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REVIEWS

Development of Cytology at the Institute of Microbiology, Russian Academy of Sciences (1934–2004)

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Cytological investigations of microorganisms have been the main line of research carried out at the Laboratory of Microbiology, USSR Academy of Sciences (1930–1934), headed by Academician G.A. Nadson, and at the Institute of Microbiology, USSR Academy of Sciences (INMI), founded on the basis of this laboratory in 1934. Within this line of research, morphology, fine structure, modes of reproduction, and developmental cycles of microbial cells were investigated and concepts of microbial evolution and classification were developed. The preference given by Nadson and his colleagues to this research line is obvious and justified: facing the enormous variety of microscopic creatures, researchers endeavored first of all to understand the nature, origin, evolution, and variability of microorganisms and their position in the system of the known kingdoms of the organic world. On the background of extremely scant information concerning the biochemical composition and physiology of microbial cells, cytological investigations performed in the 1920s and 1930s were really at the front of biology and played a role similar to that currently played by molecular biology. The discovery and description of cellular structures, organelles, and organoids (nuclei, chromosomes, cell walls, membranes, vacuoles, mitochondria, etc.) initiated the emergence of new large branches of biology.

Nadson promoted in every way the development of cytological investigations at INMI and encouraged works in which the achievements in various fields of microbiology were illustrated with microscopic examinations of the subjects of study. This becomes evident after getting familiar with the works of Nadson and his pupils collected in the two-volume *Selected Works* published in 1967 and devoted to the hundredth anniversary of Nadson's birth [1]. The extensive list of references given there allows us to not cite them in this review. Even brief acquaintance with the works of this eminent scholar and talented researcher endowed with the gift of prevision amazes the reader with the width of the sphere of Nadson's activity, the high level of his erudition, and his aspiration for a comprehensive approach to the solution of various microbiological problems.

By the time of the organization of INMI, the investigations by Nadson and his pupils had laid the groundwork for microbiological science; many ideas and approaches that were put forward by Nadson remain topical today.

Cytological and morphological investigations have been traditional at INMI; major contributions to the development of cytology were made by Nadson's pupils, future doctors of science, corresponding members of the Academy of Sciences, and academicians, A.A. Imshenetskii, M.N. Meisel', N.A. Krasil'nikov, V.I. Kudryavtsev, A.E. Kriss, Ya.I. Rautenshtein, and others, who later became classics of national science.

The personality of Nadson as a scholar was formed in his student years under the influence of the eminent plant physiologist A.S. Famintsin, head of the Department of Botany at St. Petersburg University, who considered lower algae to be excellent objects for the solution of many important problems of microbiology and physiology. Nadson developed the ideas of his teacher and focused his attention on the elucidation of relationships between the physiology of the studied microorganisms and their specific and generic features, morphology, developmental cycle, fine structure, biochemistry of metabolism, and ecology. Generalization of the obtained results allowed Nadson to develop important concepts concerning symbiotic and antagonistic interrelations between organisms, functions of morphological structures, taxonomy, evolution, and geological activity of microorganisms; these concepts formed the basis for further investigations at various departments of INMI.

Nadson paid great attention to the taxonomy of microorganisms and to isolation and description of new species of algae, fungi, yeasts, and bacteria. These studies initiated the research into the taxonomy of yeasts under the leadership of Kudryavtsev and the taxonomy of bacteria and actinomycetes under the guidance of Krasil'nikov; the obtained results were summarized in determination manuals of these groups of microorganisms. It should be noted that the morphological features and fine structure of microbial cells were at that time

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and remain now highly important for the description of novel microbial species and genera.

Later, a great number of new species of microorganisms were isolated from various ecological niches due to the efforts of soil and water microbiologists, ecologists, geochemists, and other specialists, which initiated the organization of the All-Union Collection of Microorganisms (VKM) at INMI, where it successfully developed for a long time; then, it was transferred under the jurisdiction of the Institute of Biochemistry and Physiology of Microorganisms, Russian Academy of Sciences (Pushchino). At present, intensive work on the isolation of new microorganisms is being continued at INMI. The line of research encouraged by Nadson 70 years ago is gathering force due to the efforts of many departments and laboratories, particularly those headed by Academicians G.A. Zavarzin and M.V. Ivanov, Corresponding Members of the Russian Academy of Sciences G.I. Karavaiko and V.F. Gal'chenko, Prof. V.M. Gorlenko, Dr. D.I. Nikitin, Dr. E.A. Bonch-Osmolovskaya, and others.

