J Ind Microbiol Biotechnol (2010) 37:1227–1239
DOI 10.1007/s10295-010-0859-6

ORIGINAL PAPER

General and molecular microbiology and microbial genetics in the IM CAS

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Received: 2 July 2010 / Accepted: 20 August 2010
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Abstract This review summarizes the main results obtained in the fields of general and molecular microbiology and microbial genetics at the Institute of Microbiology of the Academy of Sciences of the Czech Republic (AS CR) [formerly Czechoslovak Academy of Sciences (CAS)] over more than 50 years. Contribution of the founder of the Institute, academician Ivan Málek, to the introduction of these topics into the scientific program of the Institute of Microbiology and to further development of these studies is also included.

Keywords Academy of Sciences of the Czech Republic · Institute of Microbiology · Ivan Málek · Molecular microbiology · Microbial genetics

Introduction

The Institute of Microbiology of the Czechoslovak Academy of Sciences (CAS) was founded as an independent institute in 1962. However, its basis, the Department of Microbiology of the Institute of Biology CAS, was established by academician Ivan Málek 10 years earlier, in 1952. Ivan Málek, as the main organizer of microbiological research in Czechoslovakia, deeply supported structuralization of this department from the beginning, to ensure covering various fields of microbiology and their effective studies by individual groups of qualified scientists.

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The personal scientific interest of Ivan Málek was focused mainly on the development of methods of continuous cultivations of microorganisms, which was at that time within the Group of General Microbiology. The pioneering role of Ivan Málek in the development and use of continuous cultivations of microorganisms is the subject of another review in this memorial volume [117], therefore, I do not focus on this topic in the present review. Sporulation of bacilli as a model of cell differentiation and studies of bacterial proteolytic enzymes were the other topics studied intensively by the original Group of General Microbiology.

The basic genetic studies of bacteria started within the original Department of Microbiology in the Group of Variability of Microorganisms (remember that the word "Genetics" was taboo in Czechoslovakia in the early 1950s!). The pathogenic mycobacteria and pneumococci were used as model bacteria by this group.

General microbiology and bacterial genetics at the Institute of Microbiology during the Ivan Málek's period (1952–1969)

The basic research on physiology and genetics of microorganisms was supported by Ivan Málek since the founding of the Department of Microbiology of the Institute of Biology CAS in 1952. Establishing the independent Institute of Microbiology CAS in 1962 as well as the more free atmosphere in Czechoslovakia in the early 1960s, which allowed more intensive contacts of Czech scientists with those in Western countries including working stays in top world laboratories, were great stimuli for further development of this research.

General microbiology

Ivan Málek was deeply interested in problems of differentiation of microorganisms [123]. The mechanisms of sporulation of bacilli were therefore studied in detail during that time at the Department of General Microbiology of the Institute of Microbiology using mainly *Bacillus cereus* as a model bacterium. The content of sulphur amino acids (especially cystine) in spores of bacilli [222] and resistance of *B. cereus* spores to X-rays and heat [223] were analyzed in the early studies. The systematic analysis of effects of various factors on the process of sporulation in *B. cereus* [224–228] finally led to the discovery of the entirely new phenomenon of "microcycle sporogenesis". The microcycle sporogenesis was defined as direct transition of outgrowing bacterial spores to new sporangia without intermediate cell division [229] and it was further studied intensively by other groups abroad [65, 121, 192].

The processes of subcellular (biochemical) differentiation of a bacterial cell were also studied intensively at the Department of General Microbiology using mainly *Bacillus megaterium* as a model bacterium. This included studies of regulation of proteolytic enzymes during growth of bacterial cultures [18, 19, 22, 23, 25, 40] and of processes of cell wall turnover [20, 21, 24, 26]. The different effects of individual amino acids on formation of *B. megaterium* protease [25] and complete repression of megateriopeptidase by simultaneous presence of glucose and amino acids [27] were observed during those studies. The results obtained by J. Chaloupka's group in 1962 [20, 21] brought the first evidence of cell wall turnover in bacteria and the mechanisms of degradation and turnover of cell wall mucopeptides during *B. megaterium* life cycle were further studied in detail [26, 27]. Since that time, turnover of cell walls was described and analyzed in many bacterial species (For review see [41]).

