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Golgi Apparatus and Golgi Zone*

† I. HRŠEL

Institute of Experimental Botany, Czechoslovak Academy of Sciences, Praha**

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Abstract: The author of this paper has attempted to clarify some problems concerning the nomenclature of Golgi apparatus and Golgi zone. The actual aim of this paper is to summarize — while using the more safe nomenclature — the existing knowledge about the functional relations between nucleus and cytoplasm arising from the study of the juxtanuclear zone by electron microscopy. Some observations lead to the assumption that the juxtanuclear zone is the place where cell components are formed or transformed. Considering its temporary character in proliferating cells and taking into account the connections with endoplasmic reticulum and the presence of pores, the nuclear membrane remains apparently a barrier restraining the spontaneous movement of substances and of cell components respectively between cytoplasm and karyoplasm that can be seen e.g. in the grouping of cytoplasmic formations in the juxtanuclear zone. In plant cells, within the zone mentioned agglomerations of different cell formations have been found, either the Golgi apparatus or mitochondria, secretion granules, lipid inclusions, vacuoles or plastids. Such a gathering of cytoplasmic material has been observed especially in young embryonic cells or in cells with retarded or stopped metabolism. The older and/or intensively active cells would then absolve an expansion of the cytoplasmic material into the whole cell. Similar formative mechanisms, now available for study during some ontogenic phases or at definite functional states only, could be effective even in the course of phylogenesis. From this point of view some of the formations described could be regarded as a kind of atavisms.

It has often been observed using a light microscope that in animal cells there is in close proximity of the cell nucleus a region where cytoplasmic formations are agglomerated, among which there are also structures of the Golgi apparatus. Parat (see HIRSCH 1939) called this region the "Golgi zone". He also found there vacuoles, inclusions of fat and other formations. HIRSCH (1939) identifies the Golgi zone with the "Golgi Feld"*** and finds there besides the formations of the Golgi apparatus also mitochondria. The Golgi zone includes in this conception not only the Golgi apparatus structures, but

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** *Last address;* Praha 6 - Dejvice, Flemingovo nám. 2.

*** Further, instead of "Golgi feld" the term "Golgi field" will be used in this paper.

also other formations, situated in the region round the nucleus. Similarly, in plant cells in the so defined Golgi zone different formations were found, which are not part of the Golgi apparatus (HRŠEL 1958, HRŠEL, JURÁKOVÁ, BENEŠ 1960). More recently, however, SJÖSTRAND and HANSON (1954) used in their electron microscopic studies the term Golgi zone for all regions anywhere in the cytoplasm, provided they contain smooth membranes or — as the case may be — vesicles of the electron microscopic Golgi apparatus without any difference whether situated near the nucleus or elsewhere in the cell. In the same way, in the electron microscopy of plant objects the term Golgi zone or Golgi field is used for all regions in the cell containing agranular membranes of the electron microscopic Golgi apparatus, which in this case are revealed as dictyosomes (SITTE 1958, PERNER 1958, DRAWERT and MIX 1961, 1962).

In the above quoted studies the term Golgi zone (Golgi field, Golgi area, Golgi region) has a double meaning which must be distinguished: 1. Golgi zone means the region visible even by light microscope, which is adjacent to the nucleus; this region may contain the components of the electron microscopic Golgi apparatus [and from this point of view it partly corresponds to the conception of Golgi zone according to SJÖSTRAND and HANSON (1954)], but it may also contain all sorts of other formations. 2. SJÖSTRAND and HANSON (1954) designate as the Golgi zone regions at any place of the cell containing components of the electron microscopic Golgi apparatus. According to this conception the Golgi zone must not be adjacent to the nucleus.

By using the term Golgi zone for the region adjacent to the nucleus misunderstandings may arise in cases where it contains formations other than the Golgi apparatus. It will be more appropriate to use for this region the term juxtanuclear zone introduced by BESSIS, BRETON-GORIUS and THIÉRY (1958). The term Golgi zone would hold good especially in electron microscopic studies for regions anywhere in the cell containing the membraneous structures of the Golgi apparatus.

It is the aim of this study to summarize the existing state of knowledge about the relations between the nucleus and cytoplasm reviewing the ultrastructure of the juxtanuclear zone.

