

Boris Vasilievich Gromov (1933–2001): a microbiologist for all seasons

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This issue of *Protistology* commemorates the 20th anniversary of premature decease of Boris Vasilievich Gromov, Professor, Corresponding member of the Russian Academy of Sciences who had been the head of the Microbiology Department of St. Petersburg/Leningrad State University over a long time, as well as the head of Microbiology laboratory at Biology Institute of the same University. The issue includes a series of articles by Gromov's former students, colleagues and successors from the present staff of the Microbiology Department; these reports refer, in a varying degree, to Gromov's most important investigations and discoveries.

The heading of this introductory note is aimed to characterize *in toto* Gromov's significance for bioscience, and his personality. Indeed, he was a unique individual – at least among compatriot colleagues – as a microbiologist *sensu lato*. Thus, amazingly, he with equal success studied bacteria, protists, microscopic algae, microscopic fungi, and viruses. The absence of archaea among his research objects was not due to a lack of interest in these prokaryotes; by various reasons he was unable to sample them (as in the case of extreme halophiles and thermoacidophiles), or his laboratory was not equipped for culturing obligate anaerobes (as in the case of methanogens). Gromov's universality did not signify that he studied microbes indiscriminately. Rather, he went venturing to undiscovered and underexplored areas, and often became a pioneer.

Gromov's works can be evaluated best in historical context. The second half of XX century was

Boris Gromov in summer 1999 (watching cyanobacterial bloom ashore Gulf of Finland).

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an epoch when biochemistry tested life functions in fractionated material, and electron microscopy described fixed objects architecture. Hence, there was a general prevalence of reductionism and descriptive analysis. Besides, molecular genetics was far from routine use and second-generation microscopy *in situ* was only sporadically employed. Gromov's keeping to the scientific mainstream was combined with his ability to embody brightly the transition from classical microbiology to the microbiology of XXI century. His later works, mostly in English, were conducted in line with modern ideas and progressing methods.

Here, the aim was to review briefly Gromov's scientific heritage. His bibliography from 1957 to 2001 includes a total of 133 articles, 32 of which are in English, as well as three monographs and two manuals (see References). Not too many for a large team leader, albeit one should take into account that he did not impute his name to someone other's works, and manuscripts with his co-authorship always implied direct participation. Despite some of his discoveries were made as long as several decades ago, their priority is more or less appropriately cited in the current international literature.

Notably, B.V. Gromov did not confine himself to working with routine model objects. Rather, he preferred to deal with isolates obtained by himself or his colleagues. Although he was a convinced morphologist *par excellence* (in contrast to some today's beginner microbiologists who enjoy databases, and rarely look in a microscope), he also paid tribute to physiological and biochemical aspects, symbiotic relations in particular.

BACTERIA

Non-symbiotic species were not among Gromov's favorite objects, although he somewhat contributed to first understanding of such phenomena as bacterial chemotaxis and sensitivity to toxicants (e.g. Gromov et al., 1983). At the same time, he was among prime investigators of *Rickettsia*-related bacteria that comprise a remarkable group of internuclear symbionts of ciliates (e.g. Gromov and Ossipov, 1981; Potekhin and Nekrasova, 2021; this issue).

Starting from late 1960s he got interested in cyanobacteria (37 articles), and became one of the distinguished cyanobacteriologists; his most important discovery was also in this area (e.g. Gromov and Mamkaeva, 1980; Pinevich and Averina, 2021; this issue). Strikingly, he studied a multitude of aspects,

such as: i) diversity (e.g. Gromov et al., 1993), ii) culturing (e.g. Voloshko et al., 1996), iii) functional structure (e.g. Gromov, 1976a; Pinevich et al., 1986), iv) photosynthetic pigments (e.g. Pinevich et al., 1994), v) heat and cold shocks (e.g. Sharipova and Gromov, 1984), vi) bioactive compounds (e.g. Sivonen et al., 1992; Kozhenkova and Gromov, 1993), vii) predation by other bacteria (e.g. Gromov et al., 1972). His interest in the unusually pigmented strains has brought to recent research of far-red light photoadaptations in cyanobacteria (e.g. Averina et al., 2018).

PROTISTS

Boris Gromov was also well known for his work on protists (17 articles). As in the case of cyanobacteria, he comprehensively studied biology of these microorganisms. Among his most important achievements was a proposal of the new class *Aphelidea* – amoeboid parasites of algae (Gromov, 2000). This taxon is now considered crucially important from phylogeny viewpoint (Karpov et al., 2014). Two genera within this class, *Aphelidium* and *Amoeboaphelidium*, were studied in relation to taxonomic spectrum of their preys (e.g. Gromov and Mamkaeva, 1969), culturing (e.g. Gromov and Mamkaeva, 1970a), ultrastructure (e.g. Gromov and Mamkaeva, 1970b), molecular biology characters (e.g. Avilov et al., 1975; Pinevich et al., 1997).