The scientists of the Department of General Microbiology also studied regulation of *Escherichia coli* β-galactosidase synthesis [84, 197] and contributed to the knowledge of the role of cyclic AMP in catabolic repression in bacteria. J. Janeček took part in the pioneering work which proved that *Escherichia coli* mutants resistant to catabolic repression have defects in degradation of cyclic AMP [142, 182].

Bacterial genetics

The study of mechanisms of genetic transformation in pneumocci was the main scientific interest of the newly established Department of Microbial Genetics and Variability of the Institute of Microbiology CAS. The importance of monovalent cations in transformation of pneumocci was proved in the early studies [92]. The effects of various factors on efficiency of pneumoccal transformation [93, 95] as well as the kinetics of penetration of transforming DNA into pneumococcal cells [94] have been intensively studied since that time. The isolation and purification of a substance inducing competence of pneumococcal cells was the most important result obtained [96]. The transformation and transfection of *Bacillus subtilis* cells [186, 198, 201, 202] as well as the transduction of *Salmonella typhimurium* [72–75] were also studied.

Ivan Málek had a great personal interest in studies of mycobacteria. The factors influencing growth of *Mycobacterium tuberculosis* in blood and serum of normal and immunized rabbits were analyzed in the early studies [70, 71]. The main scientific interest of I. Málek's group was later focused on genetic analyses of mycobacteria using nonpathogenic *Mycobacterium phlei* as a model bacterium. The conditions of *M. phlei* mutagenesis were analyzed in detail [99–106, 108, 180] as well as the characteristics of individual mutants [98, 107, 109, 185]. The mechanisms of biosynthesis of *M. phlei* carotenoid pigments were also studied in detail [58–60, 97].

General and molecular microbiology and bacterial genetics at the Institute of Microbiology during the "normalization" period (1970–1989)

In 1969, Ivan Málek was forced, due to his publicly announced rejection of Soviet occupation of Czechoslovakia, to leave not only the post of the director of the Institute of Microbiology CAS but also his employment in the institute. Even his visits to the Institute of Microbiology were forbidden by the new communist authorities from that time on. The scientific contacts with laboratories abroad was very limited in this "normalization" period. Nevertheless, the scientific work on topics already studied as well as on newly introduced topics continued. The Laboratory of Electron Microscopy was included into the Department of General Microbiology. In 1976, a large Department of Molecular Biology and Genetics was formed by joining the Department of General Microbiology and Department of Bacterial Genetics.

General and molecular microbiology

The studies of proteolytic enzymes and the mechanisms of macromolecule turnover in bacteria continued intensively in this period. The mechanisms of regulation of protease synthesis in *Bacillus megaterium* were revealed [36, 37, 143]. The studies on mechanisms of turnover of cell wall mucopeptide in *B. megaterium* [28, 31] were extended to the analogous analyses in *E. coli* [29, 32]. The kinetics of

intracellular protein turnover in *B. megaterium* was studied in detail as well [30, 33–35, 38].

The effects of cyclic AMP on various cellular processes in *E. coli* was studied in detail [85, 86]. It was found that an inverse correlation between extracellular concentration of cyclic AMP and intensity of catabolic repression exists [146].

Analysis of various aspects of protein biosynthesis in streptomycetes was the new topic introduced into the Department of Molecular Biology and Genetics of the Institute of Microbiology. The elongation factor Tu from *Streptomyces aureofaciens* [242, 243] and from S*treptomyces collinus* [130] were characterized in detail. The ribosomal proteins of streptomycetes and their role in protein biosynthesis were intensively studied [129, 131–133]. The fine structure of *Streptomyces aureofaciens* mycelia [120] as well as their ribosomes [128] were analyzed by the Group of Electron Microscopy.

Bacterial genetics

The optimization of conditions of *Mycobacterium phlei* mutagenesis [110] provided a large collection of mutants. The method of sequential mutagenesis of the replication point by nitrosoguanidine was applied to synchronized cultures of *M. phlei* and used for determination of replication positions of the genes on *M. phlei* chromosome (i.e., for construction of the replication map) [111].

