Germ cell cluster in the panoistic ovary of Thysanoptera (Insecta)

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Summary. Germ cell clusters are found in the germarial region of ovarioles of Parthenothrips dracenae. Cluster mitoses are synchronized, at least initially. The intercellular bridges are filled with fusomal material, which can fuse to form polyfusomal aggregates which in turn form small rosettes. All cells develop into oocytes. Oocytes become isolated by a secondary detachment process. Intercellular bridges, together with fusomal material and cell membranes, survive for some time as isolated bodies. Phylogenetic consequences are discussed. The data provide strong evidence for a secondary panoistic ovary in thysanopterans, since cluster formation in ovaries of primary panoists has not been shown.

A. Introduction
In the ovarioles of most insects, oocytes are assisted by nurse cells during the previtellogenic growth phase. These ovaries are called meroistic ovaries. The nurse cells are the sister cells (cystocytes) of the oocyte. They develop from a mother cell, the cystoblast, by synchronized mitotic divisions, followed by incomplete cytokinesis. Among this developing germ cell cluster, only one of the two oldest cells will become the oocyte, all others will develop as nurse cells. A special cytoplasm, the polyfusome, arises between the remaining intercellular bridges or ring canals. Very often the intercellular bridges remain tightly together and the cluster cells form a rosette. These events have been known about for a long time (Giardina 1901; Hirschler 1945; King 1970; Telfer 1975; King et al. 1982). Since all meroistic ovaries can be derived from this basic plan, we have called it the basic type of meroistic ovary (Bünig 1985, 1988; King and Bünig 1985). The basic type is a character complex that can possibly be used for sister group analysis between Paraneoptera and Holometabola (Hennig 1969; Kristensen 1981). In his excellent review of the insect ovary structure, Telfer (1975) suggested that the appearance of panoistic ovaries may be ancestral or may have deviated, for example by reduction of mitotic cycles during cluster development, combined with an early decay of nurse cells. Here we report the first finding of cluster formation in a panoistic ovary and its impact on phylogeny among paraneopterans.

B. Materials and methods
The ovaries of Parthenothrips dracenae (Heeger, 1854) were investigated. The species was grown on Philodendron sp. Nymphs and imagoes were prepared for light and electron microscopy using standard methods. Serial sectioning was performed as described elsewhere (Bünig and Sohst 1988).

C. Results
1. Gross anatomy
Each ovary of P. dracenae is composed of four ovarioles. The youngest germ cell descendants are found in the tip of each ovariole, zone I (Fig. 1). They are enclosed by a layer of flat somatic cells, the inner sheath. A tightly associated basal lamina surrounds each ovariole. A loosely connected outer envelope bearing tracheoles and muscles is also associated.

Zone II comprises previtellogenic growing oocytes, ordered in a straight line. Each oocyte is enclosed by a monolayer of follicular cells, derived from prefolicular cells which form a small tissue in the transient region between zone I and II. Somatic cells of the inner sheath, the prefolicular cells and early follicular cells, cannot be distinguished by ultrastructural criteria, but only by position. Mitoses were found in the basal area of zone I and in the follicular epithelium of zone II. All events of vitellogenesis and chorionogenesis occur in zone III (not shown).

2. Ultrastructure and cluster analysis
A complete longitudinal, ultrathin serial sectioning was prepared from a whole ovariole of a young female adult, which had already started vitellogenesis (not shown). We found 25 somatic cells in zone I, enclosing 22 germ cells, whereas 15 follicular cells surround the youngest oocyte of zone II. Thus, a high mitotic activity of somatic cells must occur at the base of zone I.

In the upper half of zone I we found intercellular bridges connecting germ cell descendants (Figs. 1–4, 6). In the tip of the ovariole only one germ cell was found without any connections to others (Figs. 2, 6, cell 1). It is followed by a 4-cell cluster showing one central bridge filled with fusomal material and two lateral bridges crossed by bundles of microtubules (Figs. 1, 2). The first bridge combines the two inner cells, while the lateral bridges connect the outer...