A leading role in the development of cytological investigations at INMI was fulfilled by Meisel'; he was involved in this field of research when a student and then a postgraduate under the guidance of Nadson. The most promising studies were concerned with the effect of various extreme factors on microbial cells, which was accompanied by structural and functional intracellular reorganizations. The most striking changes were observed in yeast cells, which were later chosen by Meisel' as the main objects of his investigations. It should be noted that Nadson always emphasized the importance of the choice of research object.

The outstanding works on the effect of radium rays on biological objects started in 1924 by Nadson and G.S. Filippov and later joined by Meisel' became classics in the field of radiobiology and radiogenetics. Most of the publications related to this research line are collected in volume 2 of Nadson's *Selected Works* [1]; these works were the first to present experimental evidence for the mutagenic effect of radiation on biological objects (yeasts in particular). Radiobiological investigations, in spite of their importance, constituted only a part of the research activity of Meisel' in the earlier period of his work at INMI. His scope of scientific interests (much like Nadson's) was very wide [2]. At that time, Meisel' revealed the structural and morphological reorganizations in yeast cells in response to cell transition from aerobic to anaerobic metabolism. His works in the field of microbial vitaminology made a great contribution to the development of fundamental science and found practical application; the concepts of hyper- and hypovitaminosis were formulated. Based on investigations of the cytology and physiology of yeasts grown under vitamin imbalance, new rapid methods for the production of thiamine, riboflavin, inositol, and ergosterol were developed. The major results of these studies were summarized by Meisel' in his doctoral dissertation and in the monograph *Functional Morphology of Yeasts* [3].

In the 1950s and 1960s, Meisel' headed the Department of Functional Cytology of Microorganisms and continued investigations on the effect of ionizing radiation on microbial cells; the necessity of this research was dictated by the rising nuclear potential in the world and intensification of research on the application of nuclear energy for civil purposes. The application of functional and morphological approaches to radiobiological investigations allowed Meisel' and coworkers to obtain new important data on the mechanism of the radiation effect. Much success was achieved in the determination of the radiosensitivity of cellular structures and functional systems and viability of irradiated cells; the reasons for the retardation of the reproduction of irradiated yeast cells were established; reactions, including pathological, of the cytoplasm, nuclei, mitochondria, and cell walls in response to irradiation were studied. Cytological studies were accompanied by biochemical analyses that made it possible to elucidate the fine mechanisms of biochemical processes involved in oxidative phosphorylation, the tricarboxylic acid cycle, amination, and metabolism of nucleic acids and sterols [4–8]. A special series of investigations was devoted to the elucidation of mechanisms responsible for the reactivation of yeast cells damaged by ionizing radiation and radiomimetic chemical agents [6, 9]. The results of the fundamental investigations on the effect of radiation on microbial cells found considerable practical application. In particular, the stimulation of sterol synthesis in yeasts by irradiation was used for the development of a process for industrial production of ergosterol. The data obtained on the effect of high doses of radiation on the viability of bacteria were used to devise methods of radiosterilization [5, 7].

In the 1960s and 1970s, a large series of studies on the pathways and mechanisms of utilization of hydrophobic compounds (higher fatty acids, alcohols, and *n*-alkanes) by yeasts was carried out under the leadership of Meisel'. By using electron microscopic and fluorescent methods, it was revealed that these compounds penetrate into the periplasmic space through the system of pores in the yeast cell wall and are then transported into the cell, where they undergo oxidative conversions [10–12].

Of special importance were the investigations concerned with the assimilation and degradation by yeast and bacterial cells of carcinogenic polycyclic hydrocarbons, which are constituents of some oil fractions, coking coals, car exhausts, emissions of railway transport, tobacco smoke, etc. Meisel' was interested in this problem in his young years, but these investigations were continued at a higher methodical level only in the 1970s. By using electron and fluorescence microscopy, the cytological mechanisms involved in the accumulation of benzo(a)pyrene (which displays fluorescence under UV light) and its localization in free and bound

lipids of yeast and bacterial cells were established [13–16]. Quantitative characteristics of the degradation of this highly carcinogenic hydrocarbon by bacteria isolated from wastewater and soil of a coke-gas plant were determined [15, 16].

Meisel' and his collaborators (specialists in various fields of science—cytologists, biochemists, physiologists, and biophysicists) achieved much success in the development of fundamental problems of cytology and microbiology; this is evident from the list of their experimental articles [3–16], reviews [17–19, 26], and numerous reports made both in our country and abroad. The list of references is certainly not full; however, it shows how much was done to gain insight into the structural organization of yeast cells—the structure of the cell walls, nuclei, mitochondria, vacuolar apparatus, ribosomal system, Golgi apparatus, lysosomes, and peroxisomes, as well as into the structure of bacterial cells, particularly their nuclear apparatus [20].

