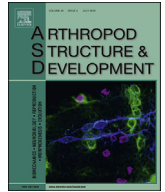




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## Egg structure and outline of embryonic development of the basal mantodean, *Metallyticus splendidus* Westwood, 1835 (Insecta, Mantodea, Metallyticidae)

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## ABSTRACT

The egg structure and outline of the embryonic development of *Metallyticus splendidus* of one of the basal Mantodea representatives, Metallyticidae, were described in the present study. The results obtained were compared with those from the previous studies, to reconstruct and discuss the groundplan of Mantodea and Dictyoptera. In *M. splendidus*, the egg is spheroidal, it has a convex ventral side at the center in which numerous micropyles are grouped, and it possesses a conspicuous hatching line in its anterior half. These are the groundplan features of mantodean eggs and the “grouped micropyles in the ventral side of the egg” are regarded as an apomorphic groundplan feature of Dictyoptera. A small circular embryo is formed by a simple concentration of blastoderm cells, which then undergoes embryogenesis of the typical short germ band type. Blastokinesis is of the “non-reversion type” and the embryo keeps its original superficial position and original orientation throughout embryonic development. During the middle stages of development, the embryo undergoes rotation around the egg’s anteroposterior axis. These features are a part of the groundplan of Mantodea. It is uncertain whether sharing of the “non-reversion type” of blastokinesis by Mantodea and blaberoidean Blattodea can be regarded as homology or homoplasy.

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## 1. Introduction

Insects are the most speciose group of animals, accounting for 75% of known animal species. Although their evolution has attracted much attention, studies reconstructing their phylogeny have left several questions unanswered (Trautwein et al., 2012; Kjer et al., 2016). For example, although the phylogeny of Polyneoptera, which comprises 10 lower neopteran orders: Plecoptera, Dermaptera, Embioptera, Phasmatodea, Orthoptera, Zoraptera, Grylloblattodea, Mantophasmatodea, Mantodea, and Blattodea (= “Blattaria” + Isoptera), has been studied in much detail, a

consensus is yet to be reached. Although the status of Polyneoptera has been long argued, recent studies pertaining to comparative morphology, embryology, and molecular phylogenetics strongly suggest that it is most likely monophyletic (e.g., Yoshizawa, 2007, 2011; Ishiwata et al., 2011; Mashimo et al., 2014; Misof et al., 2014), whereas there is no consensus among researchers on the phylogenetic relationships between polyneopteran constituents (Kristensen, 1981, 1991; Grimaldi and Engel, 2005; Terry and Whiting, 2005; Klass, 2009; Beutel et al., 2014). However, the assemblage of Mantodea and Blattodea, i.e., Dictyoptera, has been widely accepted as monophyletic on the basis of various morphological (e.g., Kristensen, 1975, 1981, 1991; Klass, 2003; Beutel and Gorb, 2006; Klass and Meier, 2006; Beutel et al., 2014) and molecular phylogenetic studies (e.g., Maekawa et al., 1999; Wheeler et al., 2001; Kjer, 2004; Terry and Whiting, 2005; Kjer et al., 2006).

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In resolving the phylogenetic issues concerning Polyneoptera, it is important to reconstruct the groundplan of Dictyoptera comprising Mantodea and Blattodea, as well as each polyneopteran order. Comparative embryology is a promising method for reconstructing the groundplan of a group and discussing its phylogenetic pattern. Recently, reviewing the embryological information covering major blattodean lineages, Fujita and Machida (2017) found that blattodeans undergo two different types of blastokinesis: the “reversion type,” i.e., blastokinesis with the reversion of the embryo’s anteroposterior and dorsoventral axes, as found in Blattodea and Isoptera, and the “non-reversion type,” i.e., blastokinesis with the embryo’s axes unchanged, as found in Blaberoidea. Several studies have discussed the embryonic development of the derived family Mantidae of the order Mantodea. These include *Mantis religiosa* (Graber, 1890; Viallanes, 1890, 1891; Giardina, 1897; Cockerell, 1898), *Tenodera* (=Paratenodera) *sinensis* (Hagan, 1917), and *Hierodula crassa* (Görg, 1959). On the basis of these studies, Fujita and Machida (2017) categorized the blastokinesis of Mantodea as the non-reversion type; however, further detailed information on mantodean embryogenesis covering major lineages is required to better understand the groundplan of Mantodea.

Egg structures provide useful information for the reconstruction of insect phylogeny, and the micropyle is one of the significant egg structural features (cf. Hinton, 1981; Mazzini, 1987; Mazzini et al., 1993; Mashimo et al., 2016). Fujita and Machida (2017) suggested that micropyles grouped on the ventral side of the egg to be a groundplan of Blattodea. The micropyles of Mantodea have been reported for a few species of Mantidae (Hagan, 1917; Görg, 1959; Iwaikawa and Ogi, 1982), wherein several micropyles and/or a single large one occur at the anterior pole of the egg. If these descriptions of mantodean micropyles have been correct, Dictyoptera would possess two disparate distribution patterns of micropyles, i.e., both the blattodean and mantodean types.

