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**REVIEWS**

# History of the Study of Biodiversity of Photosynthetic Bacteria

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**Abstract**—The tendencies in the study of anoxygenic photosynthetic bacteria (APB) are considered in the review in the historical aspect, from the discovery of APB till the present day. The contribution made by the researchers of the Institute of Microbiology, Russian Academy of Sciences, to the study of the phylogeny, ecology, and morphophysiological diversity of APB is noted. At present, molecular biological approaches play a decisive role in ecology and taxonomy. The most important task at the modern stage of the development of microbiology is to maintain the continuity of the historically formed classical approaches in the study of APB diversity.

*Key words*: anoxygenic phototrophic bacteria, history of the study of APB, biodiversity, phylogeny, molecular ecology.

At present, the term anoxygenic photosynthetic bacteria (APB) is applied to prokaryotic microorganisms capable of performing photosynthesis with the participation of chlorophyll pigments and without releasing oxygen. This physiological group includes genetically and evolutionarily remote eubacteria: purple bacteria and aerobic bacteriochlorophyll *a*–containing bacteria (ABChl-*a* bacteria), green sulfur bacteria, filamentous green nonsulfur bacteria, and heliobacteria [1].

Since the discovery of colored sulfur bacteria by Ehrenberg in 1835 [2] and up to the present day, chlorophyll-containing bacteria have attracted the attention of researchers. The focus of the attention paid to photosynthetic bacteria changed with time, but the interest in this microbial group was ever increasing. Several periods characterized by their own strategies of searching for new microbial forms can be distinguished in the history of the study of photosynthetic bacteria. The specifics of a strategy at a certain stage were determined by the level of knowledge, and its realization depended on the methodical and technological support.

Important events in the field of investigation of photosynthetic bacteria are associated with the names of distinguished scientists and the manifestation of their talent and intuition or persistence, as well as with the introduction of fundamentally new methods into research practice. The discovery of new microorganisms not infrequently led to radical changes in the concepts of the properties of the whole group of photosynthetic bacteria and gave an impetus to new directions of research.

Photosynthetic bacteria are classic subjects in the works of microbiologists, biochemists, biophysicists, and geneticists. The contribution of these bacteria to the development of concepts of the nature of prokaryotic microorganisms is very great. The history of their study is closely connected with the history of bacteriology as a whole and touches upon virtually all significant biological problems: morphogenesis, growth and development, cell structure, functioning of cell organelles, mechanisms of bioconversion of solar energy, autotrophy and lithotrophy, nitrogen fixation, metabolism regulation, extremophily, ecology, evolution of the organic world, and some other problems.

The scientists from the Institute of Microbiology, Russian Academy of Sciences, have made a tangible contribution to the development of the concepts of the ecology of photosynthetic bacteria and their taxonomic and physiological diversity.

The first, initial, period (1835–1932) of the study of photosynthetic bacteria was characterized by an extensive study of the habitats typical of colored sulfur bacteria and observation of these microorganisms in situ. The light microscope was the main instrument of research. Direct microscopy of natural samples and enrichment cultures provided the first evidence of the morphological diversity of purple sulfur bacteria and revealed green sulfur bacteria. Despite the fact that many investigators had observed small immotile straight or curved greenish cells in the enrichment cultures of purple sulfur bacteria, the first scientist to give them the name of green sulfur bacteria (in 1906) was Academician G.A. Nadson [3]. From the silt of Lake Saki, he obtained enrichment cultures of green sulfur bacteria, which he called *Chlorobium limicola.* Molish

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was the first to assign pigmented sulfur and nonsulfur bacteria to one order, *Rhodobacteria* Molish 1907 [4].

Observations of purple bacteria forming bright purple and lilac spots were made by Winogradsky, B.L. Isachenko, B.V. Perfil'ev, and A.D. Pel'sh [2]. Simple experiments showed that, like colorless sulfur bacteria, colored sulfur bacteria are capable of oxidizing hydrogen sulfide and depositing elemental sulfur. Hence, a conclusion was made that colored and colorless sulfur bacteria are physiologically related. However, this did not substantially influence the structure of the first taxonomic system, whose basis was formed by morphological characteristics [5], nor did it clear up their physiology. An outstanding contribution to the description of many genera and species of purple sulfur bacteria was made by Winogradsky [6]. Even now, species discovered by him are included in new editions of the world-renowned *Bergey's Manual.*

The second period of investigation (1932–1957) of colored sulfur bacteria is associated with the name of Van Niel. The main event of this period was the recognition of the specific type of bacterial photosynthesis [7]. This resulted in increased rates of studying purple and green bacteria. By virtue of the development of synthetic media, pure cultures of typical representatives of all the three groups of photosynthetic bacteria were isolated. Working with pure cultures was a qualitatively new stage in the research into purple and green bacteria. There appeared a possibility of conducting an in-depth study of different aspects of the metabolism of these microorganisms.

