Ring-Canals and Intercellular Communication Within the Egg-Chamber of a Tsetse Fly Species

In a number of insect groups, each ovariole consists of an alternating succession of oocytes and trophocytes (or nurse cells). As a further specialization of this polytrophic type of ovariole structure in Coleoptera, Lepidoptera and Diptera, each oocyte is accompanied by a number of trophocytes which together form a single egg-chamber[1]. According to VERHEIN[2] there are 15 trophocytes and a single oocyte in each egg-chamber of most flies belonging to the superfamily Muscoidea. Tsetse flies belong to this group. Recently, some confusion has arisen as to the number of trophocytes that are contained in each egg-chamber in tsetse flies: SAUNDERS[3] has claimed that there are only 14 trophocytes in each egg-chamber; whereas HAGAN[4] states that there are 15.

A further controversy relates to the mode of cell division which produces the number of cells contained in the tsetse

[1] R. E. SNODGRASS, *Principles of Insect Morphology* (McGraw-Hill Book Co., New York 1935), p. 557.
[2] A. VERHEIN, Zool. Jb. Anat. *42*, 149 (1921).
[3] D. S. SAUNDERS, Trans. R. ent. Soc. Lond. *112*, 221 (1960).
[4] H. R. HAGAN, *Embryology of the Viviparous Insects* (Ronald Press, New York 1951), p. 120.

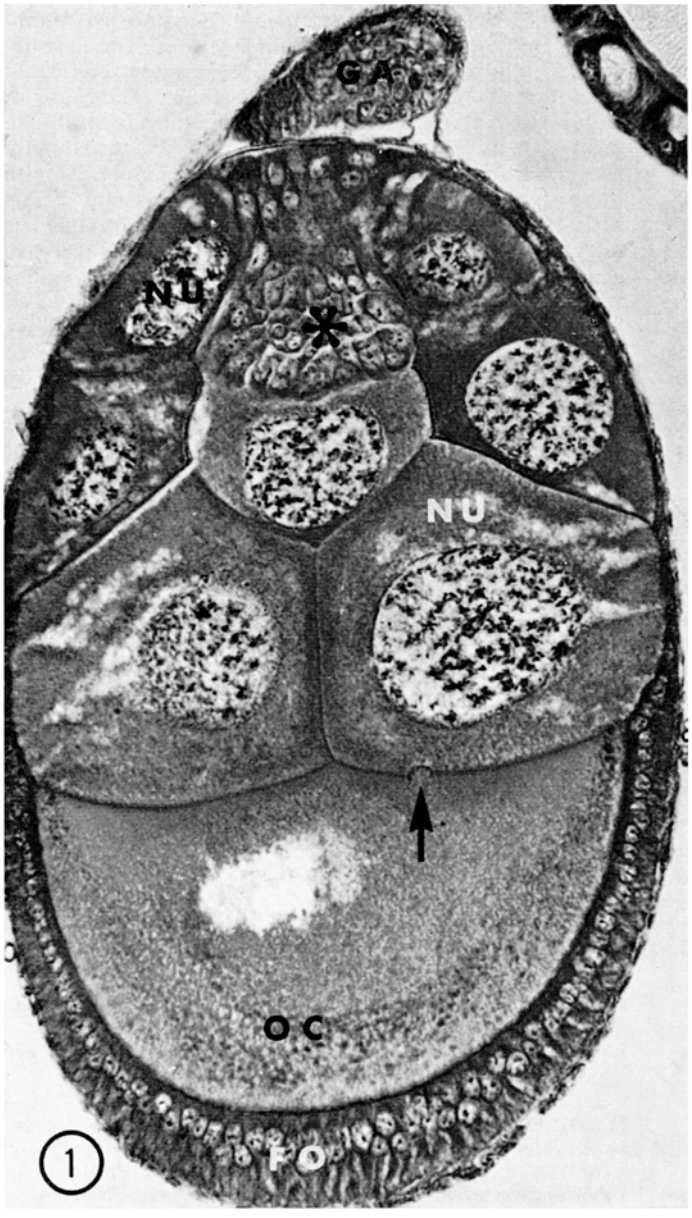


Fig. 1. Photomicrograph of a longitudinal section of a developing oocyte of *G. pallidipes*. The largest cell is the oocyte (OC) at the posterior end of the egg-chamber; the rest of the egg-chamber is occupied by 7 large trophocytes (NU) and small cells (star) which form a central column in the chamber; these small cells are derived from the follicular cells (FO) which envelop the entire egg-chamber. The arrow indicates the position of a ring-canal. Anterior to the chamber is the germarium (GA). About × 270.

