The moment this muscle will exert on the lower jaw depends on its absolute force Fm and on the moment arm h, whereby $h = r \cdot \sin \alpha$. The figure, B and C, demonstrates that assuming a constant angle $\theta$, retraction of the quadrate will cause a reorientation of the external adductor increasing its insertional angle $\alpha$ ($\alpha'$) and therewith increasing h, thus leading to a greater mechanical advantage of the muscle.

Assuming a constant size of the prey, the widening of the gape which results from quadrate retraction will necessitate further jaw elevation to hold the prey. This jaw adduction will further increase the insertional angle $\alpha$ ($\alpha''$) and thereby maximize the mechanical advantage at which the external adductor works.

The above argument can be extended to all other jaw adductors inserting into the mandible except for the m. pterygoideus.

This muscle, however, is critical during initial phases of jaw closure[7] and hence does not interfere with the system described above.

In conclusion, the acquirement of a streptostylic quadrate early during the evolution of primarily insectivorous lizards (Eolacertilia[8]) can be understood as a perfection of the static pressure system which first evolved in the earliest reptiles, the captorhinomorphs.

1 Acknowledgments. I am greatly indebted to Prof. Dr med. M. Elke who made the X-ray cinematography possible at the Röntgeninstitut, Kantonsspital Basel. I thank Dr R.L. Carroll, Montreal, Canada, Dr G.S. Throckmorton, Dallas, USA, and Dr D.G. Senn, Basel, for critically reading the manuscript.

2 O.C. Bradley, Zool. Jb. (Anat.) *18*, 475 (1903).
3 J. Versluys, Zool. Jb., suppl. 15 (2), 545 (1912).
4 T.H. Frazzetta, J. Morph. *111*, 287 (1962).
5 N.N. Iordansky, Zool. Zh. *45*, 1398 (1966, in Russian), also: Smithsonian Herp. Inf. Serv. *14*. Ed. L. Kelso and C. Gans. Washington.
6 E.C. Olson, Am. Zool. *1*, 205 (1961).
7 R.L. Carroll, Biol. Rev. *44*, 393 (1969).
8 R.L. Carroll, Linn. Soc. Symp. Ser. *4*, 359 (1977).
9 G.S. Throckmorton, J. Morph. *148*, 363 (1976).

## Nuclear lamellae in the germ-line cells of gall midges (Cecidomyiidae, Diptera)[1]

B. Jazdowska-Zagrodzińska and B. Matuszewski

*Department of Cytology, Warsaw University, Krakowskie Przedmieście 26/28, PL-00-927 Warszawa (Poland), 28 November 1977*

Summary. Lamellar structures in oogonial and spermatogonial cells of gall midges were found to form a complicated system of intranuclear compartments inside which all heteropycnotic chromosomes present in the germ-line cells of these insects are located. In this way, the heteropycnotic S-chromosomes are separated by the nuclear lamellae from the remaining, decondensed chromosomes (E-chromosomes) of the interphase germ-line nucleus.

The part of the nucleus, in the oocytes of different groups of animals, in which chromosomes are grouped, is often separated from the remaining part of the karyoplasm by structures collectively termed the chromosome or karyosphere capsule[2-7]. The structure of the capsules may differ in various animals but in most of the known cases they are transient differentiations of the nucleus which occur in a particular species in the course of oogenesis. The role of these structures remains to be elucidated.

The intranuclear chromosome capsules in the Cecidomyiids differ from similar structures in the oocytes of other animals in that they occur not only in the course of oogenesis but also in other developmental stages of the germ cells. Moreover, there is reason to presume that their occurrence in the Cecidomyiidae is connected with the functioning of a singular cytogenetic system, particular to this family of the Dipterous flies. One of the main features of this system is the presence in the germ-line nuclei of both males and females of 2 sets of chromosomes: S-chromosomes found in both the generative and somatic cells and E-chromosomes which are limited to the germ-line nuclei only.