At that time, specialized teams formed that pioneered the fields of studying the mechanism of photosynthesis, structure of the apparatus of photosynthesis, pigment composition, composition of the electron transport chain, pathways of assimilation of carbon dioxide and organic compounds, nitrogen fixation and nitrogen metabolism, and hydrogen production and utilization. The sulfur metabolism was studied to a lesser degree at that time.

The basis for the fundamental study of the metabolism of phototrophic bacteria was laid by Academician V.N. Shaposhnikov [8] and brilliantly developed by his disciple Academician E.N. Kondrat'eva [2] and, in turn, by her disciples R.N. Ivanovskii, I.N. Gogotov, E.N. Krasil'nikova, V. Uspenskaya, O.I. Keppen, Yu.V. Rodionov, and others. The collaboration between researchers from the Institute of Microbiology, Russian Academy of Sciences, and the team headed by Kondrat'eva was always fruitful and contributed to the development of the physiological trend in the study of new phototrophic bacteria.

The research strategy in this period was of an intense character and did not envisage an extensive search for new species of purple and green bacteria. From 1932 through 1960, only four new genera and ten new species of photosynthetic bacteria were described, which did not bring about any noticeable changes in the course of the investigation process. The fact that the studies were confined to a few cultures of purple and green bacteria led to the concept of a common physiological and biochemical organization in different representatives of photosynthetic bacteria. The ecological niche for the functioning of photosynthetic bacteria was outlined, characterized by the availability of light, sulfide, and carbon dioxide or organic substrate.

Worthy of note are the pioneering investigations carried out by the researchers from the Institute of Microbiology on the distribution and geochemical activity of different representatives of photosynthetic bacteria in natural ecosystems—in seas and steppe soda lakes (Isachenko, A.E. Kriss) and in hydrogen sulfide springs and meromictic lakes (S.I. Kuznetsov, Yu.I. Sorokin, M.V. Ivanov, N.N. Lyalikova). These works laid the basis for studies of the functional ecology of photosynthetic bacteria, including studies of their participation in carbon and sulfur cycles.

Of special interest was the discovery by Isachenko of red formation waters in the Apsheron oil field; these waters contained purple sulfur and nonsulfur bacteria [2]. This phenomenon has not yet been satisfactorily explained. Later, from samples of colorless water of the injection wells of this region, E.P. Rozanova and A.Ya. Khudyakova [9] isolated cultures of purple nonsulfur bacteria, and it was suggested that these microorganisms either survive in the dark by utilizing reserve substances or ferment the organic substrates present in the surrounding solution.

The development of a new taxonomic system for photosynthetic bacteria, published in the seventh edition of *Bergey's Manual* [10], was an important step forward. The bacteria capable of photosynthesis were combined into one suborder, *Rhodobacteriace,* and divided into three families: *Thiorhodaceae, Athiorhodaceae*, and *Chlorobacteriaceae.* The subdivision into genera was based on morphological principles. The physiological characteristics clearly defined the features of the families and were included in the species characteristics of green sulfur bacteria and purple nonsulfur bacteria. Many species not yet obtained as pure cultures were included in the manual. This predetermined the further primary strategy: isolation of the numerous APB species described based on examinations of natural samples.

The third period (1961–1978) was initiated by the works of N. Pfennig and his disciples [11, 12]. Pfennig developed and successfully employed a new synthetic medium suited for the enrichment and isolation of virtually all anaerobic photosynthetic bacteria. The medium is based on a carbonate buffer system and has an improved microelement composition. Growth factors (yeast extract, vitamins, sources of reduced sulfur) are added to it if necessary. The pH, salinity, sulfide concentration, and carbon source are varied depending on the expected requirements of the prospective isolates. The selective conditions for the enrichment of microorganisms with expected characteristics are provided not only by the medium composition but also by the incubation conditions (temperature, intensity and spectral characteristics of illumination).

Using modifications of Pfennig's medium, it proved possible to obtain in pure cultures virtually all types of known species of purple and green bacteria and to reveal a number of new forms. Thus, the range of subjects of physiological, biochemical, and other kinds of research into anoxygenic phototrophs was greatly extended. The third period in the history of studies of photosynthetic bacteria is marked by the combination of extensive and intensive investigations carried out with a large number of research objects (microbial isolates and natural bodies of water). The strategy of the search for new phototrophic bacteria had a firm scientific basis: the concept of the realization by microorganisms of the space of logical possibilities [11, 13].