The considerable advances made by Meisel' and his coworkers are mainly due to his constant interest in the development of microscopic and cytological methods of research and to his active participation in the organization of industrial production of microscopic equipment in our country. Meisel' emphasized the great role of Academicians D.S. Rozhdestvenskii (the founder of the State Optical Institute), S.I. Vavilov, I.V. Grebenshchikov, V.P. Linnik, and other prominent scholars and designers in providing a research and organizational basis for the development of this industry. Owing to their efforts, over 20 different types of microscopes and a great deal of facilities were produced in the USSR in 1953. Publications of Meisel' contained detailed information concerning microscopic equipment modern for that time [21, 22] and promoted its employment in laboratory practice. However, Meisel' put his high hopes on the development and wide application in our country of fluorescence microscopy and made much effort for that.

In 1945, Meisel' brought from Austria a fluorescence microscope and a small kit of dyes that allowed him to perform first experiments. These investigations initiated active employment of fluorescence microscopy in the research practice at INMI and other research and educational institutions of the USSR. In collaboration with the prominent physicist E.M. Brumberg, who at that time worked at the State Optical Institute, Meisel' laid the groundwork for the industrial production of microscopic equipment at the Leningrad Optico–Mechanical Enterprise (LOMO) [23]. Meisel' contributed a great deal to organization of the production in the USSR of fluorescent dyes and indicators and to the development of new methods for the determination of viability of yeast and bacterial cells [7, 24] and cytochemical determination of proteins and nucleic acids [25–27], lipids [28, 29], and other cellular components [30–32].

Meisel' is justly considered to be the initiator, leader, and founder of fluorescence microscopy in our country. A great contribution to the development and application of fluorescence microscopy was made by G.A. Medvedeva, one of the first pupils of Meisel', a skilled microscopist, cytologist, and highly qualified specialist, who was involved in all research carried out under the leadership of Meisel' and trained many microbiologists in the methods of luminescence microscopy [5–12, 18, 19, 30].

Further elaboration, improvement, and application at INMI of cytochemical methods, including quantitative methods of fluorescence microscopy, was provided for by M.N. Poglazova. Many of her works have been recognized and awarded with prizes at the annual competitions at INMI and found wide application at many research institutions [33–36]. An original method developed by Poglazova for the determination of the number of fluorochrome-stained bacteria directly in water suspensions was published in the journal *Microbiological Methods* by request of the editorial board [37].

Dwelling upon important milestones in the development of cytology at INMI, we must mention the research activity of M.A. Peshkov, a distinguished cytologist and unexcelled microscopist, who made a great contribution to the development of cytology in our country and exerted a profound influence on the scientific ideology of microbiologists at INMI.

The research interest of Peshkov was mainly focused on investigation of the structures of microbial cells, development of various methods for their staining, and application of special methods of light microscopy [38]. He managed perfectly phase-contrast, anoptral, dark-field, and other types of light microscopy; moreover, he constructed special objectives that allow a high-quality image of cells without aureoles to be obtained. To observe the behavior of microbial cells in dynamics, Peshkov developed a special E-type chamber (Peshkov's chamber), which has been widely applied by many generations of microbiologists for both photomicrography and film shooting.

Peshkov paid particular attention to the investigation of the structural organization of nucleoids in bacteria. This problem was actively discussed at the end of the 1930s and in the 1940s and 1950s in both the Russian and foreign literature and at conferences at INMI. The main concepts of the day on the structure of the nuclear apparatus in bacteria were summarized by Meisel' [20], Peshkov [38], and Imshenetskii [39].

A great contribution to the development of cytology at INMI was made by A.E. Kriss, who headed the Department of Marine Microbiology and founded a laboratory of electron microscopy at the Division of Biological Sciences, USSR Academy of Sciences, at the end of the 1940s, which promoted the application of electron microscopic methods to studies of the ultrastructural organization of microorganisms. V.I. Biryuzova started her scientific career as a researcher at Kriss's laboratory; she was the first to master the methods of electron microscopy and became a skilled cytologist, a repre-

sentative of the research schools of Peshkov and Kriss. At the department headed by Meisel', Biryuzova made great strides towards the elucidation of the fine structure of prokaryotic and eukaryotic microorganisms [8, 9, 18, 19, 40]. Later, Biryuzova created her own school of cytologists and promoted wide application of electron microscopy not only at INMI but also at other research institutions. She always used the current methods of electron microscopy, including techniques of preparing ultrathin sections, specimens of various cellular structures (nuclei, mitochondria, cell walls), and cell cryofractures. Biryuzova developed the concept of heterogeneity of the membrane structures (mesosomes) in bacteria [41]. The major achievements of Biryuzova were summarized in her doctoral dissertation and the monographs *Membranous Structures of Microorganisms* [42] and *An Atlas of the Ultrastructural Organization of the Yeast Cell* [43].

