LITERATURE CITED

1. B. V. Aleshin, in: Histology[in Russian], V. G. Eliseev, ed., Moscow (1963), pp. 382-416.
2. L. V. Beletskaya and É. V. Gnezditskaya, Immunologiya, No. 4, 89 (1980).
3. V. K. Beletskii and L. V. Beletskaya, Byull. Éksp. Biol. Med., No. 4, 502 (1980).
4. Sh. D. Galustyan, The Structure of the Thymus in the Light of Experimental Analysis [in Russian], Moscow (1949).
5. É. V. Gnezditskaya, L. V. Beletskaya, and D. I. Shagal, Byull. Éksp. Biol. Med., No. 1, 60 (1977).
6. I. E. Kovalev, P. V. Sergeeva, and S. E. Ishimbaev, Zh. Mikrobiol., No. 5, 85 (1971).
7. V. V. Kupriyanov, in: Morphological Bases of the Microcirculation [in Russian], No. 1, Moscow (1965), pp. 3-6.
8. Y. M. Lyampert, L. V. Beletskaya, N. A. Borodiyuk, et al., Immunology, 31, 47 (1976).
9. S. L. Clark, in: The Thymus in Immunology, New York (1964), pp. 71-78.
10. A. L. Goldstein, A. Guha, M. M. Zatz, et al., Proc. Natl. Acad. Sci. USA, 69, 1800 (1972).
11. C. Gregorie, J. Morphol., 72, 239 (1943).
12. J. A. Hammar, Die normalmorphologische Thymus: Forschung im letzter Vierteljahrhundert, Leipzig (1936).
13. J. Olah, P. Rohlich, and J. Toro, Ultrastructure of Lymphoid Organs, Budapest (1975).
14. A. H. E. Marshall and R. C. White, Br. J. Exp. Pathol., 42, 379 (1961).
15. H. Wekerle, U.-P. Ketelsen, and M. Ernst, J. Exp. Med., 151, 925 (1980).

GENESIS OF THE GOLGI COMPLEX

M. M. Kalashnikova

UDC 576.311.335

KEY WORDS: Golgi complex; genesis.

The reality of existence of the Golgi complex is no longer in doubt [5, 9, 14, 15], but the problem of its origin has not yet been finally solved. According to one view, elements of the Golgi complex arise from cisternae of the rough endoplasmic reticulum (RER) by budding from the smooth-surface regions of the membranes and conversion into Golgi membranes [10]. The functional continuity between the endoplasmic reticulum and Golgi complex has been demonstrated autoradiographically and histochemically [7, 11]. In studies on lower organisms, the cells of insects, and certain tissues of higher animals, it has been postulated that the Golgi complex originates from the outer nuclear membrane [8, 12, 13]. The object of this investigation was to study the sources of origin of the Golgi complex in cells during ontogeny.

EXPERIMENTAL METHOD

The ultrastructure of hepatocytes of rats during embryonic (daily from the 13th through the 21st days) and postnatal (1, 4, 14, and 30 days after birth) ontogeny, and of chick embryos from the 6th day of incubation until hatching, was studied. Liver tissue was fixed by Palade's method at pH 7.2-7.4 and embedded in Araldite. Ultrathin sections were stained by Reynolds' method and investigated in the HEM-7A electron microscope.

EXPERIMENTAL RESULTS

On the 13th, 14th, and 15th days the Golgi complex in the cytoplasm of the embryonic rat hepatocytes was in the immediate vicinity of the nucleus. On the 13th day of embryonic

Laboratory of Evolutionary Histology, A. N. Severtsov Institute of Evolutionary Morphology and Ecology of Animals, Academy of Sciences of the USSR, Moscow. (Presented by Academician of the Academy of Medical Sciences of the USSR V. I. Struchkov.) Translated from Byulleten' Éksperimental'noi Biologii i Meditsiny, Vol. 92, No. 9, pp. 373-376, September, 1981. Original article submitted March 25, 1981.