An increased activity in the study of the ecology, geochemical activity, and species diversity of anoxygenic phototrophic bacteria at the Institute of Microbiology, Russian Academy of Sciences, was noted in this period. The works by Kuznetsov and his disciples are worthy of note [14]. The description of unusual morphological forms of photosynthetic bacteria—purple and green bacteria containing gas vacuoles, green vibrioid and prosthecate bacteria, budding purple nonsulfur bacteria, and a new group of mesophilic green filamentous bacteria—should be considered significant events of this period [15–17].

Studies of the developmental cycles of purple bacteria revealed exospore-type (in *Rhodomicrobium vannielii*) and cyst-type resting cells (in some *Rhodopseudomonas* and *Rhodocysta* representatives and in *Lamprobacter modestohalophilus*) [18, 19]. Unfortunately, these works have not been developed further despite the fact that resting phototroph cells are of profound interest for investigation of de novo development of the photosynthetic functions of the prokaryotic cell.

Important data were obtained in studies of the fine structure of different species of purple and green bacteria [20]. Specific features of the apparatus of photosynthesis (chromatophores) of purple bacteria are important characteristics of species, genera, or even families. In several works, the unique structure of green bacteria, which possess special antenna structures—chlorosomes, was substantiated. The detection of chlorosomes in unknown organisms occurring in nature is considered to be a sufficient argument for assigning them to green bacteria. It was in this way that the prosthecate bacteria of the genus *Ancalochloris* and a number of freshwater and marine filamentous green bacteria [14] not yet obtained in pure cultures were described. At the Institute of Microbiology, Russian Academy of Sciences, the fine structure of the green sulfur bacteria was investigated by N.N. Egorova-Puchkova, T.N. Pivovarova, T.N. Zhilina, and L.L. Mityushina. The studies of recent years showed that filamentous green nonsulfur bacteria also possess chlorosomes as antenna structures; however, their chemical composition differs from that of the chlorosomes of green sulfur bacteria. In particular, green sulfur bacteria contain the water-soluble Fenna–Matthews–Olson protein, which mediates the energy transfer between chlorosomes and the reaction center. This unique protein is characteristic of only green sulfur bacteria and is currently used for their identification in natural samples by molecular biological methods [21]. At the same time, chlorosome-free filamentous bacteriochlorophyll *a*–containing phototrophic bacteria belonging to the group of green nonsulfur bacteria were revealed [22, 23]. Evidently, one should be cautious with diagnostic conclusions when using only cytological and morphophysiological characteristics for identification.

In the 1960s and 1970s, the study of the carotenoid and bacteriochlorophyll composition, as well as the functions of these pigments, was conducted in many purple and green bacteria [11, 14, 24]. The cell pigment composition is an important taxonomic characteristic and allows the differential diagnosis of new strains to be made. This may be exemplified by the recent description of a new species of the genus *Thiocapsa* (*Tc. marina* sp. nov.), containing the carotenoid okenone instead of spirilloxanthin, characteristic of the representatives of the type species *Tc. roseopersicina* [25].

Thanks to the discovery of new microorganisms, new bacteriochlorophylls (Bchl *d*, Bchl *e*, and Bchl *b* and, in the later period, Bchl *g*) and their modifications were revealed. The strategy of the search for new microorganisms by the feature of a possible but not yet revealed combination of the pigments holds much promise. In the family *Chlorobiaceae*, for almost all Bchl *c*– or Bchl *d*–containing green species, morphologically similar brown Bchl *e*–containing counterparts were discovered. The recent years were marked by new discoveries of lacking brown species of green sulfur bacteria [1]. The molecular genetic studies of most known green sulfur bacteria conducted recently showed the phylogenetic closeness between brown and green species [21]. A conclusion may be reached that the pigment variations in green sulfur bacteria are primarily of ecological significance. The presence of a considerable amount of the carotenoid isorhenieratine in brown bacteria, along with chlorosomes, specialized antenna structures, allows them to live at limiting depths where light still reaches (for example, in the chemocline of the Black Sea (100 m)) [26, 27].

At the same time, comparatively few descriptions of bacteria containing bacteriochlorophyll *b* are available, but this area of research has been expanded in recent years [28].

