

## Ultrastructure of the ovarioles in *Formica* ants (Hymenoptera, Formicidae)

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**Zusammenfassung.** Ultrastruktur der Ovariolen in Ameisen, Gattung *Formica* (Hymenoptera, Formicidae). – Die Ultrastruktur der Ovariolen von 4 *Formica*-Arten wurde untersucht. Es wird die Entwicklung von undifferenzierten Zellen aus dem Germarium in Gruppen aus Eizelle und begleitenden Nähr- bzw. Follikelzellen beschrieben, sowie die morphologischen Veränderungen dieser verschiedenen Zelltypen während der Dotterbildung. Weiterhin werden das degenerierte Stadium der Arbeiterin-Ovariolen und das Auftreten von Gelbkörpern dargestellt.

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As in most social insects, ovariole development in the worker caste of ants is suppressed. Ovaries in young *Formica* workers show a short growth phase up to a stage of maximum growth that is immediately followed by a degeneration process (BILLEN, 1982). We here report on ovariole ultrastructure and the morphological changes during its developmental cycle in 4 *Formica* species.

### Material and Methods

Workers of *Formica cunicularia* Latreille, *F. fusca* Linnaeus, *F. pratensis* Retzius and *F. sanguinea* Latreille were collected in the natural reserve „Het Leudal“ in the Netherlands. The ovaries were dissected and fixed in 2% glutaraldehyde in 0.05M cacodylate buffer with 0.15M saccharose, postfixed in 2% osmium tetroxide in the same buffer, dehydrated in acetone and embedded in Araldite. Sections were stained with uranyl acetate and lead citrate, and examined with a Philips EM 400 electron microscope.

### Results

Each ovariole consists of a tube with succeeding eggs and trophic chambers surrounded by a sheath of muscle fibres and tracheoles. Cystocyte division

occurs in the apical germarium in all stages except at final degeneration. The rounded daughter cystocytes remain interconnected by bridges with a diameter of approx. 1 µm. The cytoplasm between the rather densely stained bridge walls in general contains vesicular material (Fig. 1). During their descent towards the vitellarium, the cystocytes differentiate into clusters of an oocyte and its trophic nurse cells (trophocytes) with follicle cells surrounding both the oocyte and the nurse cell chamber. During their passage through the vitellarium all three cell types are involved in vitellogenesis.

The oocyte volume increases considerably due to the accumulation of yolk material. The ooplasm in early stages mainly contains numerous small mitochondria and a well developed RER. The latter can be found in whorls or in lineary arranged rows. During vitellogenesis, the oolemma forms an elaborated microvillar contact area where it borders the follicle cells (Figs. 2 and 3). The nucleus gradually reduces as the oocyte grows and several accessory nuclei appear. The full-grown oocyte contains high amounts of protein granules, lipid droplets and ribosomes. The accessory nuclei become smaller and finally disappear.

The development of follicle cells is the opposite of that of the oocyte. The follicular epithelium surrounding the oocyte at first consists of columnar

