karoophasma biedouwensis* or in a singular example that was found to develop normally.

Embryonic development

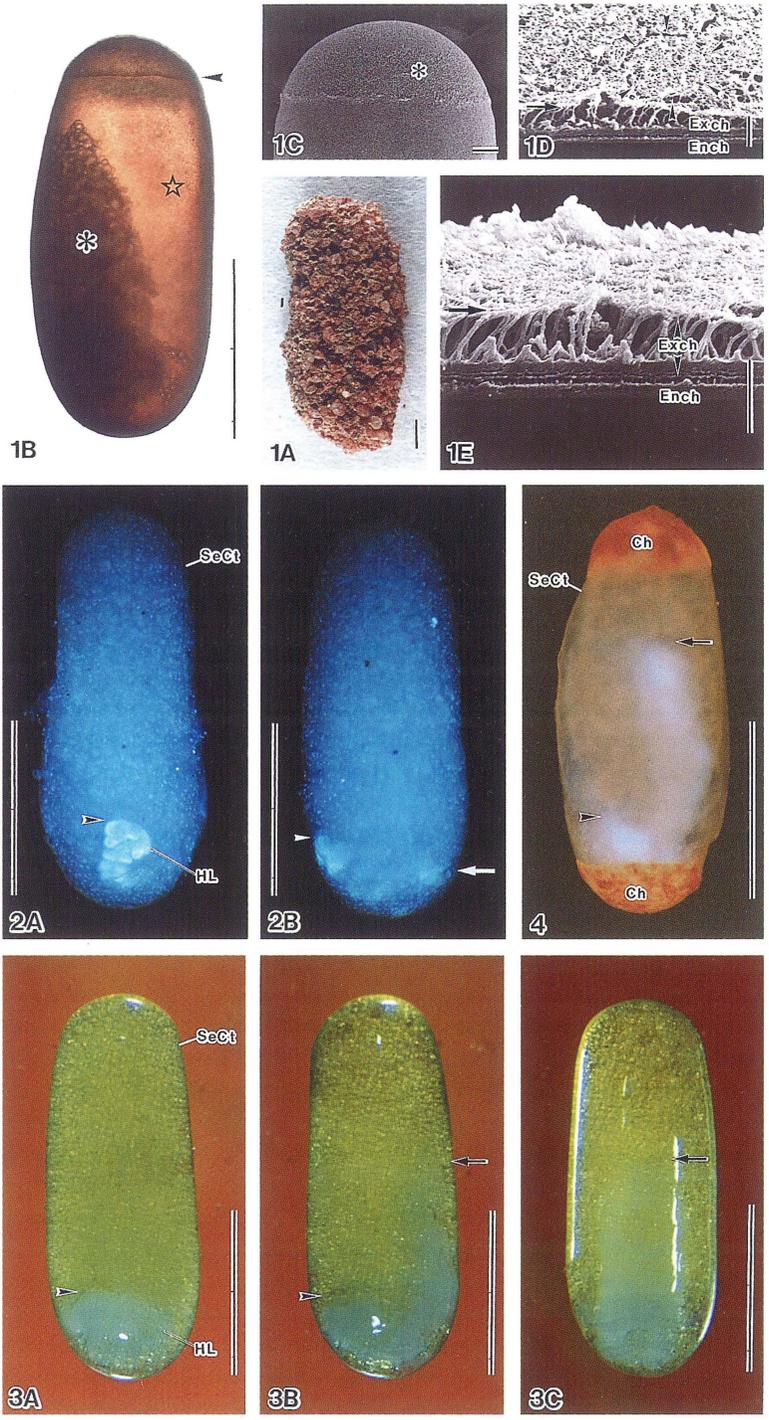
We observed several prerevolutionary stages in *Sclerophasma paresisensis*. The earliest stage concerns the early germ band, which assumes a broad pear shape of 500 μm in length (Fig. 5). The germ band had been dissected out of the egg, and so its original location within the egg is unknown. It is, however, highly likely that the germ band and the germ disc as its precursor would have been positioned in the area corresponding to the head lobe of the embryo in the next stage observed (Fig. 2), *i. e.*, on the ventral side of the egg, slightly anterior to the posterior pole (cf. Fig. 12).