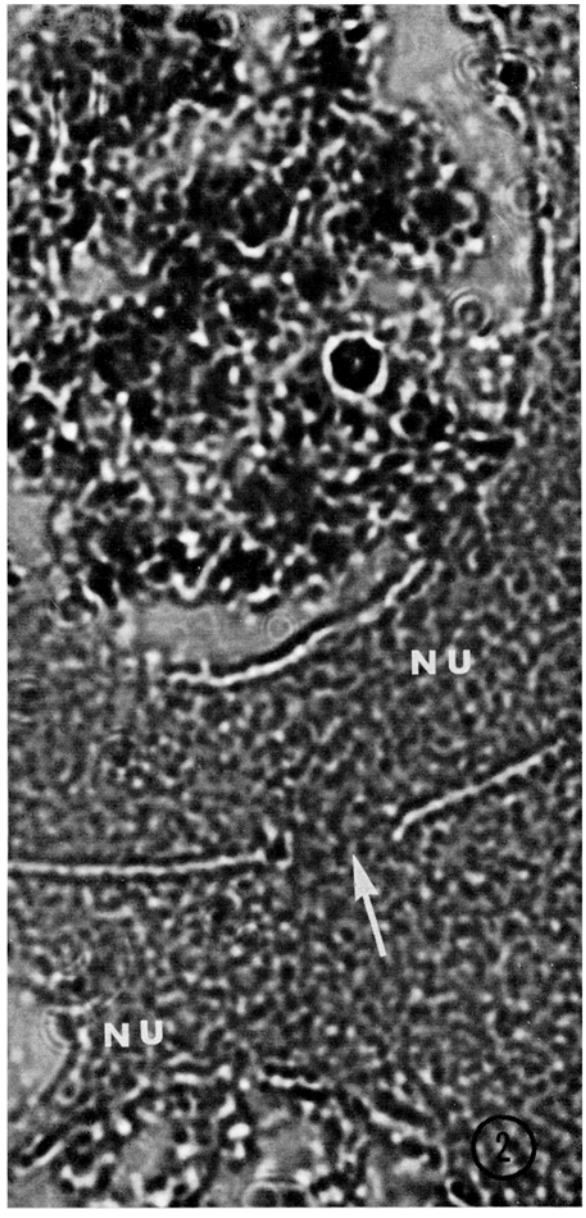


Fig. 2. Photomicrograph of a section through a ring-canal (arrow) between 2 adjacent trophocytes (NU). Note the projecting rims of the canal. About × 1500.