In this period, great success was achieved in studying the primary photosynthetic reactions and the ways of utilization of solar energy in different species of purple and green bacteria, and fundamental research into carbon, sulfur, and nitrogen metabolism and into the regularities of hydrogen photoproduction was done [29–32]. Much attention was given to investigation of the alternative pathways of metabolism in purple and green bacteria. The capacity of some purple nonsulfur bacteria to grow in the dark at the expense of respiration was studied in detail; the role of light and oxygen in the regulation of dark and light metabolism was also explored. It was established that purple bacteria capable of aerobic growth use certain segments of the electron transfer chain for both photosynthesis and respiration. This results in the inhibition of respiration when the cells are illuminated. Some of the purple nonsulfur bacteria revealed the capacity for fermentation in the dark, and purple sulfur bacteria were found to have a dark anaerobic metabolism coupled with the utilization of sulfur compounds [33].

A significant event was the discovery of the capacity for chemolithoautotrophic or chemolithoheterotrophic growth in a series of purple sulfur bacteria [34–37]. These investigations supported Winogradsky's concept of the physiological closeness between purple and colorless sulfur bacteria.

An important event extending the search for new forms was the discovery of the ability of most purple nonsulfur bacteria to utilize sulfide in the process of photosynthesis [38]. Thus, the paradigm of the sensitivity of purple nonsulfur bacteria to sulfide and of their inability to utilize it was undermined. These investigations stimulated the discovery of a number of purple nonsulfur bacteria incapable of assimilatory sulfate reduction; many of them were found to be highly tolerant of sulfide [39, 40].

The study of the ecology of photosynthetic bacteria growing in freshwater and saline stratified reservoirs was carried out at a rapid pace [14, 41, 42]. In this period, accurate recording of phototroph habitat parameters; quantitative assessment of their geochemical activity; and, importantly, generic or species identification of microorganisms were, as a rule, carried out. Every reservoir has its own physicochemical specificity, which predetermines the unique nature of the community of phototrophic microorganisms inhabiting it. The study of a large number of new sulfide-containing lakes led to the discovery and description of a series of species, mainly, of green bacteria. Thus, one of the aspects of the strategy of the search for new phototrophic bacteria is to widen the range of natural research objects. The thesis "a new reservoir (habitat) means a new microorganism" is not far from the truth. The practice showed that the most evolutionarily remote groups of photosynthetic bacteria can be revealed in extreme ecosystems: hypersaline and soda reservoirs and hot springs.

The ecological studies conducted in the 1960s and 1970s led to the coordination of the laboratory physiological–biochemical research and field ecological work [11, 14, 42, 43]. In this period, the development of microelectrode technology enabling the oxygen and sulfide content, pH, and Eh in microbial mats to be determined with an accuracy of fractions of a millimeter [44] should be emphasized. These methods offered the possibility to trace the diurnal dynamics of the anaerobic zone border in benthonic phototrophic communities and the migration of cyanobacteria and anoxygenic phototrophic bacteria and to quantify in situ their contribution to production processes and sulfide oxidation.

A number of works were devoted to studying the relations between individual species of purple and green bacteria, as well as between phototrophs and other microorganisms. The chemostat is an excellent instrument for these purposes [45]. The main event was the discovery of syntrophic interactions between green sulfur bacteria and sulfidogenic bacteria [46]. From the standpoint of the ecology of photosynthetic bacteria, syntrophy is the mode of existence of green sulfur bacteria at extremely low sulfide concentrations. Under these conditions, when the sulfate or sulfur content in the environment is limited, the sulfate-reducing or sulfur-reducing bacteria form sulfide, which is reoxidized by green sulfur bacteria. In their turn, sulfidogens utilize the organic substrates formed in the process of photosynthesis. In nature, these interactions occur in microcosms, particularly in the intercellular spaces of microcolonies of freshwater green sulfur bacteria.

The unraveling of the mechanisms of interaction between two or more microorganisms offers a strong possibility of obtaining monocultures of "uncultivated" species of green bacteria by making them coexist with sulfate-reducing, sulfur-reducing, or fermenting bacteria. This possibility has not been translated into practice yet. In our laboratory (the Laboratory of the Ecology and Geochemical Activity of Microorganisms, headed by V.M. Gorlenko), the capacity for syntrophic growth was established in sulfide-utilizing species of purple nonsulfur bacteria and sulfidogens, as well as certain strains of *Chloroflexus aurantiacus.*

Due to the efforts of a number of researchers, including researchers from the Department of the Geological Activity of Microorganisms headed by Kuznetsov (1942–1987), the strategy of the existence of ecological subgroups of phototrophic bacteria in relation to light and the sulfide concentration was clearly outlined [11, 41].