The embryo in the second earliest developmental stage observed has been completely invaginated in the yolk, and is about 1 mm in extended length (Figs. 2, 6). Its head lobe is situated just anterior to the posterior pole on the ventral side of the egg, and its axis is approximately perpendicular to the axis of the egg, with its head lobe near the egg surface and the abdominal end almost reaching the side opposite to the head lobe (Fig. 2). The segmentation has proceeded up to the fourth abdominal segment (Fig. 6). The appendages of anterior segments up to the third thoracic are now differentiating. The stomodaeum has appeared. The clypeolabrum is formed, just in front of the stomodaeum, not as a paired structure but as a single swelling. The intercalary segment, which is clearly defined, never develops appendages. The area posterior to the fourth abdominal segment remains massive, yet to segmentarily differentiate.

Then, the appendages further elongate or newly differentiate in the anterior abdominal segments, and the caudal end enlarges (Fig. 7). In the embryo shown in Figure 7, the abdomen has differentiated into seven segments. In the differentiated segments, appendages soon start to emerge. The differentiated abdominal area is followed by a massive area more thickened, in which the proctodaeum is in development (Fig. 7B). The proctodaeum is formed as a simple invagination (Fig. 7A; cf. Fig. 8A), but not in the manner found in paleopterans, paraneopterans and some oligoneopterans, *i. e.*, by the fusion of the belt-like telson (cf. Tojo and Machida, 1997). In this respect, the manner of the proctodaeum formation in Mantophasmatodea may be regarded as typical of orthopteroid orders, since it is predominant in this group (cf. Johannsen and Butt, 1941; *e. g.*, Plecoptera: Kishimoto and Ando, 1985; Phasmatodea: Thomas, 1936; Orthoptera: Roonwal, 1937; Grylloblattodea: Uchifune and Machida, in preparation; Dermaptera: Heymons, 1895; Mantodea: Hagan, 1917).

In the following stage, the development of appendages and differentiation of segments proceeds further (Fig. 8). In the maxillary and labial appendages, the endites differentiate, which are respectively the future lacinia + galea and glossa + paraglossa, and the distal parts are the future palps (Fig. 8A). The abdomen has differentiated into nine segments (Fig. 8B). As the development proceeds, the embryo moves anteriorly, with its abdominal extremity ahead.

The embryo observed in the next stage is as shown in Figure 9. The embryo is much larger and approximately 1.3 mm in extended length. The head lobes have already started to curve up, leading to the formation of the head capsule: in the lateral parts of the developing head capsule, the presumptive compound eyes are observed (Fig. 9A, B). The articulation of appendages has much proceeded (Fig. 9A, B). The maxillary and labial endites respectively differentiate into the lacinia and galea and the glossa and paraglossa (Fig. 9A, B). As a result of segmentation, 11 segments are completed in the abdomen (Fig. 9A, B). The ventral flexure lies between the seventh and eighth abdominal segments (Fig. 9B). Abdominal appendages develop in all but the 10th segment. They do not develop further except in the first and the last, 11th segment. The appendages of the first abdominal segment project laterally and develop into



Figures 1-4

embryonic organs or pleuropodia (Fig. 9B), as observed in other orthopteroid embryos (cf. Schwalm, 1988; for Grylloblattodea: Ando and Nagashima, 1982). The 11th abdominal segment is clearly defined, and the cerci differentiate as the appendicular constituents of the segment (Fig. 9A, B). In the dorsal view, one can observe the elongated, developing stomodaeum, as well as the segmentarily-arranged coelomic sacs yet to collapse (Fig. 9C), except for the posterior abdomen in which the definitive dorsal closure has already proceeded to obstruct the view of the structures.

We have only partly observed the segmentation and elongation processes of the embryo. The mantophasmatodean embryo is, however, undoubtedly of the short-germ type (cf. Krause, 1939; Sander, 1984), as are the other orthopteroid embryos (cf. Johannsen and Butt, 1941; Anderson, 1972; Schwalm, 1988), except for Dermaptera, which undergo the long-germ-type embryogenesis (Heymons, 1895; Fuse and Ando, 1983).

