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Morphogenetic functions of extraembryonic membranes in insects

Urs Schmidt-Ott and Chun Wai Kwan

Morphogenetic functions of the amnioserosa, the serosa, the amnion, and the yolk sac are reviewed on the basis of recent studies in flies (Drosophila, Megaselia), beetles (Tribolium), and hemipteran bugs (Oncopeltus). Three hypotheses are presented. First, it is suggested that the amnioserosa of Drosophila and the dorsal amnion of other fly species function in a similar manner. Second, it is proposed that in many species with an amniotic cavity, the amnion determines the site of serosa rupture, which, through interactions between the serosa and the amnion, enables the embryo to break free from the amniotic cavity and to close its backside. Finally, it is concluded that the yolk sac is likely an important player in insect morphogenesis.

Address
University of Chicago, Dept. of Organismal Biology and Anatomy, Cummings Life Science Center, 920 East 58th Street, Chicago, IL 60637, USA

Corresponding author: Schmidt-Ott, Urs (uschmid@uchicago.edu)

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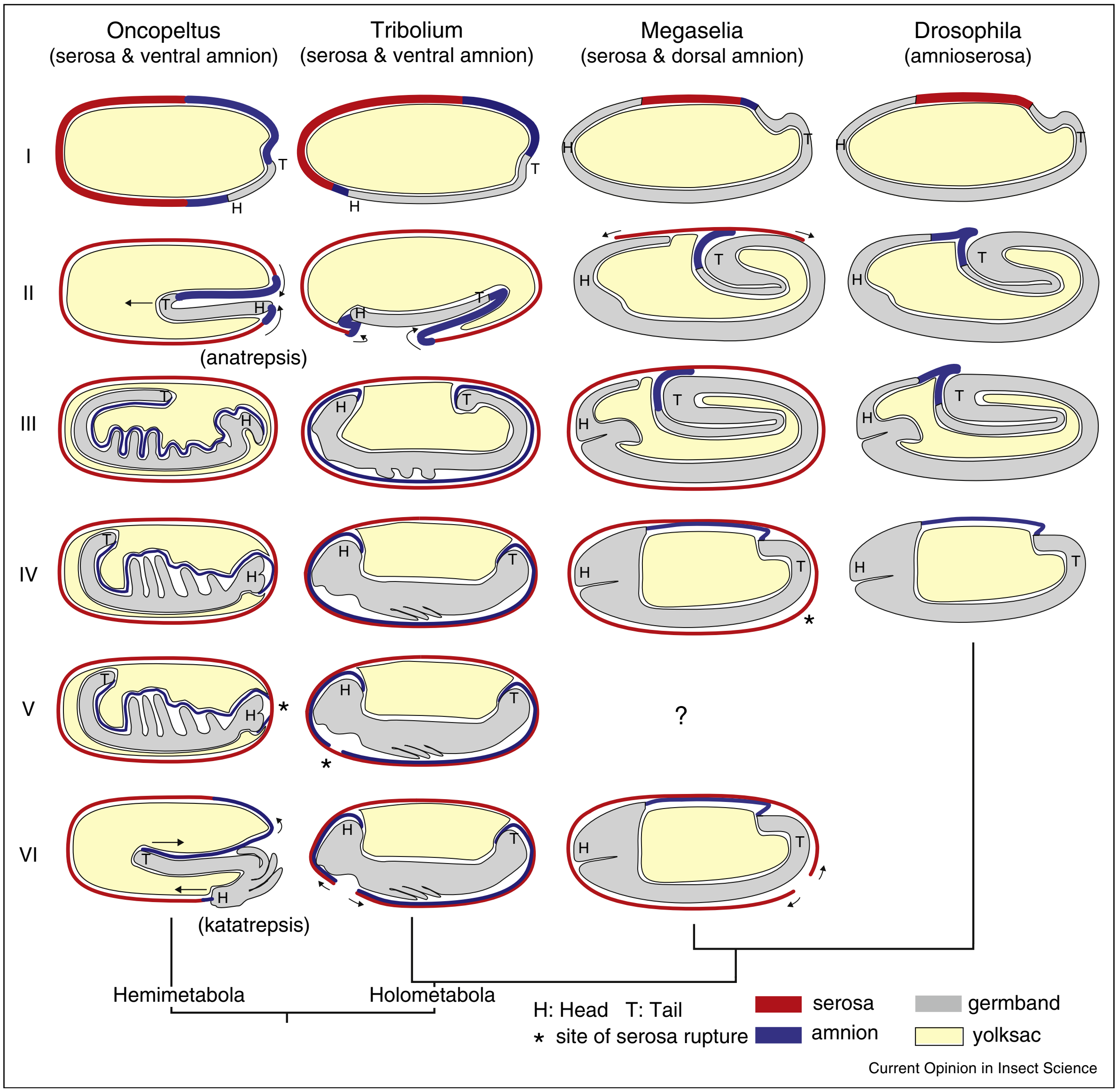
Introduction