Variations in the composition of pigments (carotenoids and bacteriochlorophylls) allow several species of photosynthetic bacteria to exist in one biotope. Using filters passing light of a certain wavelength, it is possible to selectively enrich green bacteria or, on the contrary, purple bacteria containing bacteriochlorophylls *a* or *b*. The studies of natural habitats and isolated phototroph cultures showed that green bacteria are the most shade-loving, likely due to the presence of chlorosomes in them [47]. These microorganisms are extremophiles in relation to light. They can grow even at an illuminance of 50 lx, at which virtually no growth of other phototrophs occurs.

As for the tolerance to sulfide, the most tolerant are some of the species of green bacteria of the genera *Chlorobium* and *Prosthecochloris* [11]. Sulfide is highly toxic only for certain species of purple nonsulfur bacteria. Virtually for all large taxonomic groups, three ecological subgroups were revealed: oligo-, meso-, and eurysulfidophiles (according to Pfennig's terminology). Now, this conception can be extended to heliobacteria, among which those tolerant of sulfide and utilizing it as an electron donor were revealed [48, 49]. The low tolerance of a microorganism for sulfide is usually associated with the requirement for low temperatures for growth, which is exemplified by freshwater species of the genus *Pelodictyon.*

The interest in the extreme capacities of representatives of phototrophic bacteria is indisputable. No extreme acidophiles were revealed among purple and green bacteria. It can only be noted that the species *R. acidophila, R. vannielii*, and *R. julia* prefer lowered pH values (5.5–6.0) for growth [11, 12, 40].

Certain species of the genus *Ectothiorhodospira* isolated from soda lakes are haloalkaliphilic [50, 51]. The list of alkaliphilic bacteria has been considerably augmented by the efforts of researchers from our laboratory. The phototrophic bacteria of the soda lakes of Chita oblast, Buryatia, Mongolia, and Egypt were investigated over the last 10 years (Gorlenko, I.A. Bryantseva, E.I. Kompantseva, Z.B. Namsaraev, D.Yu. Sorokin). When the slightly and moderately mineralized soda lakes of the southeastern Transbaikal region with a water mineralization of 0.5–40 g/l, alkalinity of 0.4–5.2 g/l, and pH 8.9–10.2 were explored, the existence of a new physiological–ecological group of sodophilic but not halophilic phototrophic bacteria was proved. The lakes studied were marked by considerable APB diversity, including all known groups except for green sulfur bacteria. The representatives of *Ectothiorhodospiraceae* predominated. All the APB isolated from the soda lakes were shown to be autochthonous inhabitants of these ecosystems. All of them appeared to be halo-, sodo-, and alkalitolerants or alkaliphiles requiring the presence of the carbonate ion in the medium. Three genera and six species of new and, in many respects, unique APB were described. Bacteria depositing elemental sulfur in the periplasmic space of the cells, *Thiorhodospira sibirica* gen. nov., sp. nov., were described for the first time within the family *Ectothiorhodospiraceae* [52]. They have an unusual structure of the membrane apparatus of photosynthesis, earlier unknown in APB. *Thioalkalicoccus limnetica* gen. nov., sp. nov., the first obligately alkaliphilic representative of the family *Chromatiaceae*, was also described [28]. Obligately alkaliphilic representatives of heliobacteria, assigned to the new genus *Heliorestis* gen. nov. (*Heliorestis daurensis* sp. nov. and *Heliorestis baculata* sp. nov.), were also revealed in soda lakes and described [53, 54]. They are characterized by increased tolerance of sulfide and the capacity to utilize it as the electron donor in photosynthesis.

It was interesting to go ahead with the microbiological study of the soda lakes on the territory of eastern Mongolia. More than 30 lakes with a mineralization from 3.0 to 360 g/l were investigated. The water of most of the lakes investigated was highly alkaline (pH 9.0–10.4). APB capable of growth at pH 9.0–10.0 were revealed in all samples of littoral silts and bioaccretions studied. In hypersaline reservoirs, we identified extremely halophilic species. The *Ectothiorhodospira* species were prevalent. The strains isolated from hypersaline lakes were shown to grow when the medium was fully saturated with NaCl, but the optimum growth occurred at a mineralization of 90–120 g/l. The prevalence of *Ectothiorhodospira vacuolata* and *Thiorhodospira* sp. merits attention. A unique alkaliphilic purple bacterium described as a new genus and a new species of the family *Ectothiorhodospiraceae*—*Ectothiorhodosinus mongolicum* gen. nov., sp. nov.—was revealed in a slightly mineralized lake [55]. The species diversity of the phototrophic communities in the soda lakes of eastern Mongolia was investigated for the first time. Compared to the lakes of the steppe regions of Chita oblast, the APB of the lakes of eastern Mongolia are adapted to life not only at high pH values but also at considerable salt concentrations.