 0007-4888/81/9209-1290$07.50

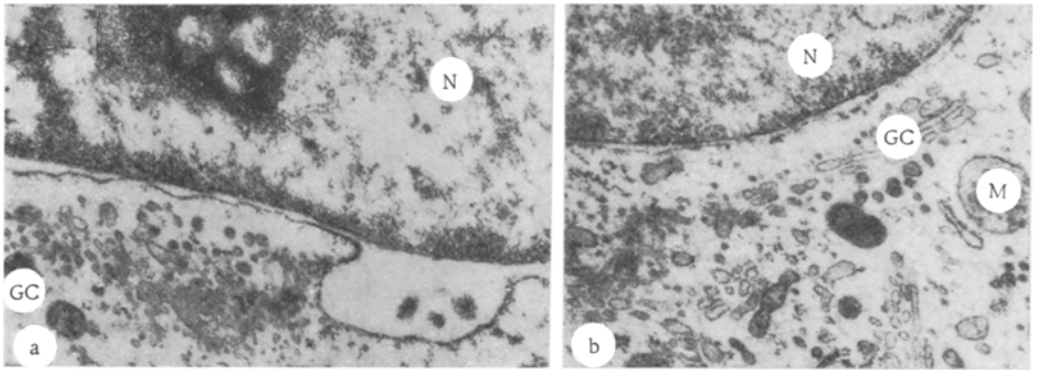

Fig. 1. Ultrastructure of rat hepatocytes on 13th day of embryogenesis: a) budding of vesicles of Golgi complex from outer nuclear membrane, 20,250 ×; b) arrangement of formative surface of Golgi complex facing outer nuclear membrane, 27,000 ×. GC) Golgi complex; N) nucleus.

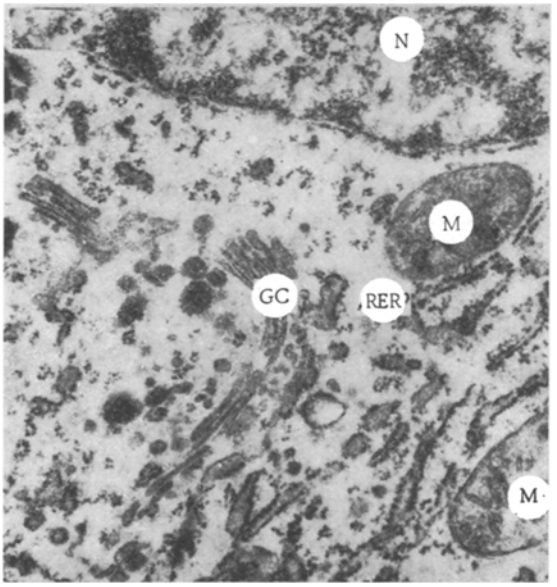

Fig. 2

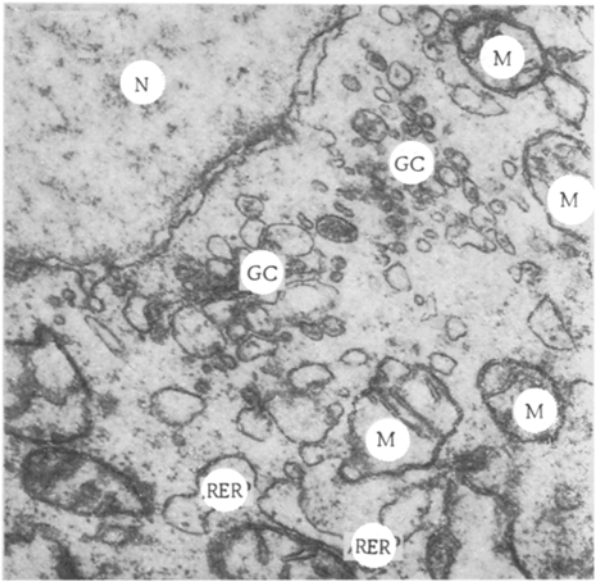

Fig. 3

Fig. 2. Arrangement of formative surface of Golgi complex facing cisternae of RER in cytoplasm of rat hepatocyte on 19th day of embryogenesis. M) Mitochondrion, 27,000 ×.