The detailed analysis of bacterial plasmids became the main scientific interest of the Department of Bacterial Genetics of the Institute of Microbiology. In the beginning, the plasmids from *E. coli* were studied and the focus was on understanding the mechanisms of resistance to streptomycin encoded by R-plasmids [12] as well as on analysis of structure of derivatives of R-plasmid R1*drd19* [11]. The plasmid R485 conferring resistance to sulphonamides was also characterized in detail [62]. Searching for agents capable to eliminate plasmids from bacterial cells [187] resulted in finding the new effective curing agent clorobiocin [17]. The association of plasmid DNA with cytoplasmic membrane was analyzed [61] and the mutants of plasmid R6K with increased number of plasmid copies in a cell were isolated and characterized [147, 148]. The new method for estimation of the number of plasmid copies in a bacterial cell was developed [63]. The new plasmid pMI10 was also isolated from the *B. subtilis* strain producing α-amylase and characterized [203].

J. Hubáček took part in the original studies characterizing the type I restriction-modification system in *E. coli* [76] and introduced this topic into the Department of Bacterial Genetics. The various temperature-sensitive mutations within the *hsd* genes, coding for subunits of *E. coli* restriction-modification complex, were isolated and characterized in detail [77–80].

The practically important amino acid-producing corynebacteria became the new model studied intensively in the late 1980s at the Department of Bacterial Genetics. The bacteriophage-like particles were isolated from *Corynebacterium glutamicum* and analyzed with an electron microscope [168]. The new bactriocin-like substance, glutamicin CBII, was isolated from the same *C. glutamicum* strain and characterized [169]. New plasmid vectors for gene cloning in corynebacteria were constructed [171] and used for transfer of heterologous genes involved in threonine biosynthesis into *C. glutamicum* [170].

Methylotrophic bacteria were the other new model microorganisms studied at the Department of Bacterial Genetics during that period. The methods of genetic transfers for Gram-negative methylotrophs were developed [67] and plasmid vectors replicating in these bacteria were constructed [171].

Molecular microbiology and microbial genetics at the Institute of Microbiology since 1990

The great changes in the Czechoslovak society after the “Velvet Revolution” in 1989 also included substantial changes in the organization of Czechoslovakian science. The grant system was established and funding of science based on competition of grant projects became gradually the main way of support of science. The structure of the Institute of Microbiology CAS also changed. Instead of 11 scientific departments, six larger units, the divisions, were founded. The Division of Molecular Biology and Genetics, which was later (in 1993) renamed to the Division of Cell and Molecular Microbiology, has been one of them (in 1993, due to the splitting of Czechoslovakia into the Czech Republic and the Slovak Republic, the Czechoslovak Academy of Sciences was also renamed to the Academy of Sciences of the Czech Republic). In addition to the groups working on various bacteria including streptomycetes, two groups studying yeasts were included in the Division of Cell and Molecular Microbiology. Renewal of the international scientific contacts, which had been interrupted forcefully in the 1970s, and their extensive growth, were the main advantages of the new period. Many young scientists from the Institute of Microbiology AS CR spent several years on working stays in the top laboratories abroad and they brought new modern topics into the institute. They founded new laboratories whose work profited from the continued cooperation with the laboratories abroad. The work of many laboratories has been co-funded from international grants. This trend was especially increased after the Czech Republic joined the European

Union in May 2004. All these activities would be undoubtedly appreciated very much by Ivan Málek, who, as a director of the Institute of Microbiology, always generously supported the international contacts of the scientists from the institute even in the less favorable conditions of the early 1960s.

The research became more interdisciplinary. Therefore, this chapter has not been divided into subchapters Molecular microbiology and Microbial genetics, since this distinguishing would be rather artificial. Instead, subchapters describing studies on individual groups of microorganisms are parts of this chapter.

Studies on bacilli and *Escherichia coli*

The effects of heat stress on the regulation of synthesis and activity of proteolytic enzymes, especially the Ca^{2+}-dependent serine proteinase [114, 207] as well as on processes of sporulation [113, 190], were studied intensively in *Bacillus megaterium.*