1. The juxtanuclear zone from a cytochemical point of view

In this part of his manuscript the author reasoned about the juxtanuclear zone as of the place of intercourse of the karyoplasm with the cytoplasm, or, according to some studies quoted at LINDBERG and ERNSTER (1954), as of a place of formative processes. In this connection the studies by RUTH, MAKINODAN and WOLFE (1957), BENNETT (1956) and LANCE (1958) are quoted further. The author refers to the fact that the karyoplasm is evidently not fully separated from the cytoplasm (see among others WHALEY, MOLLENHAUER and LEECH 1960a,b).

2. Examination of the juxtanuclear zone through a light microscope

The region in the cell where a metabolic connection between nucleus and cytoplasm is assumed was at first examined under a light microscope.

In animal and plant cells different formations behaving differently towards fixatives and to dye solutions were found in the juxtanuclear zone, which

indicates that they are of different character in different cases. Thus a complicated nomenclature originated and often there were long discussions about the definitions of these formations. It was difficult to distinguish such formations under a light microscope, because the methods for their demonstration were not specific enough and the resolving power of the light microscope was sometimes insufficient. There was also the possibility of displacing artificially the formations from the cytoplasm into the perinuclear zone. In animal cells for formations in this region terms were used like archoplasm, mitochondrial body, chondrioplast, periplast, centrosphere, centrosome, Golgi apparatus, Golgi zone etc. (see for instance HRŠEL 1958). The proper nature of these formations was reliably understood only after studying them by electron microscopy. Similar or equal formations were observed in plant cells. Among the cell components which may agglomerate around the nucleus, young vacuoles and plastids are to be considered, too. For instance in the cells of lower plants (*Selaginella*, *Anthoceros*, *Isoetes*, germ cells of *Polytrichum*, some algae) only one or two chloroplasts exist, which are also situated in the juxtanuclear zone and which at cell division move (similarly to the centrioles) to the poles of the spindle. EMBERGER (1921) compares the plastid in *Selaginella* with the mitochondrial body or with the "Nebenkern" of spermatocytes, WEIER (1932) compares the plastid in germ cells of *Polytrichum* with the Golgi apparatus in germ cells of insects, etc.

3. Observation of the relation between nucleus and cytoplasm using the electron microscope

The more detailed understanding of the possible intercourse of the karyoplasm with the cytoplasm often results from an electron microscopic study of the nuclear membrane; this membrane separates the nuclear content from the cytoplasm incompletely. In animal cells the occurrence of pores in the nuclear membrane has been observed (WATSON 1955), which means the occurrence of places with an apparently direct contact of karyoplasm with cytoplasm. In the cells of the salivary glands of *Drosophila*, the production of bladder-like formations was observed, which GAY (1956) regards as the morphological manifestation of the transportation of nuclear material into the cytoplasm. An important phenomenon is the connection of the nuclear membrane with the endoplasmic reticulum (WATSON 1955, PALADE 1955, PORTER 1957).

Under the electron microscope in the cytoplasmic region adjacent to the nucleus in both animal and plant cells various formations were found, suggesting that a mutual action between the nucleus and the cytoplasm takes place here. We shall first consider the animal cells.

The different agglomerations of formations of the endoplasmic reticulum and/or of ergastoplasm at the nucleus were observed in liver cells of a hungry and of a fed rat, which is apparently in connection with the task of the nucleus in the cytoplasmic ribonucleoproteid synthesis (BERNHARD and ROUILLER 1956). A parallelly arranged rough surfaced endoplasmic reticulum can mostly be found in the vicinity of the nucleus (pancreatic cell of a guinea pig, PALADE 1956). Ergastoplasm arranged into formations called "Nebenkern" was very often drawn to the nucleus (HAGUENAU 1958).