MICROSCOPIC ALGAE

B.V. Gromov studied microscopic algae via the same broad approach which he used in the case of cyanobacteria and protists. With few exceptions, he analyzed the strains from the St. Petersburg Culture Collection (CALU) which he initiated as early as in 1959 (e.g. Gromov, 1991; Pinevich et al., 2004). This in fact great enterprise (four decades of research; 42 articles) gained valuable information on: i) diversity and taxonomy (e.g. Gromov et al., 1991), culturing (e.g. Gromov, 1968), ultrastructure (e.g. Gromov et al., 1990), physiology (e.g. Volshko et al., 1997). In particular, the study of chemotaxis in *Chlorococcum minutum* and *Chlamydomonas reinhardtii* – a phenomenon firstly recorded by B.V. Gromov and his junior associates (e.g. Ermilova and Gromov, 1988; Ermilova et al., 1993) – proceeded until his passing away (e.g. Ermilova et al., 2000). Later, a focus of research on *C. reinhardtii* switched to molecular genetic aspects of adaptations (e.g.:

Alqoubaili et al., 2021; this issue; Zalutskaya et al., 2021; this issue).

MICROSCOPIC FUNGI

Another group of algal parasites discovered by Boris Gromov is chytridiomycetes. These understudied objects were analyzed in relation to their distribution, host specificity, and life cycle (e.g. Gromov et al., 2000). Despite being a comparatively small piece of Gromov's heritage (6 articles), this groundwork opened vast perspectives for future research. Not surprisingly, these and other chytrid parasites came into sight of international team headed by Sergey A. Karpov, a noted specialist in cytology, taxonomy, and phylogeny of lower eukaryotes (e.g. Karpov et al., 2016; 2018).

VIRUSES

Gromov's only one journey to population virology, and also the last article in his life, dealt with diversity of viruses in plankton of Lake Ladoga (Sirotkin et al., 2001). At the same time, he for several decades comprehensively studied viruses of cyanobacteria (cyanophages), as well as viruses of microscopic algae (12 articles), and he rightfully became a globally recognized authority in this field (e.g. Safferman et al., 1983).

As regards to cyanophages, Gromov reported on: i) host specificity (e.g. Gromov and Kozjakov, 1970), ii) virion morphology and DNA base composition (e.g. Kozjakov et al., 1972), iii) ultrastructure of intracellular development (e.g. Gromov et al., 1975), iv) lytic and temperate cycles (e.g. Gromov, 1983), v) dependence on host's photosynthetic metabolism (e.g. Mamkaeva et al., 1980). Noteworthy, a serendipitous discovery of unique adenine-less cyanophage S-2L (unaccountably reported without Gromov's co-authorship; see: Kirnos et al., 1977) has led, via intermediate analysis (Szekeres and Matveyev, 1987), to recent break-through in the study of 'adenine rejection' phenomenon (Czernecki et al., 2021).

Regarding viruses that infect microscopic algae, Gromov's interest was concentrated on phage-like parasite of *Chlorococcum minutum* (e.g. Gromov and Mamkaeva, 1979) that selectively infected zoospores (e.g. Gromov and Vepriiskii, 1983).

In his usual way, Boris Gromov loved working with rare and sophisticated viral symbioses with hosts

of various structure and phylogeny. In particular, he participated in early research on the tripartite symbiosis: *Paramecium*–*Chlorella*–virus (Kvitko and Gromov, 1984). Later, dsDNA containing virus, now ascribed to the family Phycodnaviridae, genus *Chlorovirus*, as the type species *Paramecium bursaria Chlorella virus* (PBCV), has become a subject of ecology and molecular genetic analyses (e.g. Vorobiev et al., 2009; Migunova and Pinevich, 2021; this issue).

Summation of Gromov's works on protists, microscopic fungi, and viruses infecting algae allows considering him as a personal founder of a separate bioscience, algopathology (e.g. Gromov, 1976b).

It should be mentioned that Professor Gromov was a thoughtful tutor and talented lecturer. His original manuals on bacteriology (Gromov, 1985; Gromov and Pavlenko, 1989) that have been used by several generations of students are helpful even nowadays.

In conclusion one could interrogate about the reason for a remarkable success in science achieved by Gromov. Indisputably, it was an excellent professional training during the study years and thereafter, great scholarship, and close attention to new trends in microbiology. However, the main reason was that he always exercised a triad such as: assiduous extensive sampling → laboratory culturing → watching objects from ontogeny and environmental/symbiotic ecology viewpoints. Simply put, that reason can be explained by biblical sermon (Matthew 7B:7–8):

Seek, and ye shall find.

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