The studies of type I restriction-modification systems of *E. coli*, proceeding in cooperation with Portsmouth University (UK), continued by isolation and detailed characterization of novel mutants in the individual subunits of these complexes [88, 244–246, 251, 252]. Localization of the individual subunits of type I restriction-modification complexes within the *E. coli* cell was defined [68], and differences between cellular localization of complexes classified into IA, IB, and IC families, respectively, were proved by immunoblotting techniques [69]. The structural analysis of the restriction-modification enzymes (in cooperation with Bristol University, UK) resulted in the construction of a structural model of DNA methyltransferase M.EcoR124I in complex with DNA [153] and in defining the nuclease motif in restriction endonuclease EcoR124I [195]. The role of the interrelationship of helicase and nuclease domains during DNA translocation by the molecular motor EcoR124I was proved [196]. The type I restriction-modification system from the commensal *E. coli* strain A0 34/86 (O83:K24:H31) was also characterized [247]. The genome of this *E. coli* strain A0 34/86, used as a live vaccine, was analyzed in detail [54] and its safer variant was constructed [191].

Studies on streptomycetes

Various aspects of metabolism and differentiation in streptomycetes were intensively studied at the Division of Cell and Molecular Microbiology. These studies included characterization of proteosynthetic apparatus of streptomycetes. The initiation and elongation factors were especially studied in detail [83, 134]. The Fts family of proteins involved in differentiation processes were analyzed in *Streptomyces collinus* producing kirromycin [138, 250]. The main scientific interest was focused on the analysis of the role of protein phosphorylation in metabolism and differentiation in streptomycetes. These studies started with isolation and characterization of protein kinases from streptomycetes [87, 135, 145, 238] and with the analysis of phosphoprotein patterns during differentiation of *S. collinus* [135]. The involvement of protein kinase in ribosome function in this kirromycin-producing strain [139] as well as in differentiation processes in *S. granaticolor* [140] and *S. coelicolor* [165] was characterized. The global analysis of effects of various stresses on metabolism and differentiation of streptomycetes was performed using transcriptomic and proteomic approaches. Developmental control of the stress stimulon was characterized [231] and the role of stress-induced proteins in diauxic lag in *S. coelicolor* was revealed [152]. Expression patterns of proteins during germination of aerial spores in *S. granaticolor* were also characterized in detail [10]. The role of cold-shock proteins in regulation of gene expression in tetracycline-producing *S. aureofaciens* was demonstrated [137]. Searching for the transfer-messenger RNA (tmRNA), which possesses both tRNA and mRNA properties and plays an essential role in recycling of ribosomes stalled on defective mRNA due to its ability to be translated and to facilitate the degradation of aberrant mRNA, in various strains of streptomycetes [164] represented the novel topic studied. Association of specific proteins to the tmRNA was found during development and differentiation of *S. aureofaciens* [141].

Studies on corynebacteria and rhodococci

The indigenous plasmids of amino acid-producing corynebacteria were studied in detail. Analysis of the replication mechanisms of plasmid pGA1 from *Corynebacterium glutamicum* revealed novel proteins positively regulating plasmid copy number and segregational stability [149, 217, 218]. The first case of complete class 1 integron in Gram-positive bacteria was described in plasmid pCG4 from *C. glutamicum* [150]. The novel plasmid pCC1 from *Corynebacterium callunae* was characterized and used for vector construction [219].

The studies of gene expression and its control in *C. glutamicum* started with detailed characterization of genes involved in biosynthesis of leucine [173] and with both global [172] and detailed [215] analyses of structure and function of *C. glutamicum* promoters using the newly constructed promoter-probe vectors [214]. The function of *C. glutamicum* promoters in heterologous hosts was proved [174] and the *C. glutamicum* consensus promoter sequences were defined [175]. In addition to the vegetative promoters, *C. glutamicum* promoters induced by heat shock were also characterized [4]. The knowledge of *C. glutamicum*

consensus promoter sequences served as a basis for their purposeful site-directed mutagenesis. The mutant promoters were used for construction of *C. glutamicum* strains producing increased amounts of pantothenate [81] and valine [64]. The valine-producing *C. glutamicum* mutant with feedback-resistant acetohydroxy acid synthase was also constructed [43]. These practically important results were obtained during the work on the international project "VALPAN" funded by the European Union. The first case of small regulatory antisense RNA in *C. glutamicum* was also described. This non-coding ArnA RNA positively regulates the expression of the *gntR2* gene coding for transcriptional regulator of GntR family, which negatively controls expression of genes involved in glucose uptake and gluconate catabolism [249].