The embryo in the next developmental stage was localized within the egg as shown in Figure 3, and about 1.4 mm in extended length. The cephalic region is near the posterior egg pole, and the embryo extends anteriorly along the dorsal side of the egg. An embryo dissected out of the egg is shown in Figure 10. The compound eyes are well developed (Fig. 10B). The development or articulation of each segmental appendage has much progressed: the thoracic appendages are furnished with a definitive number of or five tarsomeres, with a well-developed pretarsus at the tip (Fig. 10A, B): the pretarsus includes the precursors of a pair of claws and enlarged arolium, which is one of the most important characteristics of Mantophasmatodea (cf. Klass *et al.*, 2002; Tojo and Machida, 2003; Machida and Tojo, 2003). The ventral side of the mandibular to labial segments is swollen to form the hypopharynx (Fig. 10A). The most outstanding feature in the cephalic region may be the well developed paired structures, each of which is hemispherical, between the compound eyes of both sides (CP in Fig. 10B, C). The observation of sectioned materials reveals that they are organized by densely packed cells, from which thick bundles of nerve fibers run to the inside of protocerebral lobes (Fig. 10D). It may be asserted that these structures are the mushroom bodies or corpora pedunculata. Such a developed corpus pedunculatum may be singular in orthopteroid orders, and one could list this as an important characteristic of Mantophasmatodea.

The embryo has shifted its position deeper and fully sunk in the yolk (Fig. 4). The embryo continues to grow, with its extended length now about 1.7 mm, and it has fundamentally assumed a definitive body plan (Fig. 11). We could not follow the embryogenesis of mantophasmatodeans further, because the embryos entered a period of dormancy at this stage, which we failed to break: the embryos have yet to resume development, nearly 10 months since oviposition. It may be worth noting that the embryo, which is yet to experience katabolism or is still in the diapause stage, has much progressed in morphogenesis (*e. g.*, Fig. 11). This precocity of mantophasmatodean embryos may be one of the embryogenetical features of the group.

As mentioned above, in order to observe the insides of *Sclerophasma paresisensis* eggs, the chorion should be removed. Removing this layer without damaging the inside of the egg is, however, very difficult. Therefore, we could not prepare a set of specimens for precisely documenting the process of blastokinesis. Only the specimens shown in Figures 2 to 4 were successfully processed. Based on them, the blastokinesis of Mantophasmatodea, during the prerevolutionary stages, is reconstructed in Figure 12. First, a small germ disc is formed just anterior to the posterior egg pole on the ventral side of the egg (Fig. 12A). To start, the embryogenesis is of the short-germ-type, and with the

Fig. 1 Eggs of *Karoophasma biedouwensis*. A. An egg pod containing 12 eggs. B. An unfixed egg. Yolk globules are localized to a specific area (asterisk), the remaining part of the egg having a hyaline, structure-less substance (star). A circular line (arrowhead) demarcates a 'cap structure' at the anterior of the egg. C. SEM showing the 'cap structure.' D, E. SEM of a sectioned chorion: E is an enlargement, from a lower angle. The solid endochorion and thick exochorion with numerous vertical columns are distinguishable, and a faint honeycomb pattern (arrowheads in D) is visible on the outermost layer of the chorion (arrow). Ench: endochorion, Exch: exochorion. Scales = A, B: 1 mm; C: 100 μ m; D, E: 10 μ m.