The Golgi apparatus in the region of the nucleus has been mostly studied during the formation of germ cells. In *Felis domestica* the Golgi apparatus

in the region closely to the nucleus was studied during the formation of the acrosome (BURGOS and FAWCETT 1955). In the spermatocyte of the house cricket *Acheta domesticus*, the acrosome and the acroblast originating from the Golgi apparatus touch the nucleus (CLAYTON, DEUTSCH and JORDAN-LUKE 1958). In the pond-snail *Cipangopaludina malleata*, the Golgi apparatus is also in the region near the nucleus (YASUZUMI and TANAKA 1958, YASUZUMI, TANAKA, TEZUKA and NAKANO 1959). When studying the Golgi zone of the spermatid of a rat, CLERMONT (1956) found the Golgi apparatus with a developing acrosome system on the surface of the nucleus. In a similar way the Golgi complex was found in the spermatocytes of a guinea pig in close touch with the nucleus (FAWCETT and ITO 1958). In very young oocytes of the sea urchin *Echinus esculentus*, the dictyosomes are near the nucleus (AFZELIUS 1956). The Golgi apparatus can be found in the cap-like region surrounding the nucleus in cells of the gall-bladder epithelium of the mouse (YAMADA 1955). A proof regarding the relation of the Golgi apparatus to the nucleus on the basis of an ultrastructural localization of the nucleosiddiphosphatase is mentioned by NOVIKOFF et al., see HARRIS (1962). In the cells of the Reuber tumor, extensions from the outer nuclear membrane were found to be of smooth membrane type. These extensions are regarded as a sign of the relation of the nuclear membrane to the Golgi apparatus either directly or indirectly over the endoplasmic reticulum, presuming that membranes of the endoplasmic reticulum can pass gradually into membranes of the Golgi apparatus.

The centrosphere or archoplasm is likewise situated in the juxtanuclear zone. In human and laboratory animal leucocytes, in the centrosphere the centriol was found surrounded by dictyosomes (BESSIS, BRETON-GORIUS and THIÉRY 1958).

In differentiating spermatocytes mitochondria were found in the region round the nucleus. Gradually, with the formation of the spermatozoids the mitochondria agglutinate into one or two formations (mitochodrial body, "Nebenkern"*) which are situated in the immediate vicinity of the nucleus. Agglutination of mitochondria was observed by TAHMISIAN, POWERS and DEVIN (1956) in testes of the grasshopper *Lapiatacris dispar*, by CLAYTON DEUTSCH and JORDAN-LUKE (1958) in the house cricket *Acheta domesticus*, by YASUZUMI, FUJIMURA and ISHIDA (1958) in *Drosophila melanogaster*, *D. virilis* and *Gelastorrhinus bicolor* and by YASUZUMI and TANAKA (1958) in the fresh-water pond-snail *Cipangopaludina malleata*.

Relations between nucleus and cytoplasm similar to those existing in the animal cell were also observed in the plant cell.

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* "Nebenkern" was an indistinct term for formations studied under a light microscope. It was established with the aid of the electron microscope that some types of the "Nebenkern" belong to the ergastoplasmic formations as described above, others to the Golgi apparatus, for instance in the case of rat spermatids. Other formations designated "Nebenkern" originated by the fusion of mitochondria (so called mitochodrial body, HAGUENAU 1958, testes of a grasshopper). The "yolk nucleus" of egg cells also belongs to the formations called "Nebenkern". It is built by a concentrically arranged ergastoplasm (the egg cell of the mollusc *Spisula solidissima*, REBHUN 1956). The yolk nucleus of *Lycosidae* and *Thomisidae* spiders is a complex formation containing special corpuscles (capsulated body), Golgi apparatus and endoplasmic reticulum (SOTELO and TRUJILLO-CENÓZ 1957).

