How can the panoism in the Thysanoptera be understood?

Tadaaki, TSUTSUMI[1], Ryuichiro MACHIDA[2] and Kazuo HAGA[3]

[1]*Institute of Biological Sciences, University of Tsukuba, Tsukuba, Ibaraki 305, Japan*
[2]*Sugadaira Montane Research Center, University of Tsukuba, Sanada, Nagano 386-22, Japan*
[3]*School Education Center, University of Tsukuba, Ohtsuka 3-29-1, Bunkyo-ku, Tokyo 112, Japan*

Introduction

Ovaries of insects are categorized into two types morphologically and physiologically distinguished from each other. One is the panoistic type in which all oogonia develop into oocytes. The other is the meroistic type in which the differentiation of oogonia as nurse cells occurs, and this type has two subtypes, *i.e.*, the polytrophic and the telotrophic. In the polytrophic meroistic ovary, an oocyte and nurse cells grow in a single chamber. In contrast, in the telotrophic meroistic, the nurse cells are retained in the germarium, where they form a syncytium (tropharium).

These ovarian types in insects have been believed to be highly conservative at the ordinal or subordinal level (cf. King and Büning, 1985; Štys and Biliński, 1990). These ovarian types have been anagenetically explained: the panoistic type is assumed as the most ancestral because of its deficiency in transformation of oogonia into nurse cells (Telfer, 1975; King and Büning, 1985; Štys and Biliński, 1990). The polytrophic meroistic ovary has been evolved through the differentiation of nurse cells from the panoistic ovary. Finally the telotrophic meroistic type has been derived from the polytrophic meroistic by the restriction of nurse cells to the germarium (Štys and Biliński, 1990).

It is well known, however, that the panoistic type of ovary distributes in some higher taxa, such as Thysanoptera, megalopteran Corydalidae, mecopteran Boreidae and siphonapteran Pulicoidea. The sporadic appearance of panoistic ovaries in higher taxa is difficult to understand in the light of the phylogeny defined above. Pritsch and Büning (1989) found that the intercellular cytoplasmic connections are maintained between germline cells deriving from a cystocyte and the germ-line cells form clusters in terebrantian thrips, *Parthenothrips dracenae*. They proposed that the panoistic ovary in the Thysanoptera could be understood as having been constituted through the secondary regression of oocytes/nurse cell differentiation and should not be identifical to the panoistic ovaries found in lower taxa within the class Insecta. Štys and Biliński (1990) supported Pritsch and Büning's idea and coined a new term "neopanoistic" for the secondary panoism in the Thysanoptera.

In this study, we examine the ovary of thrips belonging to another thysanopteran suborder, Tubulifera, aiming at verifying whether the intercellular bridges or cluster formation can be recognized to be of a general character for the Thysanoptera. Then we discuss the "panoistic" of Thysanoptera.

Materials and Methods

Dissected-out ovaries of adults, the 1st and 2nd instar-larvae of a tubuliferan thrips, *Bactrothrips brevitubus* Takahashi were fixed with 4% paraformaldehyde in 0.05M sodium cacodylate buffer (pH 7.2) and rinsed in the same buffer. After dehydration (ethanol series), the materials were embedded in water-miscible methacrylate resin (Technovit 8100 + styrene) and polymerized at 4℃. Sections of 1.5 μm thickness were stained with hematoxylin and eosin. In order to detect the ring canals, fixed materials were rinsed in TBS-T (0.5% Tween-80 in TBS buffer), stained with rhoadaminylphalloidin in TBS-T and examined under a confocal fluorescence microscope (green excitation).