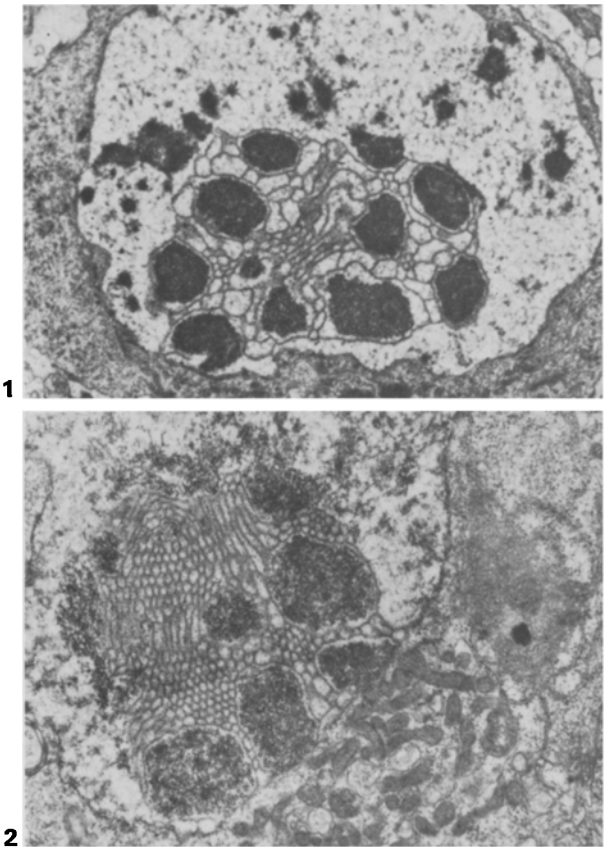
The chromosome capsule in the oocytes of the Cecidomyiidae was first described in *Mikiola fagi* as a vesicular element composed of concentric lamellae[8]. In the diplotene, these lamellar structures envelope the S-chromosomes exclusively which, contrary to the E-chromosomes, pair to form chiasmatic bivalents. In this stage of oogenesis, the E-chromosomes are found in the form of univalents on the outside of the system of lamellar vesicles. These observations, made in light microscope, have been confirmed by electron microscope studies of the oocytes of a different gall midge[9,10]. For some time there have also been clues that the chromosome capsules in gall midges occur even in the primordial germ cells[11]. Recent electron microscope studies have confirmed the presence of a chromosome capsule in the polar cells of Miastor and have revealed its lamellar structure[12].

In the light of these observations, it seemed interesting to discover whether lamellar chromosome capsules are present in the gonial cells of larval gonads in the Cecidomyiidae.

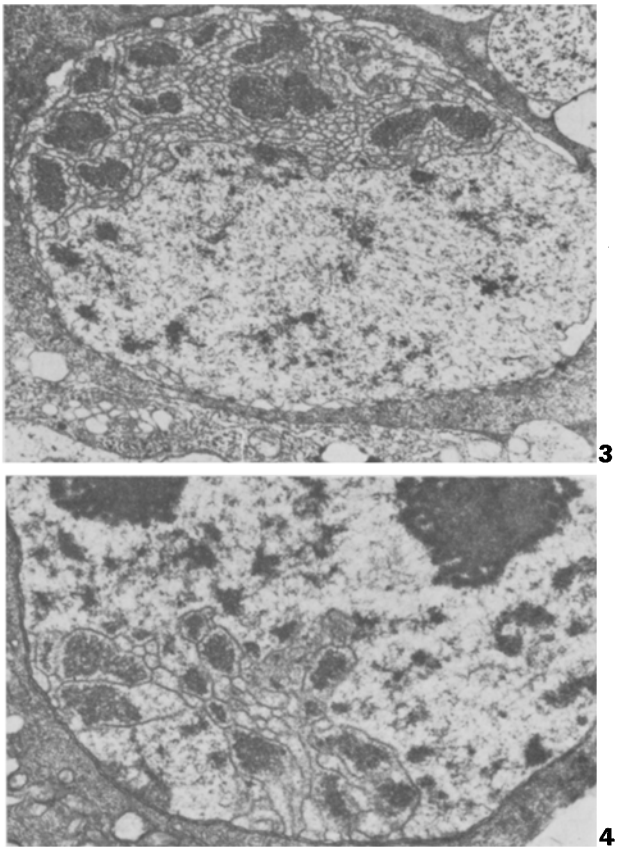
*Material and methods.* The studies were made on the larval ovary of 2 non-paedogenetic species of gall midges, *Rhabdophaga rosaria* and *Mayetiola poae*, and on the testes of larvae of the latter species. The gonads were fixed in 5% glutaraldehyde buffered at pH 7.4 with 0.1 M phosphate for 60 min, washed in 0.1 M phosphate buffer, postfixed with 2% osmium tetroxide, and embedded in a mixture of epon and araldit. Ultrathin sections were stained with uranyl and lead salts[13].

*Results and discussion.* In the early stages of embryonic development, a certain number of chromosomes in the germ-line cells of the Cecidomyiids are subjected to heterochromatinization[11,14-16]. In many species the number of chromosomes subjected to this process is the same in male and female[17-21], and there is evidence for assuming that it is the set of S-chromosomes that becomes heteropycnotic in the germ cells of both sexes[19,22].