As for their reaction to salinity, phototrophic bacteria are subdivided into five groups: freshwater; NaCl-tolerant (up to 2%); marine forms (NaCl optimum, 2–4%); weak halophiles (NaCl optimum, 4–7%); and halophiles (NaCl optimum, 10–15%) [51]. Up to now, no weakly halophilic or halophilic green sulfur bacteria or filamentous green bacteria have been revealed, whereas, among purple bacteria, halophilic species have been discovered. In our laboratory, we investigated the growth conditions and biodiversity of the anoxygenic phototrophic bacteria of the saline reservoirs of the Crimea, the northern Caucasus, and Kara-Kalpakia; mud volcanos of Turkmenistan; and the White Sea estuary zone (Gorlenko, Kompantseva, N.N. Puchkova, D.A. Starynin, and A.S. Savvichev participated in these studies). The bacteria of a genus of purple sulfur bacteria, *Lamprobacter modestohalophilus* gen. nov., sp. nov., were isolated from hypersaline lakes and described. The optimum growth of this species occurs at a NaCl concentration of 4–6% [18]. In littoral pits, we revealed new marine bacteria of the genus *Thiocapsa*, *Tc. litoralis* [56].

An important event in the history of the study of phototrophs was the discovery of *Chloroflexus aurantiacus*, a thermophilic filamentous green bacterium with the optimum growth temperature of approximately 60°C and the limiting temperature of 72°C [57, 58]. So far, no phototrophic microorganisms growing above this temperature have been discovered. The specifics of ecological conditions predetermine the development of certain ecotypes of microorganisms. Thus, R. Castenholz discovered strictly anaerobic green bacteria morphologically similar to *Chloroflexus aurantiacus* in high-sulfide hot springs [59]. Recently, a new species *Chloroflexus aggregans* inhabiting Japanese hot springs was described [60]. Of interest are, undoubtedly, the chlorosome-free thermophilic filamentous bacterium *Heliothrix oregonensis*, containing only bacteriochlorophyll *a* [22], and the recently described *Roseoflexus castenholzii* [23].

Among the green sulfur and purple sulfur bacteria and heliobacteria, only moderately thermophilic species with an optimum growth temperature of 47–49°C were found. The species *Chromatium tepidum*, later redescribed as *Thermochromatium tepidum* gen. nov., sp. nov., as well as *Chlorobium tepidum* and *Heliobacterium modestocaldum*, were isolated from hot spring samples [61–63]. When investigating the hot springs of the Baikal region, we showed for the first time the wide distribution of purple nonsulfur bacteria, ABChl-*a* bacteria, and heliobacteria in microbial mats at temperatures ranging from 18 to 55°C [64].

The presence of mesophilic species at temperatures favorable for thermophiles has not yet been satisfactorily explained [65]. A survey of our studies of alkaline hot springs of the Baikal region is presented in the jubilee issue of *Tr. Inst. Mikrobiol. RAS* (2004). Two new mesophilic species of heliobacteria—*Heliobacterium sulfidophilum* sp. nov. and *Heliobacterium undosum* sp. nov., capable of oxidizing sulfide to elemental sulfur in the process of photosynthesis—were isolated by us from hot alkaline sulfur springs [48, 49].

The first stage of the third period of investigation of photosynthetic bacteria culminated in the eighth edition of *Bergey's Manual* [15]. This manual presented a new taxonomic system, the basis of which is formed by the characteristics of the type strain. Researchers were provided with clearly defined criteria for identification of new isolates of phototrophic bacteria. The minimal set of descriptors for species description was determined by the International Subcommittee on Photosynthetic Bacteria under the Systematic Bacteriology Committee set up in the 1960s and functioning up to now. The taxonomy of photosynthetic bacteria developed by Pfennig and H. Trüpper is phenotypic, although it uses genosystematic elements (the G+C content in DNA).

The period of studying the phenotypic diversity of photosynthetic bacteria ended in the late 1970s, when the first publications comparing the molecular genetic characteristics of purple and green bacteria appeared. The widest application was found by the methods for comparison of 16S rRNA sequences [66].