Fig. 3. Arrangement of Golgi complex in immediate vicinity of outer nuclear membrane in cytoplasm of hepatocyte of 6-day chick embryo, 44,550 ×.

development the perinuclear space could sometimes be seen to be widened in a limited area in the cytoplasm of the hepatocytes. Close to the widened area of the perinuclear space a nucleolus could often be seen. Around the zone of widening there were many vesicles, some of them connected with the outer nuclear membrane, and a number of separate small flat cisternae (Fig. 1a). All these structures formed a Golgi complex. Examination of other electron micrographs showed that the outer nuclear membrane formed a projection into the cytoplasm, and a vesicle formed at its end. In the immediate vicinity there were similar small vesicles in contact with the cisternae of the Golgi complex (Fig. 1b). The formative side of the Golgi complex was on the side of the nucleus, since small vesicles of similar size were located in that zone; flat Golgi cisternae were arranged at a lower level, and on the other side of them, on the mature side, there were vesicles and quite large vacuoles resembling primary lysosomes, with fairly dense homogeneous contents (Fig. 2). It is an interesting fact that the mitochondria and many short cisternae of the RER in this case were more distant from the nucleus than the Golgi complex. The facts described above suggest that the Golgi complex is derived from the outer nuclear membrane. In the later stages of

embryogenesis, on the 19th day for example, the Golgi complex was close to the nucleus, but its formative side in this case faced the cisternae of the RER directly. Small vesicles and large granules with electron-dense homogeneous contents, resembling primary lysosomes, also were present on its mature side (Fig. 2). In the latter stages of embryogenesis and after birth of the young rats it was impossible to differentiate between the mature and the formative sides in the Golgi complex of the hepatocytes. On the 20th and 21st days the ultrastructure of the hepatocytes and bile capillaries was such that it was possible to judge that secretion of bile products into the bile capillary had begun. The Golgi complex was some distance away from the bile capillary. The bile capillaries were dilated, their outlines smooth, with few microvilli, and near the bile capillaries there were swollen mitochondria with a translucent matrix, an irregular outline, and absence of the outer membrane for a certain distance; according to our previous data [2], this is evidence that clasmatosis of mitochondrial fragments is taking place, in connection with their intensive functioning, as sources of energy for the liberation of bile products. On the first day after birth of the animals the Golgi complex in many cells were located near the bile capillaries; moreover, budding of smooth-surface regions from cisternae of the RER toward elements of the Golgi complex could often be seen, i.e., replenishing of elements of the Golgi complex from membranes of the RER. On the 4th day after birth, when the young rats were feeding on their mother's milk, the dimensions of the Golgi complex increased considerably. Cisternae, vacuoles, and vesicles were sharply dilated and contained material of varied density. On the 14th day after birth the Golgi complex remained large in size. On the 30th day the dimensions of the Golgi complex differed in different hepatocytes, an evident indication of the unequal degree of functional activity of the hepatocytes.

A study of the ultrastructure of the Golgi complex in the hepatocytes of chick embryos showed that the Golgi complex was very close to the nucleus only on the 6th day of incubation, separate small vesicles were in close contact with the nuclear membrane, and similar vesicles were located among other elements of the Golgi complex (Fig. 3). Just as in hepatocytes of the 13-day rat embryo, on the 6th day of incubation the Golgi complex in the cytoplasm of the chick embryonic hepatocytes was in the immediate vicinity of the nucleus, and cisternae of the RER and mitochondria were already located beyond it. As a result, it can be postulated that the Golgi complex is formed from the outer nuclear membrane. By contrast with the rat embryo in the early stages of development, during embryogenesis of the chick on the 6th day of incubation it was very difficult to identify the formative and mature surfaces of the Golgi complex. On the 7th day of incubation the Golgi complex increased sharply in size and consisted of flattened cisternae, many tiny vesicles, and large vacuoles arranged in parallel rows. Its morphology and arrangement are evidence that by the 7th day of incubation in individual cells, and on the 9th-10th day in most cells, bile is being secreted into the bile capillary [3], and this continues throughout embryogenesis.