The plasmids from corynebacteria were used for development of a host-vector system for related rhodococci which are practically important biodegraders of various pollutants in the environment [220] and for construction of the promoter-probe vectors applied for analysis of promoters of rhodococci [91]. These vectors were used for analysis of *catRABC* operon involved in catechol degradation in phenol-degrading *Rhodococcus erythropolis* [221]. The bacterial chlorobenzoate degraders isolated form contaminated soils in the Czech Republic were also characterized [13, 176]. Metagenomic approaches revealed abundance of *meta*-cleavage pathways of aromatic degradation in microbial communities from soil highly contaminated with jet fuel [14].

Studies on yeasts

The Laboratory of Cell Biology focused its work mainly on analysis of functions of yeast plasma membrane. Effects of external factors on membrane fluidity were studied in both *Saccharomyces cerevisiae* and *Schizosaccharomyces pombe* [48] and receptors for *S. cerevisiae* killer toxin were analyzed in detail [115, 116]. The novel time-resolved fluorescence method for measuring membrane potential was developed and used for analysis of the effects of oxidative stress and heavy metals on yeast membrane energization and transport functions [3, 46, 47, 178]. Inactivation of the plasma membrane H^+-ATPase by oxidative damage was proved [66, 193, 216]. The activities of xenobiotic-exporting multidrug resistance (MDR) pumps were studied in *S. cerevisiae* under various growth conditions [15, 55, 122].

The amino acid transporters in *S. cerevisiae* membrane were intensively studied in cooperation with Regensburg University (Germany) using reconstituted plasma membrane vesicles as experimental tool. Unidirectionality of arginine transport in *S. cerevisiae* was confirmed using this approach [154, 156]. Effects of antibiotic nystatin on transport processes were analyzed in detail [155] and mechanisms of regulation of activity of specific arginine carrier protein CAN1 was revealed [157]. The effects of phospholipids on integral yeast plasma membrane proteins were studied [183]. The phosphatidyl ethanolamine-less strain of *S. cerevisiae* was constructed [184] and it was found that phosphatidyl ethanolamine is essential for targeting the arginine transporter CAN1 to plasma membrane [158]. These results have been prerequisites for detailed analysis of the function of lipid rafts (microdomains enriched in sterols and sphingolipids) in yeast plasma membrane. Use of the fusion membrane proteins differentially labeled with green or red fluorescent markers made it possible to prove differences in distribution of individual proteins in yeast plasma membrane [124, 125]. The existence of at least two stable compartments in yeast plasma membrane [49, 159] and the key role of membrane potential changes on lateral segregation of plasma membrane proteins and lipids [50] were demonstrated. The plasma membrane microdomains were found to regulate turnover of transport proteins in yeasts [51].

The mechanisms of yeast cell aging, especially the role of the RAS2 protein in these processes [57, 177], were studied in detail using the centrifugal elutriation technique. The influence of oxidative stress on aging of *S. cerevisiae* cells was proved [1, 118]. Yeast colonies were studied as a model of organized multicellular structures. The role of transcription factor Sok2p in the long-term survival of *S. cerevisiae* colonies was demonstrated [208]. The mechanisms of regulation of cell death in yeast colonies by ammonia were analyzed in detail [209]. The control of expression of *ATO* genes (coding for ammonium exporters) by ammonia and localization of Ato proteins in plasma membrane were proved [181]. Metabolic diversification of cells during development of yeast colonies [16, 211] and formation of colony architecture [210, 239] were studied in detail.

Analysis of yeast cytoplasmic microtubules was another topic studied in the Division of Cell and Molecular Microbiology. The new *S. cerevisiae* gene *ISW2* was found to code for a microtubule-interacting protein involved in control of cell morphology [205, 206]. The *S. cerevisiae* strain lacking Isw2 showed activation of the cell wall integrity pathway [45]. The large subunit of translation initiation factor 3 (eIF3), the Rpg1p protein, was found to interact with microtubules [112] and was studied in detail [53, 212, 213]. Accumulation of translation initiation factors into cytoplasmic aggregates (stress granules) were observed for the first time in *S. cerevisiae* cells after robust heat shock [52]. The mechanisms of interactions of N-terminal domain of *S. cerevisiae* eIF3a subunit with 40S ribosomal subunit were revealed and their involvement in the translation initiation process was suggested [199].