The connection between the nuclear membrane and the endoplasmic reticulum was described by LANCE (1957) in the apical cells of *Chrysanthemum segetum*. In these cells, besides the pores there appear vesicular extensions of the nuclear membrane; these extensions communicate with the endoplasmic reticulum (LANCE 1958). Further cases of the connection of the nucleus with the endoplasmic reticulum were found by many authors in other material (WHALEY, MOLLENHAUER and KEPHART 1959, PORTER and MACHADO 1960, MARINOS 1960, MOORE and MCALEAR 1963, BUVAT 1963 and others). WHALEY, MOLLENHAUER and LEECH 1960a,b studied in detail the connections between the nuclear membrane and the endoplasmic reticulum in the apical cells of *Zea mays* primary root tips. Besides the simple connection of the nuclear membrane and the endoplasmic reticulum these authors found different cases, such as, for instance, a circularly arranged extension of the nuclear membrane into the cytoplasm. There was an extension of the nuclear membrane orientated towards the inside of the nucleus. In some cases broad gaps in the nuclear membrane were also observed, whose size much exceeded the diameter of the pores (WHALEY, MOLLENHAUER and LEECH 1960a, b). In cells of the fungus *Neobulgaria pura* a disintegration of the nuclear membrane was observed; this membrane is apparently regenerated later on (MOORE and MCALEAR 1963). At the differentiation of gametes in fungus *Allomyces macrogyrum* an agglomeration of the ribosomes was observed around the nucleus in a so-called paranuclear body (BLONDEL and TURIAN 1960, PREVOST-MONNOT 1960). Ergastoplasmic "Nebenkern" of the same appearance as in the animal cell, bipolarly placed near the nucleus, were found subsequently to an experimental anoxia in the meristematic root cells of *Hyacinthus orientalis* (GAVANDAN, POUSSEL and GUYOT 1960). Similarly anoxia caused formations connected with the nuclear membrane WRISCHER (1960) found in the root meristem of *Sinapis alba*.

Near the nuclear membrane vacuoles were also observed. By electron microscopy a characteristic central vacuole adjacent to the nucleus was found in the yeast *Saccharomyces cerevisiae* (AGAR and DOUGLAS 1957, HASHIMOTO, CONTI and NAYLOR 1958). The vacuole here is not part of the nucleus, as assumed by some authors. POUX (1962) mentions the possibility of a relation of the vacuoles to the nucleus in higher plants, but admits that this is a rare case. On her micrographs POUX 1961, 1962 recorded vacuoles in the proximity of the nucleus in some cells of young leaves of *Anthoxanthum odoratum* and *Dactylis glomerata* (POUX 1961 Fig. 7, POUX 1962 Planche I, II, IIIa, VIa). ESAU (1963) draws attention to the closeness of the vacuole and the nucleus in the root meristem of *Vitis vinifera*. The present author found in the root meristem of *Fagopyrum* the juxtanuclear position of light and dark vacuoles by both light and electron microscopy. The vacuoles are mostly originated near the nucleus bipolarly from small primordia. The tonoplast of the central vacuoles, which are visible, was often observed quite close to the nuclear membrane.

A closer relation of the Golgi apparatus to the nucleus in the plant cell was not always observed. BUVAT (1958) studied the Golgi apparatus in the root meristem of *Allium cepa*, *Triticum sativum*, *Phajus Wallchii*, *Lens culinaris*, in the apex of *Chrysanthemum segetum* and *Elodea canadensis*.

He states that, concerning the Golgi apparatus there is a difference between the animal and the plant cell: the Golgi apparatus of the animal cell is situated near the nucleus, whereas in the plant cell the dictyosomes are spread all over the cytoplasm. PERNER (1958) did not find in the root meristem of *Zea mays*, *Cucurbita pepo* and *Trianea begotensis* a striking agglomeration of dictyosomes near the nuclear membrane either. Nor did SITTE (1958) observe in the root meristem of *Pisum sativum* the position of the Golgi apparatus round the nucleus as a regular phenomenon. When studying the alga *Micrasterias rotata*, DRAWERT and MIX (1962) compared the structures of living cells as seen using a light microscope with fixed cells observed by an electron microscope. They found that the corpuscles described as "karyoids" using the light microscope correspond to the dictyosomes observed by the electron microscope. They are often agglomerated in the region near the nucleus (DRAWERT and MIX 1961/1962). The authors explain this phenomenon saying that the nucleus and the chloroplasts are obstacles restraining the free movement of the dictyosomes within the living cell. Otherwise they did not observe a nearer relation of the dictyosomes to the nucleus (DRAWERT and MIX 1961). HEITZ (1957) determined in the apex of *Antirrhinum majus* an agglomeration of dictyosomes near the nucleus. MANTON (1960) observed in the spore mother cell of *Anthoceros* relations between the dictyosomes, the new nuclear membrane and the endoplasmic reticulum before the onset of meiosis. The possibility of a neoformation of dictyosomes and mitochondria from the so-called neocytoplasm which is gathered round the nucleus of the coenocytic proembryo of *Pinus laricio*, is discussed by CAMEFORT (1961). A close relation between the Golgi apparatus and the nuclear membrane has been observed in the alga *Pediastrum biradiatum* (MONER and CHAPMAN 1960). In cells of *Dictyota dichotoma* (*Phaeophyceae*) dictyosomes in an apparently active state (BERKALOFF 1962) were found in the proximity of nuclear membranes. In the apothecia of fungus *Neobulgaria pura* dictyosomes were found in connection with the nuclear membrane and the origin of the dictyosomes from the nuclear membrane is thus assumed (MOORE and MCALEAR 1963). In *Volvocaceae* and *Astrephomenaceae*, a juxtanuclear position of dictyosomes was found (LANG 1963). Identically located are the dictyosomes in *Diatomaceae* (DRUM 1963, DRUM and PANKRATZ 1964a, b) and in the brown alga *Laminaria hyperborea* (SCHNEPF 1963).