Analysis of the ultrastructure of the Golgi complex during embryogenesis in rats and chicks shows that its dimensions differ considerably. For instance, the Golgi complex in hepatocytes of the rat embryo are represented until birth by all its proper components, but they are very small in size. This, in the writer's opinion, is evidence that synthetic processes of moderate intensity are taking place in the hepatocytes of the rat embryo. Active secretion of bile products into the bile capillary does not begin until the 20th day of embryonic development, and a sharp increase in size of the Golgi complex takes place only after the animal's birth, when the young rat begins to feed on its mother's milk. In hepatocytes of chick embryos at the 7th day of incubation, the Golgi complex is large in size and bile products are secreted into the bile capillary. It can be tentatively suggested that these differences in the size of the Golgi complex and in the times of the beginning of secretion of bile products into the bile capillary in rat and chick embryos are connected with differences in the mode of embryogenesis: In the chick embryo exogenous feeding begins as early as on the 9th day (swallowing amniotic fluid), and this requires secretion of bile into the intestine, and the supplying of the liver by the blood stream, starting with the 7th day of incubation [4], of all the necessary nutrients providing the material basis for the rapid synthesis of bile products. The dimensions of the Golgi complex were thus determined by the level of functional activity of the hepatocyte.

In the cells of certain other organs, as a rule, the formative and mature surfaces of the Golgi complex simply differentiated, and in the hepatocytes this may happen extremely rarely, evidently because of the polyfunctional nature of these cells, as a result of which

the movement of substances liberated from the Golgi complex takes place toward both the biliary and the sinusoidal poles of the hepatocyte.

In the writer's view, the genesis of elements of the Golgi complex from the outer nuclear membrane and, correspondingly, their location near the nucleus in early embryogenesis, are not accidental. The localization of organelles in the cell is known to be determined by their function. It follows from data in the literature that the nuclei can synthesize a specific protein and secrete it into the cytoplasm [1, 6]. It can be tentatively suggested that vesicles of the Golgi complex are formed from the outer nuclear membrane in the early embryonic period because either in the nucleus or in the zone of the nuclear membrane, proteins destined to be secreted into the cytoplasm are synthesized during this period, in the same way that in the later period the protein synthesized and accumulated in the cisternae of the RER enters the vesicles budding from their smooth-surface areas, which later come into contact with the cisternae of the Golgi complex present in the hepatocyte. In early embryogenesis this is evidently connected with the fact that very few cisternae of the RER are yet present in the cytoplasm to synthesize specific proteins.

LITERATURE CITED

1. V. Ya. Brodskii, Cell Nutrition [in Russian], Moscow (1966).
2. M. M. Kalashnikova, Byull. Éksp. Biol. Med., No. 7, 84 (1979).
3. M. M. Kalashnikova, in: Abstracts of Proceedings of the 11th All-Union Conference on Electron Microscopy [in Russian], Tallin, p. 94.
4. V. V. Rol'nik, The Biology of Embryonic Development of Birds [in Russian], Leningrad (1968).
5. H. W. Beams and R. G. Kesse, Int. Rev. Cytol., 23, 209 (1968).
6. W. Bernhard, in: The Cell Nucleus. Morphology, Physiology, Biochemistry [in Russian], Moscow (1972), p. 15.
7. L. Caro and G. E. Palade, J. Cell Biol., 20, 473 (1964).
8. M. Chretien, J. Microscop. (Paris), 14, 55 (1972).
9. A. J. Dalton, in: The Cell, J. Brachet and A. E. Mirsky, eds., Vol. 2, New York (1961), pp. 603-617.
10. E. Essner and A. Novikoff, J. Cell Biol., 15, 289 (1962).
11. D. S. Friend and M. J. Murray, Am. J. Anat., 117, 135 (1965).
12. R. G. Kessel, J. Ultrastruct. Res., 34, 260 (1971).
13. A. Massalski and G. F. Leedale, Br. Phycol. J., 4, 159 (1969).
14. D. J. Morre, H. H. Mollenhauer, and C. E. Bracker, in: Origin and Continuity of Cell Organelles, H. Reinett, ed., Berlin (1971), pp. 82-126.
15. W. G. Whaley, The Golgi Apparatus, Springer, New York (1975).