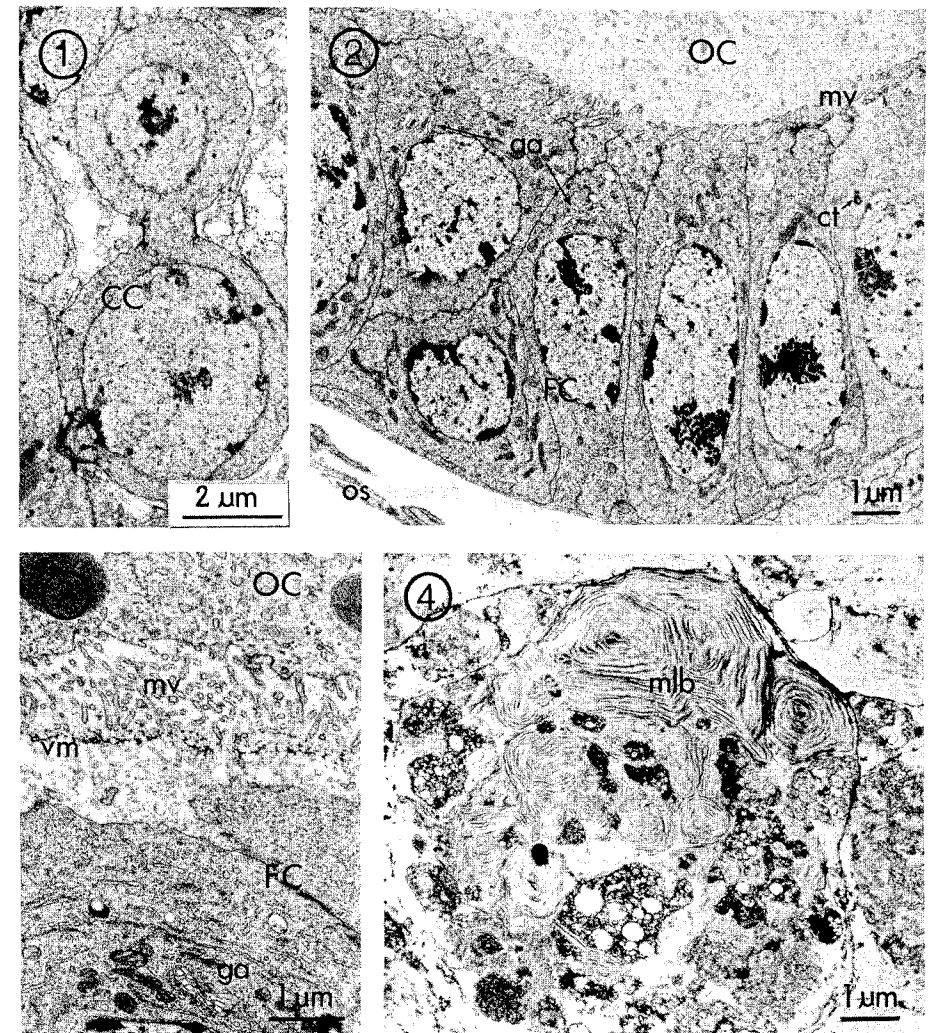


Fig. 1. Electron micrograph of cystocytes with intercellular bridges in the germarium of *F. cunicularia*.

Fig. 2. The follicular epithelium in a young *F. fusca* worker showing the columnar follicle cells and the microvillar region lining the oocyte.

Fig. 3. Contact area between the oocyte and the follicle cells at the end of vitellogenesis in *F. sanguinea*.

Fig. 4. Detail of the yellow body content in a degenerated ovariole of a *F. cunicularia* worker showing the large amounts of multilamellar bodies.

CC, cystocyte; ct, centriole; FC, follicle cell; ga, Golgi apparatus; mlb, multilamellar body; mv, microvilli; OC, oocyte; os, ovariole sheath; vm, vitelline membrane.

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cells which gradually become cuboidal and end as flattened cells with large intercellular spaces. During their columnar and cuboidal phase the cytoplasm contains many mitochondria, a well developed Golgi apparatus and only scattered RER (Fig. 2). In the apical region intercellular bridges between follicle cells (diameter  $\pm 0.3 \mu\text{m}$ ) are often found. In the squamous follicle cells a well elaborated RER occurs as well as a Golgi system. At the end of vitellogenesis, a vitelline membrane is deposited between the follicle cell epithelium and the oocyte (Fig. 3).

Nurse cells also at first show a considerable growth when moving towards the oviduct before degeneration sets in. The cytoplasm contains many very small mitochondria and huge amounts of ribosomes. The cells remain interconnected by bridges (diameter  $\pm 1.2 \mu\text{m}$ ) that resemble those between cystocytes. When vitellogenesis comes to an end, the nurse cells degenerate and probably give rise to yellow bodies. These can reach a diameter of over  $50 \mu\text{m}$ . They have a multinuclear appearance and contain large amounts of multilamellar bodies (Fig. 4).

### Discussion

The oogenesis as reported in this contribution on *Formica* workers is very similar to that in the queens

of *Atta* (DA CRUZ-LANDIM, 1978). Intercellular bridges which occur in dividing cystocytes will remain between differentiated nurse cells and between a nurse cell and the oocyte. Also the follicular epithelium shows intercellular bridges. Such cell contacts are important for transport of cytoplasmic material and probably also have a synchronizing function for the different cells during oogenesis (RAMAMURTY and ENGELS, 1977).

After maximal growth has been reached, worker ovarioles undergo a rapid degeneration with formation of yellow bodies. The abundance of multilamellar bodies indicates the degeneration process. Formation of yellow bodies still remains unclear, their position next to an oocyte and the multinuclear appearance, however, suggest their nurse cell origin.

### Summary

The ultrastructure of the ovarioles has been studied in 4 species of *Formica* ants. The evolution of undifferentiated cells in the germarium into groups containing an oocyte and its accompanying nurse cells and follicle cells is reported as well as the morphological changes of these different cell types during vitellogenesis. The degenerated stage of worker ovarioles and the appearance of yellow bodies is also described.

### Literature

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