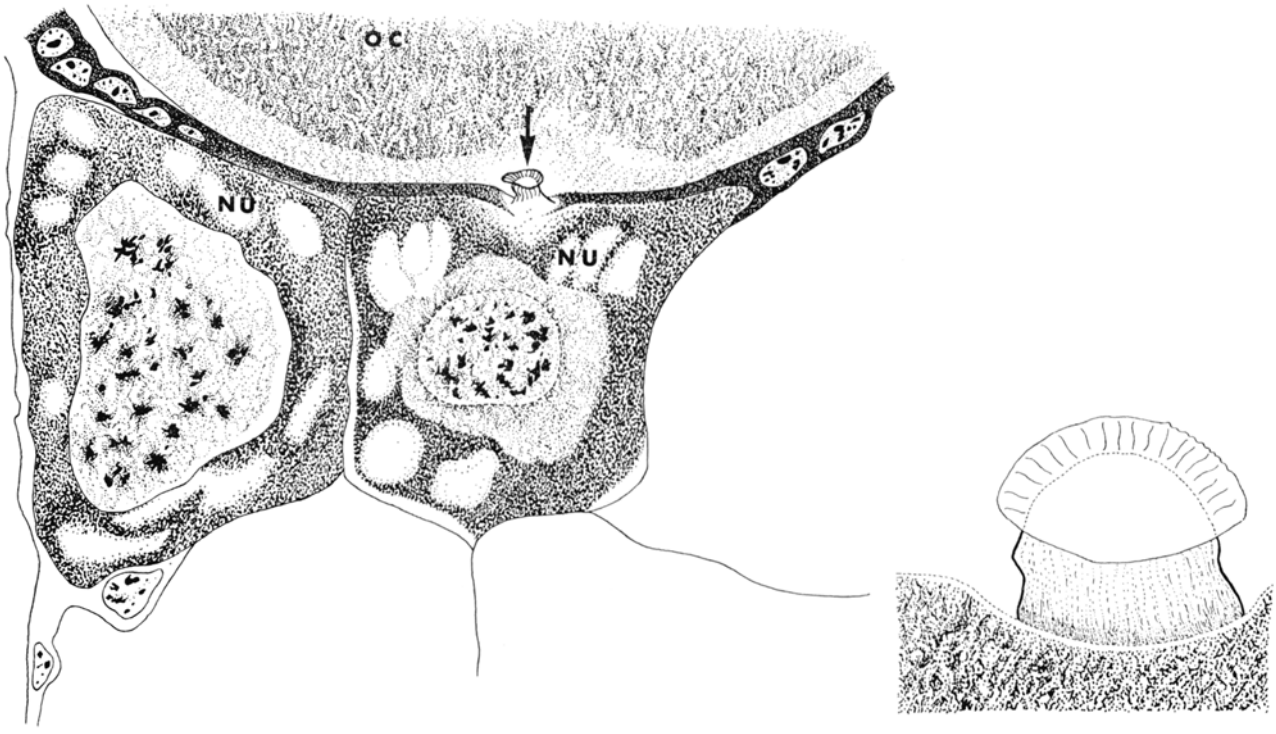
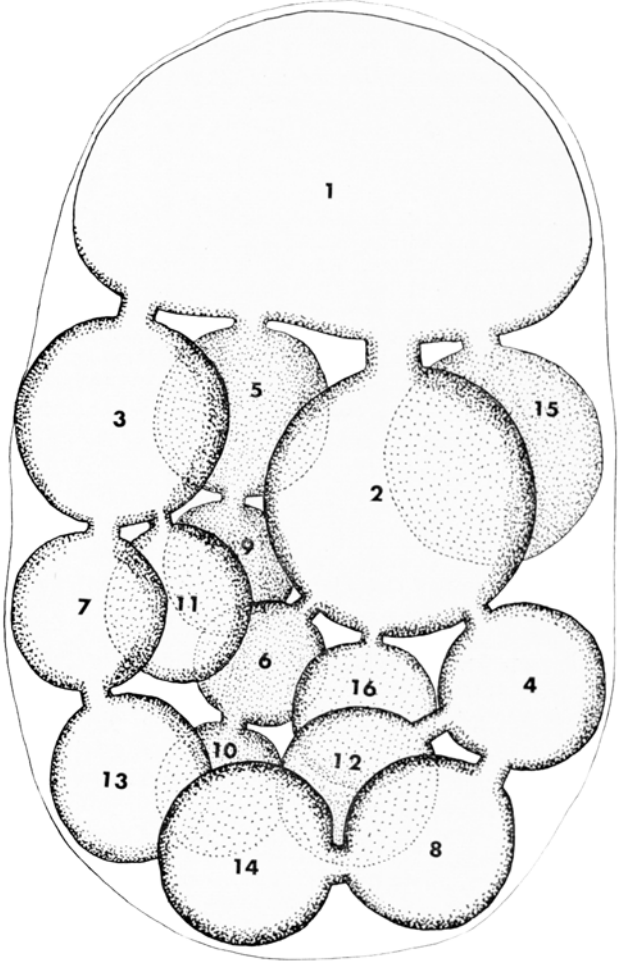