WHALEY, MOLLENHAUER and LEECH (1960a) found mitochondria and plastids agglomerated at those places where the nuclear membrane shows discontinuities. WILSENACH (1963) found in meristematic cells of *Anthoceros* a young plastid closely adhering to the nucleus at a place where the nuclear membrane was enormously perforated. WEIER (1963) observed in cells of young leaves of *Vicia*, extensions of nuclear membranes passing between the adjacent plastids. MÜHLETHALER and BELL (1962) found in archegonium of *Pteridium aquilinum* the separation of sacculiform formations from the nucleus. After separation these formations pass into the cytoplasm and are according to the authors the primary forms of mitochondria and plastids. In the algae *Ochromonas danica* and others, the endoplasmic reticulum, forming a closed envelope around the chloroplasts, communicates with the nuclear membrane (GIBBS 1962). Morphologically, a relation between the

plastid and the nucleus was observed in cells of the root apical meristem of *Isoetes Howellii* (PAOLILLO 1962). The relation between the nucleus and the cytoplasmic formations in the plant cell is discussed by WEIER (1963).

4. The juxtanuclear zone in plant cells during ontogenesis and at different physiological states

In higher plant cells the gathering of cytoplasmic material near the nucleus was observed mainly in embryonic cells. Later, during differentiation, an expansion of this material into the surrounding cytoplasm takes place. Dark vacuoles in the youngest cells of the root meristem of *Fagopyrum* are also first formed in the neighbourhood of the nucleus. Then they spread over the whole cytoplasm. In a similar way the light vacuoles are also formed mostly near the nucleus. PAS positive material behaves in the same way in *Fagopyrum* (HRŠEL, JURÁKOVÁ and BENEŠ, 1960) and *Echinochloa* (HRŠEL, unpublished results). But in some animal and higher plant cells the cytoplasmic material remains in the form of compact formations all the time adhering to the nucleus (acrosome and mitochondrial body of spermatocytes). In lower plants, containing one or two plastids, the plastids remain near the nucleus.

The agglomeration of cytoplasmic material in the juxtanuclear zone occurs also in cells, where the metabolic processes are strongly slowed down or stopped. At an excitation the cytoplasmic material expands into the whole cell. O'BRIEN (1951) found in young cells of the scutellum of *Triticum* and *Secale* young proplastids in the so-called aggregate, which adhere to the nucleus and contains dense cytoplasm. In older cells the plastids expand into the whole cytoplasm. This presupposes the influence of the nucleus on the aggregate. The observation of young wheat embryos before dehydration of the seed in the period of milk maturity (HRŠEL, unpublished results) also showed, that plastids in the third leaf are normally differentiated and distributed throughout the cell. In the dry embryo, however, these plastids gather into one or two compact formations which can be strongly coloured by hematoxylin and which mostly adhere to the nucleus. Cells with such formations thus resemble cells containing one or two plastids only (*Anthoceros*, *Selaginella* and others). During germination under certain experimental conditions (temperature 0° C, exstirpated embryos) the formations disunite into single plastids which still remain agglomerated into one whole and only after some days expand into the whole cytoplasm. Under the usual conditions for germination this expansion is quick and, therefore, hardly noticeable. The agglomeration of plastids in the region of the nucleus and their expansion was also observed in the cells of the apex of *Peperomia* and elsewhere.