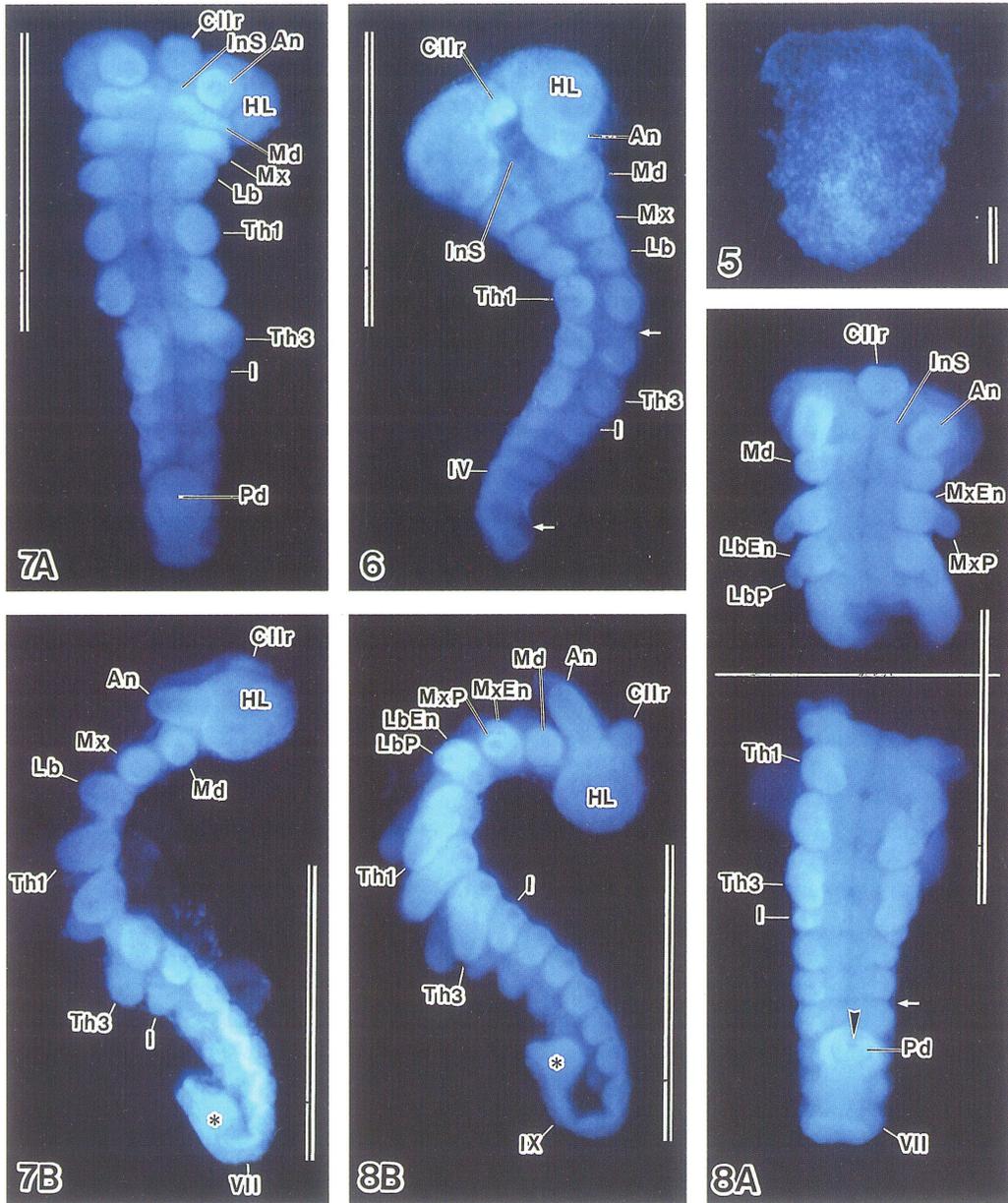
Figs. 2-4 *Sclerophasma paresisensis* eggs in different developmental stages, showing the localization of the embryo in the egg. Anterior egg pole to the top. The chorions were removed (the egg shown in Fig. 4 failed to be dechorionated in the anterior and posterior regions). Arrowheads and arrows respectively indicate the cephalic end and posterior limit of the embryo. See the text.

Fig. 2 Ventral (A) and lateral (B) views, DAPI staining.

Fig. 3 Ventral (A), lateral (B) and dorsal (C) views, an unfixed, unstained egg.

Fig. 4 Lateral view, DAPI staining.

Ch: chorion, HL: head lobe, SeCt: serosal cuticle. Scales = 1 mm.



Figs. 5–8 *Sclerophasma paretisensis* embryos in different developmental stages (I). DAPI staining. See the text.