Results and Discussion

The observation of resin sections reveal that intercellular connections between germ-line cells exist in a tubuliferan thrips, *Bactrothrips brevitubus* (Fig. 1) as in *Parthenothrips dracenae*. With rhoadaminylphalloidin staining, the intercellular connections are detected as brilliant spots. Many spots are detected at one or two regions in the ovaries of the first to the early second larval stage (Fig. 2A), but in the late second larval stage those come to be fewer in number (Fig. 2B). Even in the germarium of a mature adult in which ovarioles con-

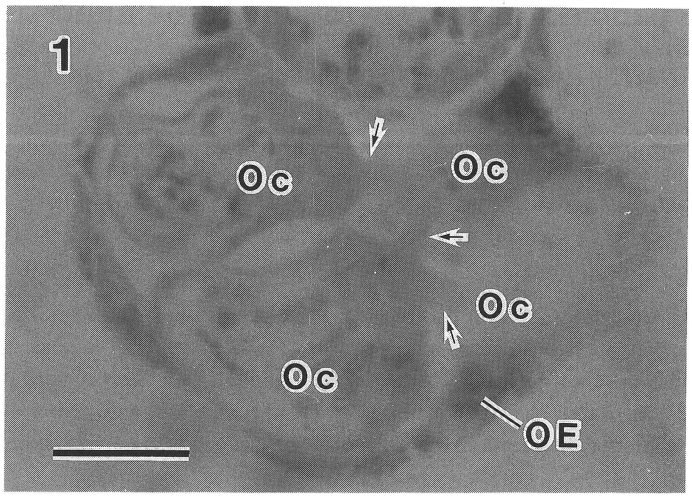

Fig. 1 Cluster of oocytes in late second larval stage of *Bactrothrips brevitubus*. Four cells are observed to be connected with three bridges (arrows). Scale=10μm. Oc: oocyte, OE: ovarian epithelium.

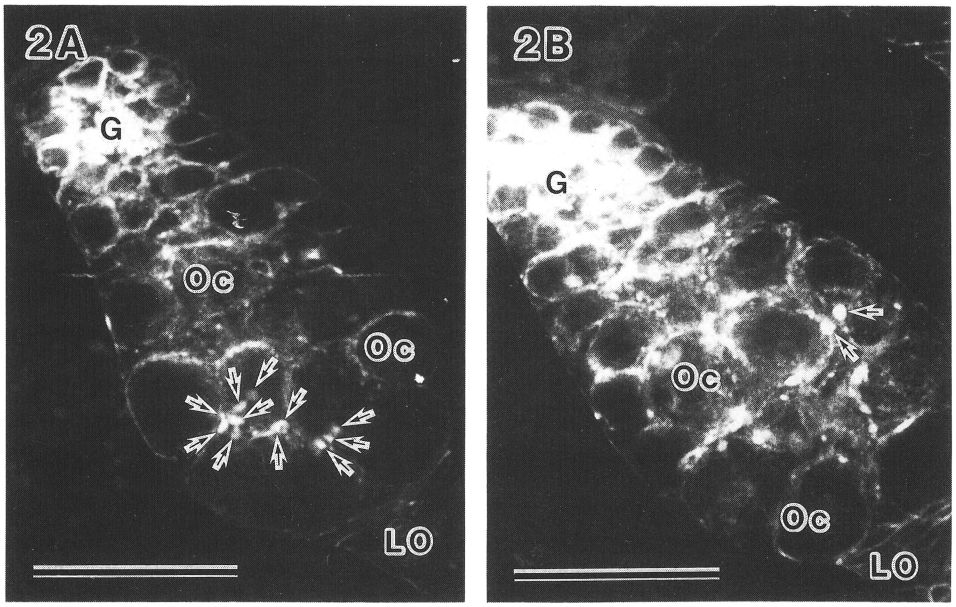

Fig. 2 Confocal fluorescence microscopy of ovary in early (A) and late (B) second larval stage of *Bactrothrips brevitubus*, processed into 1μm thickness. A. Intercellular connections between oocytes are detected as brilliant spots (arrows), localized in small areas. B. Intercellular connections (arrows) decrease in number in comparison with in the early stage (A). Scales=50μm. G: germarium, LO: lateral oviduct, Oc: oocyte.

tain ovoviviparously developing eggs, a small number of the intercellular connections between germ-line cells are still observed. Electron microscopy demonstrated in the same species that intercellular connections are present between germ-line cells (Haga and Matsuzaki, unpublished data). The intercellular connection between germ-line cells of *B. brevitubus* can thus be regarded as a structure comparable to the intercellular bridge or ring canal in the polytrophic ovaries, *e.g.* in *Drosophila*. Our finding, together with the previous report, may allow us to consider that the cluster formation with intercellular bridges of germ-line cells is characteristic for the Thysanoptera.