The main line of research at the department headed by Meisel' was devoted to the elucidation of the relationship between the structure and functions of cells under various physiologically normal and extreme conditions. In this connection, not only the effect of ionizing radiation, radiomimetic chemical agents, and other unfavorable factors on the structural and functional organization of cells was studied, as mentioned above [4–8, 10–16], but researches were also concerned with the influence of factors promoting the transition of microorganisms into the resting (anabiotic) state, as, for example, under the action of some antibiotics, antiseptics, and other antimetabolites or dehydration [40, 44, 45]. The pioneering studies along this line, aimed at investigating anabiosis in yeast cells, were performed by I.M. Nadirova under the guidance of Meisel' and summarized in her candidate's dissertation and a number of experimental papers [46]. These basic researches were continued by Meisel's pupil A.I. Rapoport, who was the first to get important data on the ultrastructural changes and molecular mechanisms responsible for the dehydration and rehydration of yeast cells [47].

By using various methods of fluorescence microscopy, Poglazova, in collaboration with S.S. Abyzov and I.N. Mitskevich, for the first time characterized microorganisms that, due to their transition to the anabiotic state, survived for many hundred thousand years within the ice at the Central Antarctic [48–50]. In this field of research, where the microbiology of our country occupies leading positions, the employment of the methods of fluorescence microscopy is of cardinal importance; these methods allowed novel data on the cell number, morphological diversity, and viability of microorganisms in the ice thickness of the Antarctic to be obtained (Fig. 1). These findings attracted much attention from Russian and foreign researchers [51, 52].

A somewhat different line of research concerning microbial anabiosis was carried out at the Laboratory of Cytology of Microorganisms, founded in 1986 and headed by V.I. Duda; the attention was focused on the structural and functional organization of resting forms of bacteria, such as endospores, cysts, and cystlike cells. The major achievements recognized both in Russia and abroad are outlined below.

(1) The phenomenon of polysporogenesis in bacteria was described. It has been proved experimentally that a single bacterial cell may form up to five to seven spores (Fig. 2), which are similar to endospores of bacteria in their structure, composition, and physiological properties [53–55]. The results of these investigations made it possible to change a concept that had prevailed in microbiology for more than a hundred years and according to which endogenous sporulation was considered to be a way of cell preservation not related to the reproduction process in bacteria. The phenomenon of polysporogenesis was described due to the isolation in a pure culture of the novel anaerobic bacterium *Anaerobacter polyendosporus* gen. et spec. nov. in 1985; the detailed study of this bacterium opened up new horizons in both cytological research and the genetics of sporulation.

(2) The concept was developed of a special type of resting forms of cells that provide for the survival of non-spore-forming bacteria under superprolonged anabiosis in extreme natural biotopes. These forms, designated as cystlike resting cells (CLC), possess a number of peculiar characteristics typical of specialized resting cells [56, 57]. Recent detailed ultrastructural investigations carried out at INMI (the group headed by G.I. El'-Registan) and at the Institute of Biochemistry and Physiology of Microorganisms, Russian Academy of Sciences (the laboratory headed by Duda) revealed that structural transformations that occur during the transition of vegetative cells into CLC in non-spore-forming bacteria (micrococci, arthrobacters, pseudomonads) are complex and systemic and involve changes in the envelopes (cell walls, capsules) (Fig. 3), cytoplasmic membrane, cytoplasm, and nucleoid. A great number of CLC similar in their ultrastructural organization were revealed in the permafrost of Eastern Siberia and in tundra soils. The observed peculiarities of CLC with respect to their morphology, ultrastructural organization, and physiological properties indicate that a constitutive resting stage is typical of non-spore-forming bacteria [58]. The results obtained are of importance for solving the problem of the resting state of non-spore-forming microorganisms; they made it possible to explain the reasons and mechanisms for prolonged preservation of non-spore-forming microorganisms under extreme natural conditions.