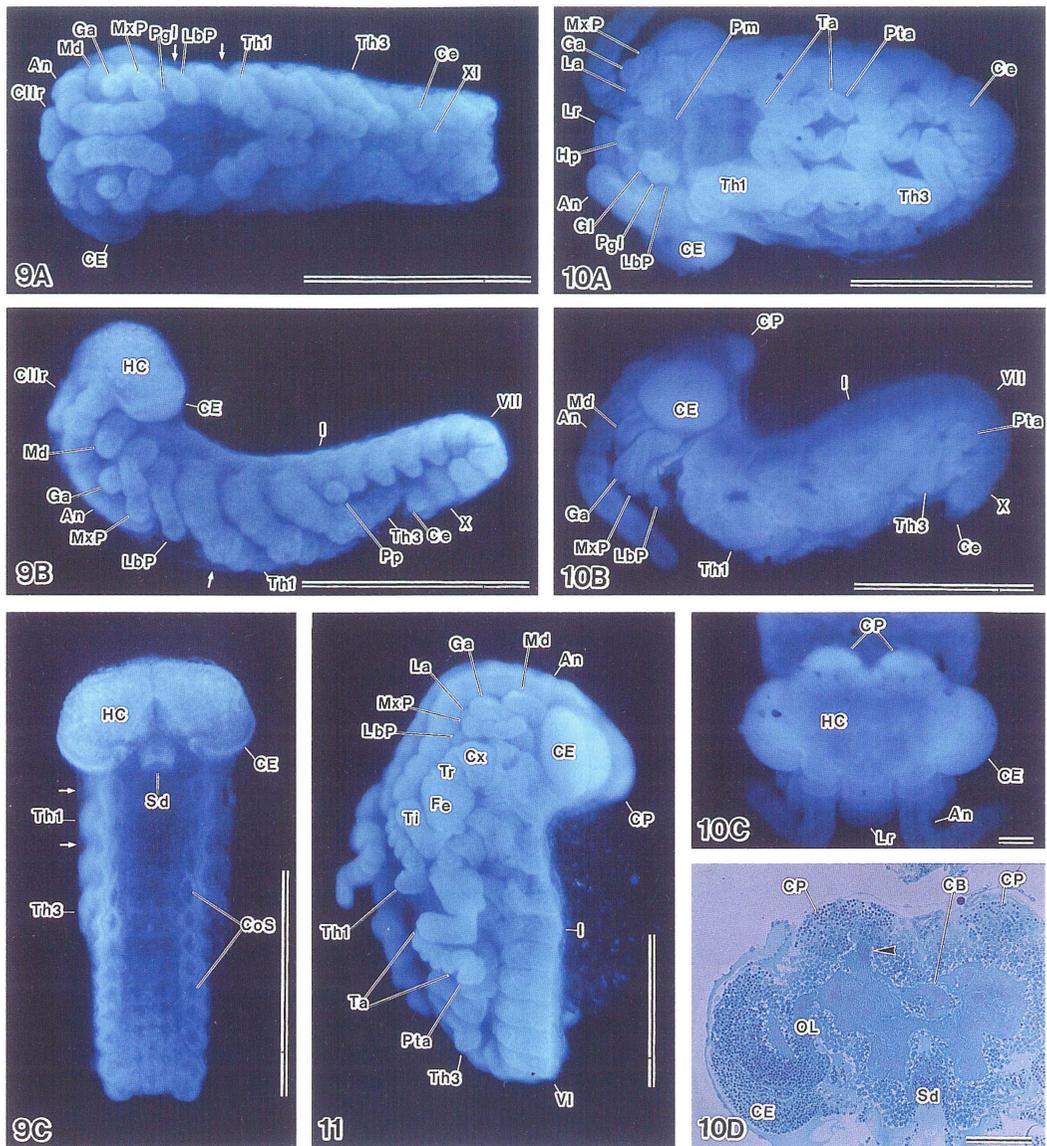
Fig. 5 Pear-shaped early germ band, ventral view. Anterior to the top.

Fig. 6 Embryo at approximately the same stage as in Fig. 2, ventral view. Arrows show the amnion.

Fig. 7 Ventral (A) and lateral (B) views. An asterisk shows the thickened area yet to segmentarily differentiate, in which the proctodaeal formation is in progress.

Fig. 8 A. Ventral view. The upper and lower halves of the figure are respectively the anterior and posterior parts of the same embryo. Arrowhead and arrow respectively show the proctodaeal invagination and amnion. B. Lateral view. An asterisk is the same as in Fig. 7B.

An: antenna, Cllr: clypeolabrum, HL: head lobe, InS: intercalary segment, Md: mandible, Mx: maxilla, MxEn: maxillary endite, MxP: maxillary palp, Lb: labium, LbEn: labial endite, LbP: labial palp, Pd: developing proctodaeum, Th1, 3: prothoracic and metathoracic legs, I–IX: first to ninth abdominal segments. Scales = 5: 100 μm ; 6–8: 500 μm .