5. Phylogenic view on the juxtanuclear zone of plant cells.

The author considers in this part of his work the relationship between the juxtanuclearly localized formations in the cells of higher plants, which in some cases can be observed in certain phases of the ontogenesis or in some extreme situations and between the distribution of cytoplasmic components in cells of lower plants. Agglomerations of plastids for instance, visible under some extreme conditions in higher plants, thus appear as a kind of atavism — taking into account the few or single large plastids of algae — and the way of formation and disintegration of such agglomerations could be identical to or analogous with the mechanisms active in phylogenesis.

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† I. HRŠEL, Ústav experimentální botaniky ČSAV, Praha: **Golgiho aparát a Golgiho zóna.** — Biol. Plant. **9** : 157—167, 1967.

Autor se v této práci nejprve pokouší objasnit některé terminologické problémy z okruhu Golgiho aparátu a Golgiho zóny. Vlastním cílem této práce je shrnout s použitím bezpečnější nomenklatury stávající znalosti o funkčních vztazích mezi jádrem a cytoplasmou vyplývající z elektronmikroskopického studia juxtanukleární zóny. Některá pozorování vedou k domněnce, že juxtanukleární zóna je místem, kde se utvářejí nebo transformují buněčné složky. Přes její dočasný charakter v proliferujících buňkách a přes souvislost s endoplasmatickým reticulem a přítomnost pórů zůstává jaderná blána zřejmě překážkou bránící spontánnímu pohybu látek, příp. buněčných složek mezi cytoplasmou a jádrem, což se mj. projevuje hromaděním cytoplasmatických útvarů v juxtanukleární zóně. U rostlinných buněk bylo v uvedené zóně zjištěno nahromadění různých buněčných útvarů, ať už to byl Golgiho aparát, mitochondrie, sekreční granula, lipidové inkluse, vakuoly, plastidy. Takovéto soustředění cytoplasmatického materiálu bylo pozorováno především u mladých, embryonálních buněk, a dále u buněk se zpomaleným nebo zastaveným metabolismem. Buňky starší, resp. intensivně činné by pak absolvovaly expansi cytoplasmatického materiálu do celé buňky. Podobné utvářecí mechanismy, které lze nyní studovat jen v určitých obdobích ontogenese nebo za jistých funkčních stavů, mohly se uplatňovat během fylogenese. Některé z popsaných útvarů lze tedy považovat za jakési atavismy.

† И. Гршел, Институт экспериментальной ботаники ЧСАН, Прага: **Аппарат Гольджи и зона Гольджи.** — Biol. Plant. 9 : 157—167, 1967.

Автор сперва занимается некоторыми терминологическими вопросами имеющими отношение к аппарату Гольджи и зоне Гольджи. Собственная цель работы — суммировать с применением более разработанной номенклатуры имеющиеся в настоящее время данные о функциональных отношениях между ядром и цитоплазмой, полученные при электронмикроскопическом изучении юкстануклеарной зоны. Некоторые наблюдения приводят к предположению, что именно эта зона является тем местом, где формируются или трансформируются компоненты клетки. Ядерная оболочка, несмотря на ее временный характер в пролиферующих клетках, связь с эндоплазматическим ретикулом и присутствие порбостается, очевидно, преградой, препятствующей свободному движению веществ или образований между цитоплазмой и ядром, следствием чего является также скопление цитоплазматических образований в юкстануклеарной зоне. В растительных клетках было действительно в этой зоне установлено накопление различных клеточных образований, таких как аппарат Гольджи, митохондрий, выделительные гранулы, липидные включения, пластиды. Скопление цитоплазматических структур было найдено прежде всего у молодых, эмбриональных клеток а также у клеток с замедленным или остановленным обменом. У более взрослых и очень жизнедеятельных клеток цитоплазматические образования, по этому представлению, распространяются в остальные части клетки. Подобные процессы формирования, которые в настоящее время можно изучать лишь в определенные периоды онтогенеза или при некоторых функциональных состояниях могли иметь большее значение в филогенезе. Некоторые из описанных образований можно таким образом считать атавизмами.