Already the first results of molecular genetic investigations demonstrated the high-level genetic divergence of anoxygenic phototrophs. By now, the phylogenetic position of almost all currently recognized species of photosynthetic bacteria has been determined. According to the data from the 16S rDNA sequence analysis, photosynthetic bacteria belong to four evolutionary lineages of bacteria. The longest evolutionary distance separates the following groups of anoxygenic phototrophs: purple bacteria together with ABChl-*a* bacteria, green bacteria, green nonsulfur bacteria, and heliobacteria. Green nonsulfur bacteria, represented until recently only by the thermophilic filamentous bacterium *Chloroflexus aurantiacus*, seem to have the most ancient origin. *Heliobacterium chlorum* and other species of heliobacteria belong to the gram-positive evolutionary lineage (the *Bacillus–Clostridium* group with a low G+C content of DNA).

The evolutionary lineage of purple bacteria includes all representatives of purple sulfur and nonsulfur bacteria and their chemotrophic relatives (*Proteobacteria*). Purple bacteria have a common ancestor and are divided into three subgroups: alpha, beta, and gamma. Most purple nonsulfur bacteria belong to the alpha subgroup, and only *Rhodocyclus* representatives were assigned to the beta subgroup. The data from the 16S rDNA sequence analysis revealed close relatedness between all known purple sulfur bacteria and considerable heterogeneity (divergence) of purple nonsulfur bacteria.

Owing to the fact that the phylogenetic studies were conducted with a large number of species of phototrophic bacteria, it became possible to correct the earlier phenotypic taxonomic system of phototrophic bacteria. The taxonomic system published in the eighth edition of *Bergey's Manual* [15] was a compromise system that retained, in large measure, the continuity with the old phenotypic system. However, the new system widely uses genosystematic and chemotaxonomic data.

Some contradictions between the new phylogenetic conceptions and the old phenotypic ones remain unsolved until now. This is connected with the absence of information about the molecular genetic characteristics of certain taxa and the still existing distrust in the correctness of the genosystematic methods used.

One of the most important results of the new molecular biological approach is the conclusion as to the ancient and multiple origin of the process of photosynthesis. It is clear that different groups of phototrophic bacteria have traversed independent paths of evolution. Many phototrophic bacteria are closely related to chemotrophic bacteria. Sometimes, this relation is closer than that between the phototrophic representatives in one group; numerous examples of this phenomenon were discovered for purple nonsulfur bacteria and the ABChl-*a* bacteria. It may be suggested that both phototrophic and chemotrophic bacteria originated from one ancestor capable of photosynthesis.

The achievements of molecular genetic research allowed the strategy of the search for new microorganisms to be extended. A search for the yet-unknown chemotrophic relatives of photosynthetic bacteria has become topical. The strategy of the modern period also implies a search for new evolutionary branches that include photosynthetic bacteria. Now we are aware of aerobic bacteria in which Bchl *a* does not manifest itself phenotypically (and it is only possible to reveal a dormant gene responsible for the synthesis of bacteriochlorophyll) or bacteriochlorophyll manifests itself only under certain cultivation conditions.

It is not long ago that all photosynthetic bacteria were considered to belong to gram-negative bacteria. However, the discovery of heliobacteria destroyed this paradigm. These microorganisms, which form endospores, are the only representatives of phototrophic bacteria in the gram-positive evolutionary lineage. In the nearest future, other anoxygenic phototrophs related to gram-positive bacteria may be discovered. An important event was the discovery of the group of ABChl-*a* bacteria [67]. Freshwater and marine forms, as well as methylotrophic and nonmethylotrophic species, were found to occur among them [67, 68]. ABChl-*a* bacteria appear to be a new ecophysiological group of anoxygenic phototrophs: they are obligately dependent for life on oxygen. Photosynthesis in them functions only in the presence of oxygen and is an additional source of energy. Genetically, according to the data of 16S rDNA sequence analysis, both methylotrophic and nonmethylotrophic bacteria belong to the alpha subgroup of purple bacteria. There are reasons to believe that, like purple nonsulfur bacteria, ABChl-*a* bacteria are a highly diverged group, both phenotypically and genotypically. An example may be the bacteria (revealed in the rhizosphere of plants) that are phylogenetically close to the genus *Rhizobium* but contain bacteriochlorophyll *a* (the so-called *"Photorhizobium"*). Obviously, the search for new aerobic chlorophyll-containing anoxygenic bacteria will be rewarding.

