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'Paraneoptera': A Comparison of Ovarian Structures*

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Insect ovaries are usually composed of two clusters of egg tubes termed ovarioles. Traditionally, two basic categories of insect ovarioles are recognized, meroistic and panoistic. In meroistic ovarioles, incomplete cytokinesis of gonial cells leads to the cluster formation of germ cells connected with each other by intercellular cytoplasmic bridges. One or several cells in each germ cell cluster develop into oocytes, while the others differentiate into trophocytes. Relationships between the oocytes and trophocytes allow the subdivision of meroistic ovarioles into two types: polytrophic and telotrophic. In polytrophic ovarioles, each oocyte is accompanied by its sibling trophocytes (nurse cells) and an egg chamber (oocyte–nurse cell complex) is formed. In telotrophic ovarioles, all trophocytes are retained in the germarium, thereby forming a tropharium. Elongated intercellular bridges referred to as nutritive cords ensure the supply of nutrients from the tropharium to the growing oocytes, which migrate to the vitellarium. In panoistic ovarioles, all oogonia develop into oocytes. However, detailed ultrastructural investigations revealed that germ cells, interconnected by intercellular bridges, form a cluster in the thysanopteran panoistic ovarioles (Pritsch and Büning, 1989; Tsutsumi *et al*., 1995). This ovariole type is regarded as a derivative of the meroistic one with a secondary loss of nurse cell differentiation; the term "secondary panoistic" or "neopanoistic" has been proposed (Pritsch and Büning, 1989; Štys and Biliński, 1990; Büning, 1994).

These insect ovariole types correspond to insect taxa at the ordinal, subordinal or family levels (King and Büning, 1985; Štys and Biliński, 1990; Büning, 1994, 1998). Analysis of the distribution of ovariole types in various insect taxa leads to the following anagenetical hypothesis. Panoistic ovarioles without the germ cell cluster are regarded as the most basic type, and polytrophic meroistic ovarioles are derived from panoistic ovarioles. Telotrophic meroistic ovarioles and neopanoistic ones originate independently from polytrophic meroistic ovarioles, respectively (Štys and Biliński, 1990).

Taxonomically, the 'Paraneoptera' is composed of four neopteran orders: Zoraptera, Psocodea ('Psocoptera' + 'Mallophaga' + Anoplura), Thysanoptera (Terebrantia + Tubulifera) and Hemiptera (Heteroptera + Coleorrhyncha + Auchenorrhyncha + Sternorrhyncha) (Kristensen, 1975, 1981; Hennig, 1981). The 'Paraneoptera' has all insect ovariole types, *i. e*., panoistic in Zoraptera, polytrophic meroistic in Psocodea, neopanoistic in Thysanoptera and telotrophic meroistic in Hemiptera. Below, I outline the ultrastructural features of ovarioles in the 'paraneopteran' orders, except for Zoraptera.

We have very incomplete information on the ovarian structures and oogenesis of Zoraptera. The ovarioles of Zoraptera are normally four to six in number per ovary and contain only oocytes in various stages of development (Gurney, 1938; Matsuda, 1976). Their ovariole type is said to be panoistic but the ultrastructural features of their ovarioles remain unknown. Recently, it was suggested that Zoraptera has phylogenetic affinity with some polyneopteran orders, *e. g*., Embioptera, Dictyoptera or Dermaptera (Yoshizawa and Johnson, 2005; Yoshizawa, 2007). 'Paraneoptera' without Zoraptera is referred to Acercaria and all the orders of Acercaria have the ovarioles secondarily derived from panoistic ovarioles.