Figs. 9–11 *Sclerophasma paretisensis* embryos in different developmental stages (ID). See the text.

Fig. 9 Ventral (A), lateral (B) and dorsal (C) views, DAPI staining. Arrows show the amnion.

Fig. 10 A. Ventral view, DAPI staining. B. Lateral view, DAPI staining. C. Dorsal view, DAPI staining. D. Horizontal section of the head through the compound eye. Arrowhead shows the fibrous stalk of the corpus pedunculatum.

Fig. 11 Lateral view, DAPI staining.

An: antenna, CB: central body, CE: compound eye, Ce: cercus, Cllr: clypeolabrum, CoS: coelomic sac, CP: corpus pedunculatum, Cx: coxa, Fe: femur, Ga: galea, Gl: glossa, HC: head capsule, Hp: hypopharynx, La: lacinia, LbP: labial palp, Lr: labrum, Md: mandible, MxP: maxillary palp, OL: optic lobe, Pgl: paraglossa, Pm: postmentum, Pp: pleuropodium, Pta: pretarsus, Sd: stomodaeum, Ta: tarsus, Th1, 3: prothoracic and metathoracic legs, Ti: tibia, Tr: trochanter, I–XI: first to 11th abdominal segments. Scales = 9, 10A, B, 11: 500 μ m; 10C, D: 100 μ m.

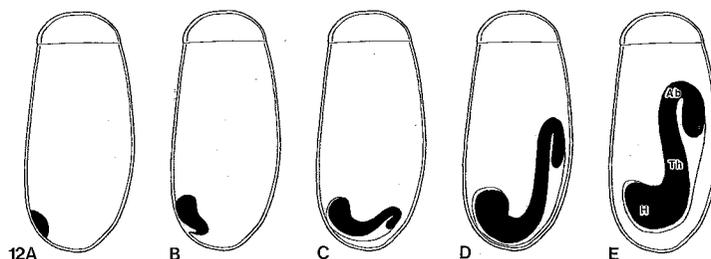


Fig. 12 Blastokinesis and localization of the embryo during the prerevolutionary stage in Mantophasmatodea. See the text. Ab: abdominal region, H: cephalic region, Th: thoracic region.

elongation of the embryo, the posterior end begins to invaginate (anatrepsis stage) (Fig. 12B). When the invagination or anatrepsis is complete, the embryo is positioned along the surface of the egg at the posterior pole, with its axis approximately perpendicular to that of the egg (diapause stage from this point onward) (Fig. 12C). The embryo further elongates and moves anteriorly along the dorsal side of the egg, with its abdominal region ahead and with its axis being reversed to that of the egg (Fig. 12D). Finally, the embryo shifts and settles deeper into the yolk (Fig. 12E). After continuing to develop for a time in this condition, the embryo enters a period of dormancy.

The blastokinesis during the prerevolutionary stage in Mantophasmatodea is characterized by: i) the small germ disc forms near the posterior pole of egg, ii) it grows and elongates with its abdominal region ahead, along the dorsal side of egg, resulting in the reversed orientation of embryo to the egg's anteroposterior axis, and then, iii) the elongated embryo is fully immersed into the yolk. In this respect, the blastokinesis during prerevolutionary stage of Mantophasmatodea resembles that of Grylloblattodea (Ando and Nagashima, 1982; Uchifune and Machida, in preparation). On the other hand, Mantophasmatodea are like neither Mantodea nor Phasmatodea. In both of them, the embryo does not sink into the yolk, and the orientation of embryo is not (Mantodea: Hagan, 1917) or not so substantially (Phasmatodea: Leuzinger *et al.*, 1926; Anderson, 1972) changed during the prerevolutionary stage.

Conclusions

In this paper, we reported the general features of eggs and some prerevolutionary stages in Mantophasmatodea, using *Karoophasma biedouwensis* and *Sclerophasma paresisensis* as materials. Our observation, however, could provide only references of low resolution to phylogenetical issues, only to suggest a resemblance of Mantophasmatodea with Grylloblattodea.

By improving techniques of incubation and obtaining many more samples, we intend to elucidate the whole developmental process of the group in detail, to provide a basis for comparative embryological and phylogenetical discussion concerning Mantophasmatodea, this leading to testing the problematic status of 'Polyneoptera.'

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