The results of the application of genosystematics methods dictated the necessity of reevaluation of the taxonomic significance of various phenotypic characteristics. The period between the publication of the ninth edition of *Bergey's Manual* and the appearance of the first volume of the new edition of *Bergey's Manual of Systematic Bacteriology* [1] was marked by the ongoing advance of molecular biological methods into the taxonomy, phylogeny, and ecology of anoxygenic phototrophic bacteria. During this period, new phylogenetic methods were developed and tested. The data from 16S rDNA sequence analysis, which are of primary importance in determining the taxonomic position of isolates, have been used as the main criterion in many works. On the other hand, the significance of DNA–DNA hybridization data in the diagnosis of species and, less frequently, genera has grown [66]. The data of this method are increasingly being used to solve disputable taxonomic problems. Thus, by virtue of high DNA homology, a number of earlier independent species of the genus *Ectothiorhodospira* have been united: *Ect. shaposhnikovii* absorbed *Ect. vacuolata*, and *Ect. mobilis* assimilated *Ect. merismortii.*

The pace of describing new species has somewhat increased in the last decade, mainly because the genetic characteristics, primarily the 16S rDNA sequence data, have become decisive in diagnosing microorganisms and the method has become routine in many microbiology laboratories. The morphological characteristics have receded to the background, and the physiological characteristics only accompany the molecular biological database, even when higher taxa are characterized. Phototrophic and nonphototrophic bacteria are closely intertwined in the phylogenetic tree. This circumstance actually made researchers reject the habitual concepts of orders and families that include only phototrophs. This process was aided by the development of molecular ecology methods and the results obtained with them. In general, the scheme of molecular ecological work is as follows: from natural samples, industrial reactors, or enrichment cultures, total DNA is isolated with the subsequent amplification by PCR of either the 16S rRNA gene (for phylogenetic analysis) or conservative functional genes. The undisputable advantage of such methods is the possibility of monitoring the composition of complex microbial communities without isolating pure cultures. Moreover, the molecular genetic methods enabled us to determine the taxonomic position of bacteria known earlier but not amenable to isolation as pure cultures. Such microorganisms include the filamentous green bacterium *Chloronema giganteum* [16, 69], which occupied its taxonomic position among other mesophilic freshwater green nonsulfur bacteria of the family *Oscillochloridaceae.* The filamentous green bacteria inhabiting hypersaline microbial mats and not yet available as pure cultures are said to be candidates for the new genus *"Chlorothrix."*

The following large phylogenetic branches of anoxyphotobacteria are considered in the new edition of *Bergey's Manual* [1]: all purple bacteria are included in the new class *Proteobacteria*, which also contains their chemotrophic relatives. Purple sulfur bacteria are included in the phylum *Gammaproteobacteria* as constituents of two families—*Chromatiaceae* and *Ectothiorhodospiraceae.* Purple nonsulfur bacteria are subdivided into two phyla: *Alphaproteobacteria* and *Betaproteobacteria.* The family *Athiorhodaceae* was abolished because of the wide divergence of the group of purple nonsulfur bacteria. *Alphaproteobacteria* also includes aerobic bacteriochlorophyll-*a*–containing bacteria, among which more than 17 new genera and about 30 species have been described. The name of the old family *Erythrobacteriaceae* was excluded from the manual owing to the obvious heterogeneity of this group of anoxyphotobacteria. Green sulfur bacteria are included in the phylum *Chlorobi*, the class *Chlorobia*, the order *Chlorobiales*, the family *Chlorobiaceae.* The discovery of *Chlorobium ferrooxidans*, a new species of bacteria that utilize ferrous oxide salts instead of sulfide as electron donors, was a notable event [70, 71]. This undermined the established opinion that green sulfur bacteria are obligate sulfidophiles. Green nonsulfur bacteria (filamentous green bacteria) belong to the phylum *Chloroflexi*, the class *Chloroflexia*, the order *Chloroflexales*, which is subdivided into two families: *Chloroflexaceae* and *Oscillochloridaceae*. However, the names of these families, although mentioned, are not valid, as they would be if published in *IJSB*. Heliobacteria were assigned to the phylum of gram-positive bacteria, the subgroup of low G+C bacilli and clostridia.

Thus, the new edition of *Bergey's Manual* shows a tendency to do without large taxa, habitual in former systematics, and to replace them with phyla (phylogenetic lineages), in which phototrophic and chemotrophic bacteria are intermingled. The new taxonomic regulations have not yet been legalized, and the old ones are being abolished by the compilers of *Bergey's Manual* on their own volition.

It may be concluded that the modern period of investigation of phototrophic bacteria led to the discovery of a number of novel microorganisms the study of which has changed the concepts of the phenotypic features, evolution, and phylogeny of anoxygenic phototrophic bacteria.

The strategy of the search for new APB has arrived at a still higher molecular genetic level. The most important task of the modern stage is to maintain the continuity of the historically formed classical approaches to the study of the taxonomy and biodiversity of APB.

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