The leading understanding on phylogenetic passage of insect ovarian types is that the panoistic type is the fundamental and the meroistic type is derived from the former (cf. Štys and Biliński, 1990). We, however, have a different opinion. It is well known that the sister germ-line cells are generally connected by intercellular bridges to make a cluster in the male germ line of metazoans (Fawcett, 1971) and in the female germ line of vertebrates (Franchi and Mandl, 1962; Zamboni and Gondos, 1968; Ruby *et al.*, 1970; Skaklo *et al.*, 1972; Filosa and Taddei, 1976; Gondos, 1987). It has also been found that not a few invertebrates besides insects develop nurse cells which are sister cells of the oocyte, and form germ-line cell clusters (oocyte-nurse cells) during oogenesis. This is known in animals such as Tardigrada (Weglarska, 1979), Annelida (Heacox and Schroeder, 1981; Eckelbarger, 1983), crustacean Branchiopoda (Tommashini and Scanabissi Sabelli, 1992). In addition, clusters composed only of oogonia or oocytes are reported in Arthropoda such as in the Acari (Brinton, 1971), and in the Myriapoda (Kubrakiewicz, 1991) which is the sister group of Insecta. The intercellular connections between the germ-line cells (the oogonia, oocyte and nurse cells) have thus been widely observed basic characteristics of the germ line in animals including Insecta, as Gottanka and Büning (1990) noticed. In fact, germ-line cell clusters are found even in the most primitive insect group, the Entognatha: as oocyte-nurse cells cluster in the meroistic ovaries of collembolans (Krzysztofowicz, 1971; Matsuzaki, 1973; Kisiel, 1987) and dipluran *Lepidocampa* (Asaba and Ando, 1978) and as a cluster composed only of oogonia or oocytes in the proturan panoistic ovary (Klag and Biliński, 1984). Provided that the cluster formation should be a basic attribute in the Entognatha (cf. Gottanka and Büning, 1990), it may be reasoned that the intercellular connections between germ-line cells have been maintained through the establishment of the sister taxon of the Entognatha, the Ectognatha. Concerning the problem which should be ancestral between the two types that retain the inter-germ-line cell connections, *i.e.*, one composed only of oogonia or oocytes and the other composed of an oocyte and nurse cells (meroistic), further discussions are needed (Tsutsumi *et al.*, in preparation). However, it may be safely asserted that the ovarian type of which the cluster consists exclusively of oogonia or oocytes should be basic to the meroistic, in which the nurse cell differentiates.

Let us further extend our argument. From the ovarian type with the homogeneous cell cluster, the meroistic evolves in one hand through functional differentiation of nurse cells, generally found in higher groups; in the other hand the panoistic develops, in association with the loss of intercellular connections acquired by complete cytokinesis, occurring generally in lower groups. Štys and Biliński (1990) argued that the ovarian type of the Thysanoptera to be yielded as a result of reversal reduction from the polytrophic type to the panoistic one, and they proposed the term "neopanoistic" for it. Their idea indeed may be in good agreement to the current insect phylogeny, and it may be also the most parsimonious hypothesis. However, as discussed above, we have an opinion that the ovarian type with homogeneous cell clusters should be the most plesiomorphic in Insecta and that the ovary of the Thysanoptera should be in this category: the ovarian type of Thysanoptera is to be regarded as primary or fundamental one in Insecta, as those of the Protura and Plecoptera.

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