(3) New cellular structures of bacteria were described, such as appendages and gas caps on spores and extracellular gas balloons (EGBs). In recent years, special attention has been given to the ultrastructural organization, composition, and functions of EGBs. It was found that EGBs have a thin membranelike wall, which differs from a typical biological membrane in its structure and composition; it holds air but is watertight [59–61]. EGBs are

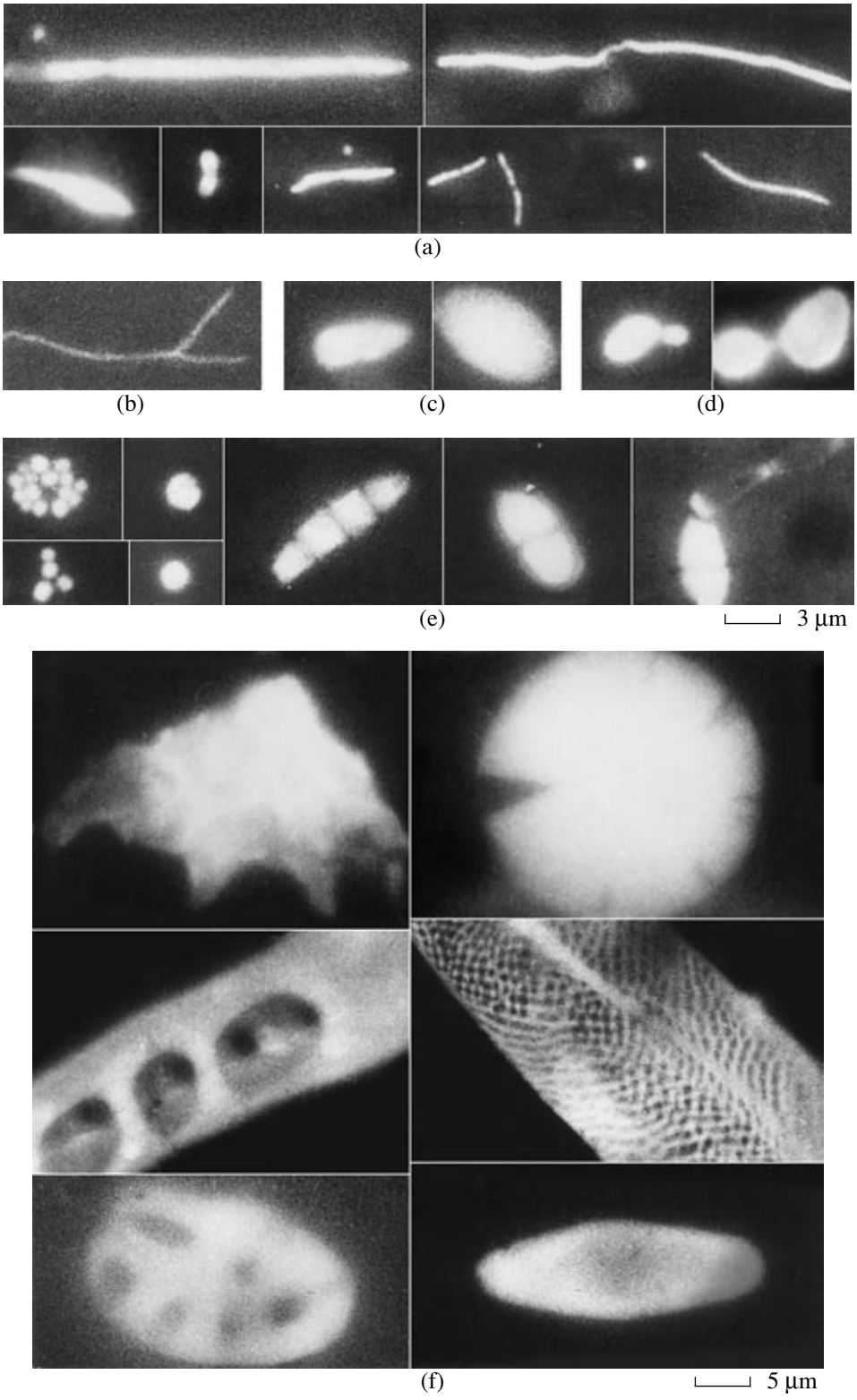

Fig. 1. Prokaryotic and eukaryotic microorganisms from different horizons of the ice sheet in the Central Antarctic, trapped on membrane filters, stained with fluorescamine, and viewed under a luminescence microscope: (a) bacteria; (b) actinomycetes; (c) cyanobacteria; (d) yeasts; (e) conidia of mycelial fungi of different genera: *Penicillium, Mucor, Fusarium, Trichotecium*, etc.; (f) unicellular microalgae.