Fig. 3. (a) A diagram of a ring-canal (arrow) between a trophocyte (NU) and the oocyte (OC). The section from which the diagram was made went obliquely through one half of the ring-canal, the portion within the oocyte. About × 450. (b) A high-magnification drawing to show the structure of the ring-canal (half of it).



and other muscoid egg-chambers, where 4 successive cell divisions of the original cystoblast produce the oocyte and its accompanying trophocytes. It is claimed that in the tsetse fly, *Glossina morsitans*, 8 daughter cells arise by oogenesis in the germarium and then descend to the vitellarium; one of these becomes the definitive oocyte, while the other 7 divide once more to form the 14 trophocytes in the egg-chamber[3]. On the other hand, in the fruitfly, *Drosophila melanogaster*, all the 8 daughter cells divide once again while still in the germarium to form 16 cells, one of which will be the future oocyte when the cells eventually descend into the vitellarium[5,6].

The problem has been re-examined by histological methods using Carnoy-fixed, paraffin-imbedded ovaries of *G. pallidipes*.

Serial sections of 5–7 μ thickness have revealed that there are 15 trophocytes and a single oocyte in each egg-chamber of the tsetse fly. These cells are all interconnected by a series of ring-canals (Figures 1 and 2) of definite size that are arranged in a precise manner. In a mature egg-chamber, the ring-canals are about 8–10 μ in diameter; at the 16-cell stage within the germarium, the ring-canals are only about 3 μ in diameter. This size difference in ring-canals is in keeping with the enormous growth of the 16 cells once they have reached the vitellarium (Figure 1). The 16 cells within the egg-chamber are closely adherent

[5] E. H. Brown and R. C. King, Growth *28*, 41 (1964).
[6] E. A. Koch, P. A. Smith and R. C. King, J. Morph. *121*, 55 (1967).

Fig. 4. A schematic diagram of the disposition of all the cells of an egg-chamber of *G. pallidipes* including their ring-canal interconnections, based on serial sections. 1, the oocyte; 2–16, trophocytes.