Psocodea is composed of three traditional groups, *i. e*., 'Psocoptera,' 'Mallophaga' and Anoplura. All of these traditional groups have polytrophic meroistic ovarioles (Gross, 1906; Ries and van Weel, 1934; Biliński and Jankowska, 1987; Büning and Shost, 1990; Büning, 1994). The ovarian structure and oogenesis of three traditional groups are extremely similar to each other, except for the number of nurse cells in each germ cell cluster, three in 'Psocoptera,' seven in 'Mallophaga' and five in Anoplura. Five nurse cells and one oocyte in each cluster of Anoplura show a reduction in gonial cell mitosis and similar reductions are also known among

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endopterygotan (holometabolous) polytrophic meroistic ovarioles (Büning, 1994). The large taxon Psocodea is supported by some obvious similarities in the features of the ovarian structure and oogenesis among 'Psocoptera', 'Mallophaga' and Anoplura.

Psocodea and Endopterygota with polytrophic meroistic ovarioles share a set of common characters: 1) germ cells form a branched cluster, 2) a nurse chamber is formed by interaction of follicular cells with nurse cells, 3) 2^n-1 nurse cells support one oocyte and the oocyte always originates from one of the two oldest cells with the maximum number of intercellular bridges, 4) nurse cell nuclei enhance their DNA contents by endomitotic polyploidization (Büning, 1994). Polytrophic meroistic ovarioles in endopterygotan orders show some variations or deviations, but such variations or deviations are seldom found in Psocodea (Büning, 1994). These allow us to assume a common origin of the polytrophic meroistic in Psocodea and Endopterygota and fundamentality in the polytrophic meroistic of Psocodea (Büning and Shost, 1990; Büning, 1994, 1998).

In Thysanoptera, germ cell cluster analysis has been performed in both suborders, Terebrantia and Tubulifera, and it has been demonstrated that their ovariole types are neopanoistic (Pritsch and Büning, 1989; Tsutsumi *et al*., 1995). Germ cell cluster formation is always observed in ovarian rudiments of larvae and germaria of imaginal ovarioles, but nurse cells never differentiate. The germ cells forming a cluster are separated into several small subclusters, and each of the germ cells finally becomes a solitary oocyte. In the aspect of no tropharium, thysanopteran ovarioles are to be derived from psocodean polytrophic meroistic ovarioles.

In Hemiptera, though the ovariole type of Coleorrhyncha remains unknown, all the other three suborders have telotrophic meroistic ovarioles (Matsuzaki, 1975; Książkiewicz-Kapralska, 1985, 1991; Szklarzewicz and Biliński, 1995; Simiczyjew *et al*., 1998; Štys *et al*., 1998; Szklarzewicz, 1998). The telotrophic meroistic ovarioles of Hemiptera are uniform in structure and are supposed to be derived from the polytrophic meroistic ovarioles of Psocodea. However, the architecture of tropharium shows some obvious differences among suborders and among infraorders of Heteroptera (Simiczyjew *et al*., 1998; Szklarzewicz, 1998). In primitive heteropterans, their tropharia are composed of individual, usually mononucleate nurse cells, while in more advanced ones, *e. g*., Pentatomomorpha, their tropharia are built of syncytial lobes containing several nurse cell nuclei. The syncytial areas seem to arise as a result of membrane fusion between some nurse cells. Mononucleate nurse cells in the tropharium are also observed in primitive hemipterans, such as Auchenorrhyncha and Sternorrhyncha. Mitotically active nurse cells in the apical region of tropharium are observed in more advanced heteropterans, while in primitive ones, nurse cells in the apical region of imaginal tropharium do not divide mitotically. A similar situation has also been found in Auchenorrhyncha and Sternorrhyncha. It is probable that the individuality of nurse cells and absence of mitotic activity of nurse cells in the apical zone of imaginal tropharium are primitive conditions in hemipteran telotrophic ovarioles.

The ultrastructural features of the ovarian structures and oogenesis support a recent phylogeny and classification of the orders belonging to 'Paraneoptera' or rather Acercaria. In order to confirm the certainty of relationships among and within four orders, Zoraptera, Psocodea, Thysanoptera and Hemiptera, ultrastructural investigations of the ovarian structures and oogenesis of Zoraptera, primitive thrips (*e. g*., Merothripidae), fulgoromorphan Auchenorrhyncha, Coleorrhyncha and primitive heteropterans (*e. g*., Enicocephalomorpha) are much desired.

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