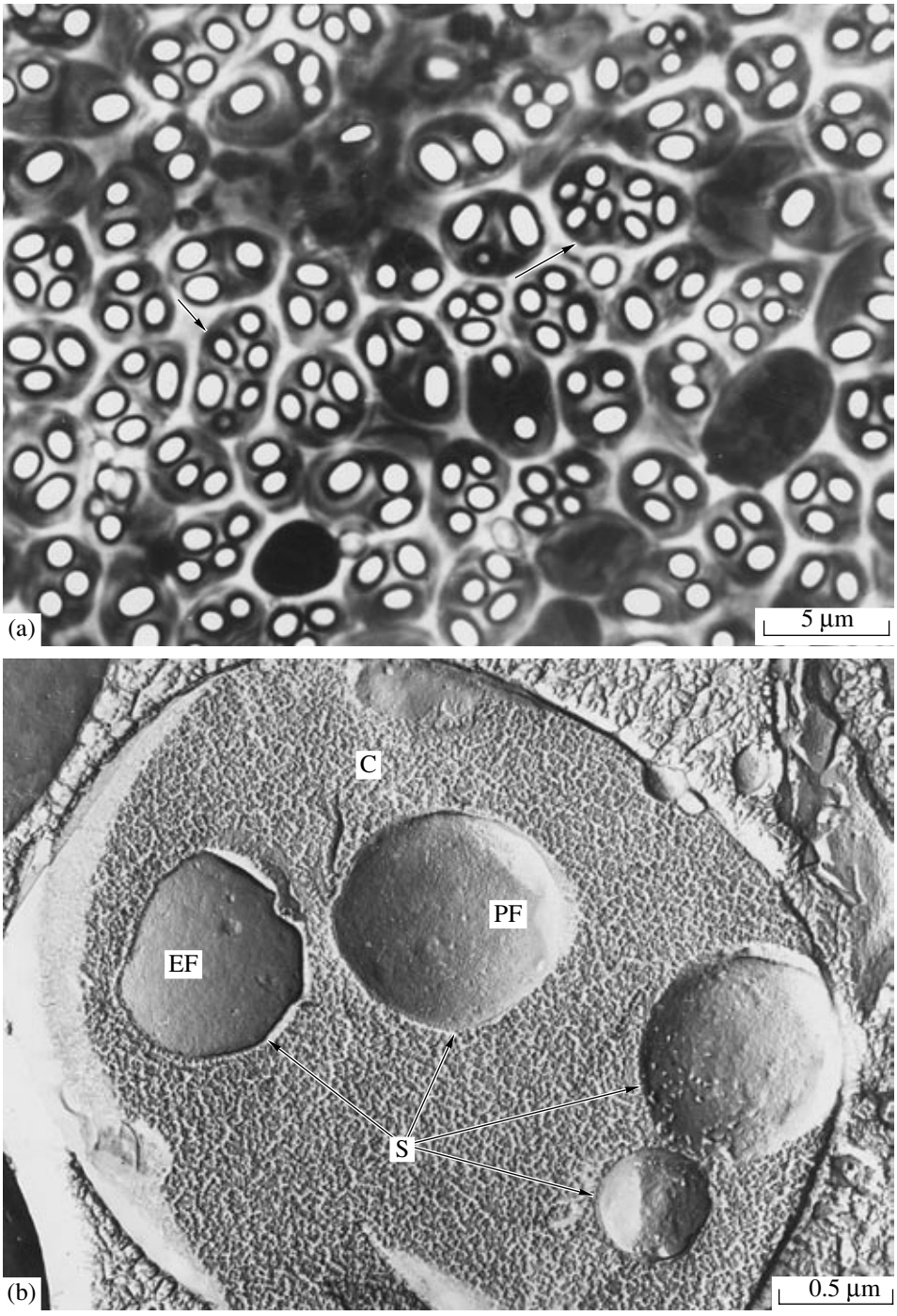

Fig. 2. Sporulating cells of *Anaerobacter polyendosporus* strain PS-1: (a) living culture under a phase-contrast microscope (arrows indicate sporangia with six or seven spores) and (b) cross cryofracture of a sporangium containing four spores. S, spore; PF, protoplasmic face of the fracture of the internal membrane of a spore; EF, exocellular face of the fracture of the internal membrane of a spore; C, cytoplasm [53–55].

tightly attached to the cell walls of individual cells or their aggregates, promoting cell buoyancy. In colonies of some bacteria, EGBs form air-conducting channels, which improve aeration of the colonies (Fig. 4). These findings extend our knowledge of the diversity in the structural and functional organization of prokaryotes and have provided a closer insight into the biology of the bacterial cell.