Studies on pathogenic bacteria

Molecular biology of bacterial pathogens became the new topic studied intensively in the Division of Cell and Molecular Microbiology after P. Šebo had returned from his long-term stay in the Institut Pasteur (Paris, France) and had founded the new laboratory within the division. The whooping cough agent *Bordetella pertussis* has been the original model bacterium studied in this laboratory and scientific work has been focused predominantly on detailed analysis of structure and function of its adenylate cyclase toxin (ACT). The role of posttranslational fatty-acylation in biological activities of *B. pertussis* ACT [5, 6, 127] and the mechanisms of ACT translocation across cellular membranes [163] were revealed. Using the collection of ACT mutants selectively blocked in distinct steps of toxin action enabled dissection of the complex mechanism of ACT toxicity into individual enzymatic and channel-forming activities [42]. Binding of calcium to the ACT molecule was proved to cause its functional switching [90]. Membrane restructuring by ACT penetration into lipid bilayer was observed [126] and correlation between the pore-forming activity and capacity of ACT to form oligomers in cell membrane was documented [8, 9, 237]. The novel activity of *B. pertussis* ACT, promoting the calcium influx into monocytes due to membrane translocation of AC domain, was proved [44] and the mechanism of recognition of β_2 integrin receptors by ACT was revealed [144]. The role of ACT in rearrangements of actin cytoskeleton was also demonstrated [89].

In collaboration with the Cellular Immunology Group of Institut Pasteur, the use of modified *B. pertussis* ACT as a novel non-replicative vector, capable of delivering passenger antigens into dendritic cells and inducing the specific immune response against pathogenic microorganisms, viruses, and tumors, was tested [119, 160, 194]. The genetically detoxified ACT derivatives (dACT toxoids) carrying mycobacterial antigens not only induced T-lymphocyte responses against *Mycobacterium tuberculosis* [39, 56, 248] but also served as a novel tool for rapid diagnosis of latent tuberculosis infections [2]. The dACT toxoids delivering antigens of *Plasmodium berghei* were shown to be a potent vaccine against malaria in mouse model [200].

Neisseria meningitidis is the other model bacterium that has been studied at the Laboratory of Molecular Biology of Bacterial Pathogens. Detailed analyses of *N. meningitidis* genes regulated by iron level [7] and of structure and function of the FrpC protein found in all tested clinical isolates [161, 162, 179] were performed. The self-processing FrpC activity was used for affinity purification of recombinant antigens [188].

A new signaling pathway, in which serine/threonine protein kinase had been involved, was demonstrated in *Streptococcus pneumoniae* [151, 166] and in *Streptococcus mutans* [82]. The *S. pneumoniae* genes regulated by the serine/threonine protein kinase StkP were identified by transcriptomic analysis [189].

Bioinformatics

The bioinformatical approaches were used mainly for analysis of proteomes obtained in different developmental stages of *Streptomyces coelicolor* [230, 235, 236]. A mathematical model of kinetics of transcription and translation using artificial neural networks to model the dynamics of gene expression was also developed [232, 234] and tested on the bacteriophage lysis/lysogeny decision circuit [233]. This model was employed for prediction of transcriptional regulators and their target genes and applied to analysis of microarray cell cycle data obtained in *Saccharomyces cerevisiae* [240, 241] and for gene expression profiling in *Streptomyces coelicolor* [204]. Biocomputational approaches were also used for prediction of small non-coding RNAs in streptomycetes [167]. The newly formed Laboratory of Bioinformatics also hosts the developmental proteomic databases of streptomycetes and *Caulobacter* (http://proteom.biomed.cas.cz).

Outlook

The results obtained recently in the individual laboratories of the Division of Cell and Molecular Microbiology of the Institute of Microbiology ASCR provide a good basis for further development of studies on molecular biology and genetics of microorganisms in future. The many grant-supported projects go on and the cooperation with the top laboratories abroad as well as with Czech universities and institutes of applied research and biotechnological companies continues. All these efforts can be considered as fulfillment of the academician Ivan Málek's legacy, who founded the Institute of Microbiology as an institution studying a broad range of perspective fields of microbiology and generously supported all scientific activities and cooperations.

Acknowledgments This work was done within the Institutional Research Concept No. AV0Z50200510.

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