The full complement of extraembryonic membranes in insects includes the serosa, the amnion, and the yolk sac (reviewed in [1–4]). They play important roles in embryo immunity, desiccation resistance, and morphogenesis, and may fulfill additional physiological roles (reviewed in [5–7]). This comparative review focuses on the functions of extraembryonic membranes in morphogenesis. Insect embryos undergo intertwined morphogenetic and blastokinetic functions. The former refer to cell and tissue movements within the embryo, whereas the latter refer to movements of the whole embryo within the egg but for the purpose of this review we will refer to them collectively as morphogenetic movements. Most research on the role of extraembryonic membranes in insect morphogensis has been done with the genetic model organism *Drosophila melanogaster* because of its exceptional amenability to functional analysis, and this work has been reviewed extensively in the context of dorsal closure (for a concise summary of that literature, see [8•]). However, in this species, the extraembryonic membranes are partly reduced, and it is not well understood how findings in Drosophila can be applied to insects with the full complement of extraembryonic membranes. In this brief 'opinion paper', we compare the morphologies and discuss specific functions of the diverse extraembryonic membranes in insects, drawing mostly from recent studies in flies (Drosophila, Megaselia), beetles (Tribolium), and bugs (Oncopeltus).

Diversity of extraembryonic membranes in insects

The extraembryonic membranes of insects differ morphologically between species (Figure 1) (reviewed in [1–5,9,10]). Nearly all insects develop a serosa after germ band formation. This epithelium lines the inner side of the eggshell and originates from the blastoderm cells that do not contribute to the germ rudiment (prospective embryo and amnion). The amnion develops from the rim of the germ rudiment but its topography varies between species. In most insects, it closes over the ventral side of the germ band and forms an 'amniotic cavity', a term that refers to the closed space between the amnion and germband. In butterflies and some beetles (e.g. Chrysomelidae and Curculionidae), the amnion closes ventrally, like in most species, but then also dorsally, forming an outer circumferential amnion and an inner dorsal amnion that covers the yolk sac [2]. In wasps [11] and lower cyclorrhaphan flies such as phorids and syrphids [12], the amnion only grows dorsally over the yolk sac, forming a dorsal amnion. Higher cyclorrhaphan flies (Schizophora), such as Drosophila develop an 'amnioserosa' instead of distinct serosa and amnion epithelia. The final topography of this tissue is comparable to the dorsal amnion in phorids and syrphids but the modes of dorsal amnion and amnioserosa formation differ. While the dorsal amnion of phorids and syrphids grows from the rim of the germ rudiment over the dorsal yolk sac and is completed after germ band elongation, the amnioserosa of Drosophila develops from blastoderm cells that form a narrow stripe along the dorsal midline and covers the yolk sac at all stages until dorsal closure occurs. The yolk sac of Drosophila is a membrane-lined multinucleate yolk cell that forms underneath the blastoderm. In other species, yolk nuclei underneath the yolk cell membrane cellularize and form a yolk cell lamella (primary entoderm), or the yolk cell cleaves into large

Figure 1



Sketches of embryos and extraembryonic membranes of four insect species (based on data reported in [12,27,48,50,51,52•,56,68]). Consecutive developmental stages are depicted from top to bottom. Oncopeltus embryos are shown at the beginning of gastrulation (I), during anatrepsis (II), after serosa and amnion completion (III), after serosa-amnion adhesion (IV), after hole formation in the amnion (V), and after serosa rupture (VI). Developmental stages of other species are roughly matched. The serosa is shown in red, the amnion in blue, the embryo in gray, and the yolk sac in yellow. The eggshell is omitted. In Drosophila, amnioserosa cells are depicted in red or blue depending on whether *zen* is expressed (red) or repressed (blue). We propose that after the repression of *zen*, amnioserosa cells are comparable to amnion cells (see main text). Arrows indicate directed movement of extraembryonic epithelia. Anterior of the egg is left and dorsal up. H, head end. T, tail end.

membrane-lined mono-nucleate or multi-nucleate yolk cells.

Functions of the serosa

The serosa can mount a strong innate immune response to counter bacterial infection [13,14,15••] and secretes a cuticle underneath the eggshell that increases resistance to desiccation [16–23]. In many species, the serosa also controls dorsal closure by promoting the rupture of the amniotic cavity and pulling the amnion to the dorsal side [10]. Many non-holometabolous insects undergo longitudinal axis inversion and, in these species, the serosa also plays an important role in realigning the axes of the embryo with those of the egg (see Box 1) [5]. There is consensus among early and current investigators that, as the serosa ruptures and recedes to the anterior or dorsal