(4) Peculiarities in the ultrastructural organization of a great number of new forms of microorganisms (at the level of novel taxa) isolated and investigated at

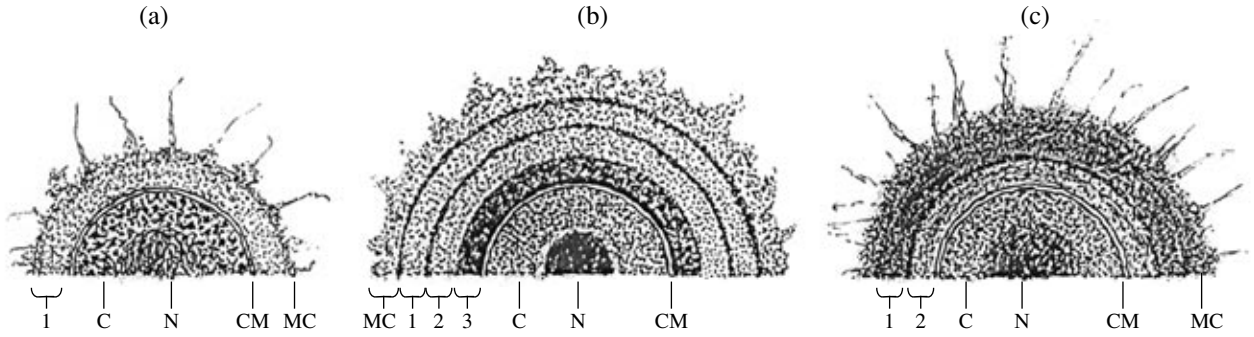

Fig. 3. Scheme of the surface structures of resting cystlike cells (CLC) of micrococci based on electron microscopic examinations: (a) cell of a 3-day culture; (b) CLC of a 9-month culture; (c) CLC of a 14-day culture supplemented with C_6-alkyl hydroxybenzene. Numerals designate the cell wall layers; C, cytoplasm; MC, microcapsule; CM, cytoplasmic membrane; N, nucleoid [58].

different laboratories of INMI and other institutions were characterized by researchers of the Laboratory of Cytology of Microorganisms; this provided for a high level of publications (in Russian and foreign journals) concerned with the description of new forms of microorganisms.

It should be noted that important cytological studies of undoubted priority have been carried out not only at the specialized cytological laboratories, but practically at all other laboratories of INMI; they involved a wide spectrum of poorly known, rare, and new forms of microorganisms and were concerned with the important problem of the structural and functional organization of microbial cells (the description of all the achievements at these laboratories is impossible within the limits of this paper).

However, the important role of a specialized cytological laboratory is evident; the functions of such a laboratory involve not only performing its own complicated studies but also participation in joint interlaboratorial studies, providing methodical help to researchers from other laboratories, the mastering and elaboration of new cytological methods, and training of skilled specialists in cytology. It is noteworthy that current cytological investigations are highly complicated and require costly equipment, e.g., a setup for cryofracturing, and the application of advanced methods of cytochemistry and molecular biology. The employment of a confocal laser microscope and flow cytometry is of special importance for the solution of a number of problems in microbiology.

Although molecular biological and genetic laboratories are now also involved in developing the cytology of microorganisms, the number of questions and problems to be solved at the cellular or ultrastructural levels is proliferating considerably, which can be explained by two reasons. Firstly, the description of a great number of novel forms of microorganisms is in progress, which calls for the characterization of ultrastructural peculiarities of these objects; these studies often result not only in the description of new cell morphotypes but also in the discovery of radically novel cellular structures. Thus, the study of sulfobacilli isolated at the Laboratory of Chemolithotrophic Microorganisms (headed by Karavaiko) and a polysporogenic anaerobic bacterium isolated at the Laboratory of Cytology of Microorganisms (headed by Duda) brought about the discovery of a new type of membranous structures designated as lamellar intramembrane lipid structures [62, 63] (Fig. 5). Similar examples were given above (see items 1–3 above). Secondly, in recent years, much attention has been given to the study of the composition, structure, and functioning of microbial communities in situ. This initiated a new line of research, molecular ecology, which is based on the application of fluorescence microscopy and methods of molecular biology (PCR and FISH) for the identification of microorganisms in situ. Of importance also is the employment of the methods and approaches of present-day high-resolution transmission electron microscopy. As early as in the