In both species examined, the S-chromosomes of the interphase germ-line nuclei show strong positive heteropycnosis and, as in most gall midge species, form a compact group on one side of the nucleus. The E-chromosomes, which take up the remaining part of the nucleus are represented by diffuse chromatin and a certain number of relatively small and irregularly shaped heterochromatin blocks (figures 1, 3 and 4). Moreover, it is seen from these figures that the part of the interphase nucleus, in which the S-chromosomes are grouped, is occupied by a system of interconnected electron dense sheets or lamellae, which form an irregular network with honey-comb-like structure



Figs. 1 and 2. Lamellate bodies in the oogonial nuclei of *Rhabdophaga rosaria*. The presence of large compartments containing heteropycnotic S-chromosomes, and of small chromatin free compartments is clearly visible in each nucleus. In figure 2, a honeycomb-like arrangement of numerous small compartments formed by nuclear lamellae is very distinct; it can also be seen that some of the compartments occupied by the condensed S-chromosomes are formed partly by the lamellae and partly by the nuclear envelope. Figure 1, × 8000; figure 2, × 12,000.



Figs. 3 and 4. Nuclear lamellae in oogonial nucleus (upper) and in spermatogonial nucleus (lower) of *Mayetiola poae*. As in oogonial nuclei of *Rhabdophaga*, the condensed S-chromosomes in germ cells of *Mayetiola* are located in large compartments of the lamellate bodies. Numerous small compartments which are free of chromosome material can also be seen in each nucleus. In the upper part of figure 4, 2 large and darkly stained nucleoli are visible. Figure 3, × 9600; figure 4, × 14,000.

(figures 1-4). The large compartments of this lamellate body seem to be occupied by separate S-chromosomes, but most of its numerous small compartments or canals are apparently free of chromatin material (figures 1-3). Some of the nuclear lamellae in the gonial cells, otherwise than in the polar cells or oocytes, directly contact the nuclear envelope. This results in the formation of a certain number of compartments whose walls are formed partly by the lamellae and partly by the nuclear envelope. These compartments may also contain single S-chromosomes (figures 2 and 3). No gaps were observed in the lamellae which are apparently continuous in their structure.

The occurrence of the nuclear lamellae in the polar cells[12], primordial germ cells[16], oocytes[8-10] and, as demonstrated in this paper in the gonial cells indicates that these structures exist continuously in the germ-line cells, at least of the female, throughout the life cycle of gall midges. The presence of a lamellar capsule containing the S-chromosomes in its compartments also in the spermatogonial cells (figure 4), gives strong support to the suggestion[9] that nuclear lamellae in the germ-line cells of gall midges are a device for isolating the set of S-chromosomes from the E-chromosomes. The existence of such compartmentization in the germ cell nuclei of the Cecidomyiidae would also explain the different behaviour of the chromosomes of both sets, in both males and females[23], the likely high degree of homology of the 2 sets notwithstanding[9,10,21,22,24,25].

1 This investigation was supported in part under Contract DPKBN/52/76-II.1.3.10. with the Polish Academy of Sciences.

2 M.N. Gruzova, Citologija *4*, 335 (1962).
3 M.N. Gruzova, Z.P. Zaichikova and I.I. Sokolov, Chromosoma *37*, 353 (1972).
4 A. Fiil, J. Cell Sci. *14*, 51 (1974).
5 A. Fiil, Cell Tissue Res. *167*, 23 (1976).
6 B. Matuszewski and M. Kloc, Experientia *32*, 34 (1976).
7 B. Matuszewski, P. Hoser, G. Hoser and M. Michalak, Experientia *33*, 883 (1977).
8 B. Matuszewski, Chromosoma *12*, 741 (1962).
9 W. Kunz, Verh. dt. zool. Ges. *64*, 42 (1970).
10 W. Kunz, H.H. Trepte and K. Bier, Chromosoma *30*, 180 (1970).
11 W. Kahle, Zoologica, Stuttg. *21*, 1 (1908).
12 A.P. Mahowald, Wilhelm Roux Arch. *176*, 223 (1975).
13 J.H. Venable and R. Coggeshall, J. Cell Biol. *25*, 407 (1965).
14 A. Reitberger, Chromosoma *1*, 391 (1940).
15 I. Geyer-Duszyńska, J. exp. Zool. *141*, 391 (1959).
16 S. Panelius, Chromosoma *23*, 333 (1968).
17 M.J.D. White, J. Morph. *79*, 323 (1946).
18 M.J.D. White, J. Morph. *80*, 1 (1947).
19 M.J.D. White, Univ. Texas Publ. No. 5007, 1 (1950).
20 Z. Kraczkiewicz, Zool. pol. *5*, 73 (1950).
21 Z. Kraczkiewicz, Chromosoma *18*, 208 (1966).
22 S. Panelius, Chromosoma *32*, 295 (1971).
23 M.J.D. White, Animal cytology and evolution. 3rd ed. University Press, Cambridge 1973.
24 R. Camenzind, Chromosoma *18*, 123 (1966).
25 W. Kunz and R.A. Eckhardt, Chromosoma *47*, 1 (1974).