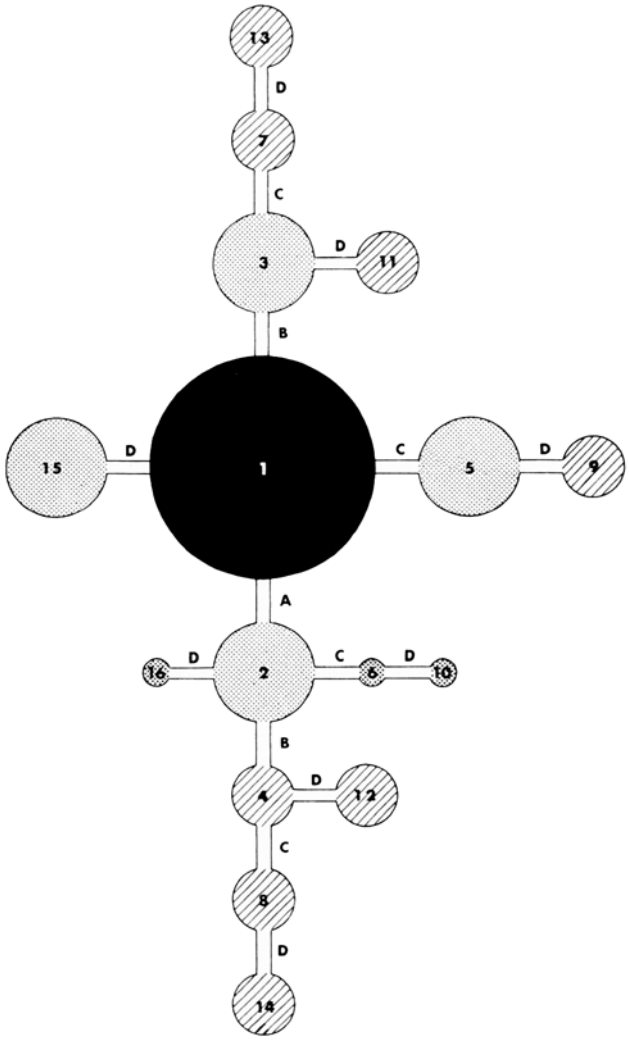


Fig. 5. A schematic model of the cell divisions that result in the 16 cells of a tsetse-fly egg-chamber and its ring-canals. The numerical numbering follows that in Figure 4; the alphabetical numbering indicates A, first cell division; B, second division; C, third division; and D, fourth division. The sizes of the cells in the diagram give an (exaggerated) indication of the size differences between the various cells of the egg-chamber towards the end of the yolk-deposition stage.

to each other, and each ring-canal is simply a short tube projecting into the 2 adjacent cells (Figures 2 and 3).

There are in all 15 such ring-canals in each egg-chamber. Two cells (including the oocyte) have 4 ring-canals, 2 cells have 3, 4 cells have 2, and 8 cells have 1 ring-canal each (Figure 4). Taking into consideration this very precise location of ring-canals, and the suggestion that ring-canals are a result of arrested cytokinesis[5,7], a model has been constructed to indicate the manner in which the cells comprising the egg-chamber may have been derived by mitosis (Figure 5). It is clear then that the 16 cells arise from the division of all the 8 third-generation cells.

It is not certain what the function of the ring-canals is in insect egg-chambers. There is some suggestive evidence that cytoplasmic contents flow through this canal: (1) cytoplasmic contents apparently stain similarly on either side of a ring-canal[8]; (2) large or distinctive cytoplasmic organelles are often seen within the canal[7,9]; and (c) radioautographic studies of the incorporation of injected tritiated uridine demonstrates that the labelled RNA appears in the cytoplasm adjacent to a ring-canal before it is noted in the cytoplasm of the adjoining cell[10]. However, the intercommunication through ring-canals and the manner in which this is regulated has still to be unequivocally demonstrated[11].

Zusammenfassung. In der Ovariole der Tsetsefliege werden 15 Trophozyten und eine Oozyte festgestellt, die in wohlgeordneter Weise durch 15 Ringbildungen miteinander verbunden sind. Eine Anordnung, welche die Rekonstruktion der vorausgegangenen Mitosen dieser 16 Zellen möglich macht.

T. R. ODHIAMBO

Department of Zoology, University College, Nairobi (Kenya), 15 January 1961.

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[9] G. F. MEYER, Z. Zellforsch. mikrosk. Anat. *54*, 238 (1961).
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[11] This work was supported by a grant from the Rockefeller Foundation. I wish to thank Mrs. D. MCLACHLAN and Mr. P. LISAMULLA for technical assistance and the East African Trypanosomiasis Research Organization, Tororo, for the provision of tsetse flies.

COGITATIONES

Chromosomes and Systematics of some North American Species of the Genus *Marmota* (Rodentia: Sciuridae)

The North American members of the genus *Marmota*, the marmots, were last revised by A. H. HOWELL[1]. He recognized 3 groups of species: the woodchuck, *M. monax* (Linnaeus); the yellow-bellied marmot, *M. flaviventris* (Audubon and Bachman); and the hoary marmot group, consisting of the hoary marmot, *M. caligata* (Eschscholtz), the Olympic marmot, *M. olympus* (Merriam), and the Vancouver Island marmot, *M. vancouverensis* Swarth. Subsequently, a new form was described[2] from the Brooks Range of northern Alaska as a race of the hoary marmot, *M. c. broweri* Hall and Gilmore. ELLERMAN[3] retained these latter forms in the *caligata* group, and added the black-capped marmot, *M. camtschatica* (Pallas), of eastern Siberia to it. He then went further[4] submerging the entire *caligata* group within the *M. marmota* group, which as he

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[3] J. R. ELLERMAN, *The Families and Genera of Living Rodents* (British Museum, Natural History, London 1940), vol. 1.
[4] J. R. ELLERMAN and T. C. S. MORRISON-SCOTT, *Check List of Palaearctic and Indian Mammals: 1758 to 1946* (British Museum, Natural History, London 1951).