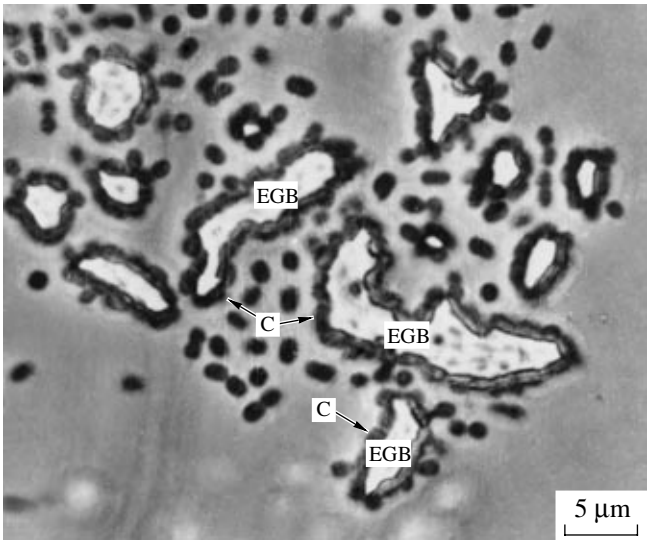

Fig. 4. Extracellular gas balloons (EGBs) in a colony of *Alcaligenes* sp. strain d_2 (a preparation of live cells under a phase-contrast microscope). Layers of cells attached to the EGBs can be seen. C, cells.

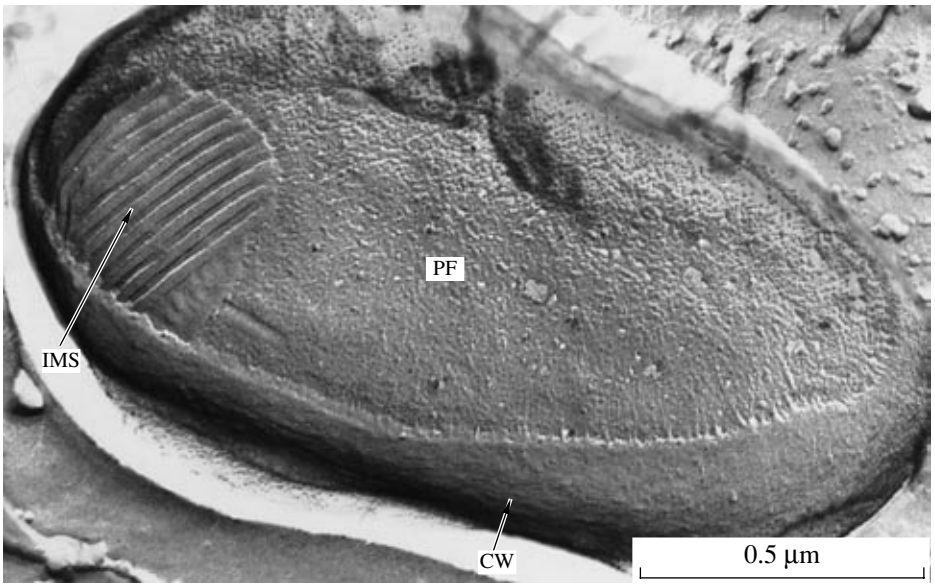

Fig. 5. Electron micrograph of a cryofracture of a cell of *Sulfobacillus thermosulfidooxidans* strain VKM B-1269. Intramembrane structures (IMS) in the form of wrinkled lipidic leaflets are arranged at a protoplasmic face (PF) of the cytoplasmic membrane fracture [63].

early 1960s, D.I. Nikitin and his collaborators were the first to use transmission electron microscopy for the examination of intact microbial cells in natural substrates [64, 65]. These studies were recognized in both the Russian and the foreign literature and resulted in the discovery of several new forms of microorganisms. Further development of this line of research will be apparently concerned with the employment of methods of high-resolution electron microscopy such as cryofractography and the use of ultrathin sections (including cryosections) in combination with the methods of electron cytochemistry, X-ray microanalysis, and molecular biology. The currently available methods for the fractionation of microbial cells from natural substrates are also of essential importance. Realization of the described approaches and methods will allow data to be obtained on the ultrastructural and molecular organization, composition, and metabolic activity of microbial cells in situ, i.e., in natural substrates.

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