The inadequate knowledge of the embryology of Mantodea, which is restricted only to a higher group of Mantidae, has been challenging in reconstructing the embryological groundplan of Dictyoptera, and more embryological information is needed on the major mantodean lineages, especially the “basal Mantodea,” i.e., Mantoididae, Chaeteessidae, and Metallyticidae. With this background, we commenced an embryological study of *Metallyticus splendidus* Westwood, 1835, of Metallyticidae. In the present study, we examined its egg structure, outlined its embryonic development, and compared the obtained information with the previous studies on other dictyopterans and polyneopterans, with the aim of discussing the groundplan of Mantodea and Dictyoptera.

## 2. Material and methods

Six females and four males of *M. splendidus* were collected in Rawang, Selangor, Peninsular Malaysia in April 2011. The collected specimens were reared in a laboratory and fed small insects (Fig. 1A, B). We obtained 13 oothecae deposited by females, each of which contained 20–30 eggs. For observing egg structure, the eggs from the newly deposited oothecae were cleaned in 0.1 M phosphate buffered solution (pH 7.2), transferred to Karnovsky’s fixative (2% paraformaldehyde + 2.5% glutaraldehyde in 0.1 M HCl-sodium cacodylate buffer, pH 7.2), perforated with a fine needle to facilitate the penetration of the fixative and fixed overnight. Fixed eggs were rinsed with 0.1 M HCl-sodium cacodylate buffer and observed under an S8 APO Leica stereomicroscope (Heerbrugg, Switzerland). For more detailed observation of their structure, the eggs were postfixed with 1% OsO<sub>4</sub>, dehydrated in a graded ethanol series, dried using a tousimis Samdri-PVT-3D CO<sub>2</sub> critical-point dryer (Rockville, USA), coated with gold in a JEOL JFC-1100 ion sputter (Tokyo, Japan), and observed under a TOPCON SM-300 scanning

electron microscope (Tokyo, Japan) at an accelerating voltage of 15 kV. Some of the eggs were postfixed with 1% OsO<sub>4</sub> solution, dehydrated in a graded ethanol series, and embedded in an Agar LV epoxy resin (Essex, UK). Semi-thin or ultra-thin sectioning was performed at a thickness of 0.5 μm and 75 nm, respectively, using an RMC MT-XL ultra-thin microtome (Arizona, USA) equipped with a histo-diamond knife. Semi-thin sections were stained using 1% toluidine-pyronine solution or 1% toluidine solution, and observed under an Olympus BH2 biological microscope (Tokyo, Japan). Non-stained ultra-thin sections were observed under a Hitachi HT7700 transmission electron microscope (Tokyo, Japan).

To observe the external features of embryonic development, the exochorion was carefully removed from the eggs and fixed with Karnovsky’s fixative. Fixed materials were stained with DAPI (4’,6-diamidino-2-phenylindole dihydrochloride diluted to about 0.5 μg/ml using distilled water) and observed under a Carl Zeiss SteREO Lumar.V12 fluorescence stereomicroscope (Oberkochen, Germany) or a Leica M165 FC fluorescence stereomicroscope (Heerbrugg, Switzerland) under UV excitation at 360 nm.

## 3. Results

### 3.1. Egg structure

The orientation of insect eggs is defined relative to the embryo position just before hatching (Wheeler, 1893). However, in *M. splendidus*, as in other mantodeans (e.g., Hagan, 1917), the embryos undergo a 180° rotation around the anteroposterior axis of the egg during development. Therefore, we define the ventral side of the egg as the side on which the embryo develops, and the side opposite to it is the dorsal side.

Eggs of *M. splendidus* are yellowish white (Fig. 1C, D) and spheroidal (about 3.2-mm long and 1-mm thick), with a pointed anterior pole, a little convex ventral side, and a straight or slightly concave dorsal side (Figs. 1C and 2A).

A coronal line assumes a long, inverted U-shape at the anterior half of the ventral side of the egg (Fig. 2A, B, E, F). The prolarvae hatch by opening the eggshell along this line, and this may be called the “hatching line.” The hatching line is a deep cleft, as shown in the sagittal section (black arrow in Fig. 3E), and easy to tear. Numerous aeropyles of about 0.5 μm in diameter are seen as deep, branching canals in section (white arrows in Fig. 3E) and are scattered at the anterior pole of the egg and along the hatching line (white arrowheads in Fig. 2E, G). About 80 funnel-shaped micropyles are located in the central area of the ventral side of the egg (Fig. 2A, B, D, black arrowheads in Fig. 2C). Fig. 3D is a sagittal section through a micropyle. The micropylar canal (white arrowhead) penetrates the exo- and endochorion, running obliquely toward the posterior.

The eggshell comprises three distinct layers: an approximately 15-μm thick exochorion with columnar structures at its bottom, a 2-μm thick endochorion, and an extremely thin vitelline membrane (Fig. 3A, B, D). The endochorion is composed of a thin outer layer (layer I) that has a high electron density and an inner layer (layer II) with numerous, short, columnar structures (Fig. 3B). The layer I shows an appearance of piled laminae (Fig. 3C).

### 3.2. Embryonic development

A blastoderm region with a high cellular density appears at the egg’s ventral side, slightly biased toward the posterior (Figs. 4A, 5A, and 6A). This represents the newly differentiated embryonic area, where the blastoderm cells of the embryonic area simply concentrate further to form a circular, small germ disc or embryo approximately 400 μm in diameter. The extraembryonic area is now called the “serosa” (Figs. 4B, 5B, 6B, and 7A). The embryo

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