ISSN 0026-2617, Microbiology, 2013, Vol. 82, No. 5, pp. 547–553. © Pleiades Publishing, Ltd., 2013.
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EXPERIMENTAL ARTICLES

Comparative Study of Metabolism of the Purple Photosynthetic Bacteria Grown in the Light and in the Dark under Anaerobic and Aerobic Conditions

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Received December 24, 2012

Abstract—For three species of anoxygenic phototrophic alphaproteobacteria differing in their reaction to oxygen and light, physiological characteristics (capacity for acetate assimilation, activity of the tricarboxylic acid (TCA) cycle enzymes, respiration, and the properties of the oxidase systems) were studied. Nonsulfur purple bacteria *Rhodobacter sphaeroides, Rhodobaca bogoriensis*, and aerobic anoxygenic phototrophic bacteria *Roseinatronobacter thiooxidans* were the subjects of investigation. All of these organisms were able to grow under aerobic conditions in the dark using the respiratory system with cytochrome aa_3 as the terminal oxidase. They differed, however, in their capacity for growth in the light, bacteriochlorophyll synthesis, and regulation of activity of the TCA cycle enzymes. Oxygen suppressed bacteriochlorophyll synthesis by *Rha. sphaeroides* and *Rbc. bogoriensis* both in the dark and in the light. Bacteriochlorophyll synthesis in *Rna. thiooxidans* occurred only in the dark and was suppressed by light. The results on acetate assimilation by the studied strains reflected the degree of their adaptation to aerobic growth in the dark. Acetate assimilation by light-grown *Rha. sphaeroides* was significantly higher than by the dark-grown ones. Unlike *Rha. sphaeroides*, acetate assimilation by *Rbc. bogoriensis* in the light under anaerobic and aerobic conditions was much less dependent on the growth conditions. Aerobic acetate assimilation by all studied bacteria was promoted by light. In *Rha. sphaeroides*, activity of the TCA cycle enzymes increased significantly in the cells grown aerobically in the dark. In *Rbc. bogoriensis*, activity of most of the TCA cycle enzymes under aerobic conditions either decreased or remained unchanged. Our results confirm the origin of modern chemoorganotrophs from anoxygenic phototrophic bacteria. The evolution from anoxygenic photoorganotrophs to aerobic chemoorganotrophs included several stages: nonsulfur purple bacteria → nonsulfur purple bacteria similar to *Rbc. bogoriensis* → aerobic anoxygenic phototrophs → chemoorganotrophs.

Keywords: anaerobic anoxygenic phototrophs, aerobic anoxygenic phototrophs, bacteriochlorophyll, tricarboxylic acid cycle, respiration, cytochromes, acetate metabolism

DOI: 10.1134/S0026261713050056

Nonsulfur purple bacteria (NPB) belong to the alphaproteobacteria and are able to grow either under anaerobic conditions in the light or in the dark, obtaining the energy from aerobic respiration. Under anaerobic conditions in the light they possess the photochemical apparatus and fix CO_2 via the Calvin cycle. Under aerobic conditions, the synthesis of these systems is suppressed [1–3]. Aerobic anoxygenic phototrophs are able to grow only under aerobic conditions in the light or in the dark. They are obligate chemoorganotrophs and use the light as an additional energy source [4]. In contrast to the classical anaerobic anoxygenic phototrophs, all aerobic anoxygenic phototrophic bacteria studied in this respect were unable to assimilate CO_2 autotrophically, which correlates with the absence in their genome of the gene coding for ribulose bisphosphate carboxylase [5, 6]. These two groups of bacteria also differ significantly in the regulation of bacteriochlorophyll synthesis. In anaerobic anoxygenic bacteria, oxygen suppresses bacteriochlorophyll synthesis, while in aerobic anoxygenic phototrophs this process requires the presence of oxygen. An effect of the light on these bacteria is also different. In anaerobic anoxygenic phototrophs, bacteriochlorophyll synthesis does not depend on the light. In aerobic anoxygenic bacteria, in contrast, light suppressed bacteriochlorophyll synthesis, so that pigmentation was observed only in the dark [4].

According to their physiological characteristics, the purple anoxygenic phototrophic bacteria *Rhodobaca bogoriensis* [7] and *Rbc. barguzinensis* [8] isolated recently from soda lakes occupy an intermediate position between these two groups. Similar to anaerobic anoxygenic phototrophs, they are able to grow under anaerobic conditions in the light, while, similar to aerobic anoxygenic phototrophs, they lost the capacity for autotrophic CO_2 assimilation.

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Table 1. Growth and bacteriochlorophyll *a* synthesis of *Rba. sphaeroides, Rba. bogoriensis*, and *Rna. thiooxidans* in the medium with acetate in the dark and in the light (the growth is shown as μg/mL, bacteriochlorophyll concentration as μg/mg protein)

Growth conditions	*Rha. sphaeroides*		*Rbc. bogoriensis*		*Rna. thiooxidans*	
	Growth	Bchl	Growth	Bchl	Growth	Bchl
Light, anaerobic	306	7.3	400	5.8	None	None
Light, aerobic	214	0.7	356	0.6	252	0.02*
Dark, aerobic	100	0.82	272	0.7	230	0.45*

* Indicates the data of Sorokin et al. [13].

The goal of the present work was to study the physiological and enzymological characteristics of the photosynthetic bacteria belonging to the three described groups of phototrophic alphaproteobacteria.

MATERIALS AND METHODS

Bacterial strains and cultivation conditions. *Rba. sphaeroides* strain *2R* (323 CM MSU) was obtained from Culture Collection of the Department of Microbiology of the Moscow State University and *Rbc. bogoriensis* strain LBBI (DSM 18756) were the subjects of the study. The type strain *Rna. thiooxidans* was obtained from the collection of V.M. Gorlenko (Winogradsky Institute of Microbiology, Russian Academy of Sciences). The bacteria were grown in the media described earlier [3, 7, 9]. The cultures were grown in the presence of acetate in the light (1000 lx) in a luminostat under anaerobic and aerobic conditions and in the dark under aerobic conditions at 30°C. Cultivation under aerobic conditions was carried out in 500-mL flasks containing 150 mL of the medium under shaking (200 rpm).

Assimilation of the labeled substrates. The exponential-phase cells were separated from the medium by centrifugation (5000 *g*, 10 min), washed with 0.01 M potassium phosphate buffer, and resuspended in the same buffer. The pH of the buffer was adjusted to that of the culture medium. For *Rbc. bogoriensis* and *Rna. thiooxidans*, the buffer was supplemented with NaCl (1 and 2%, respectively). Experiments on the assimilation of 2-[^{14}C]acetate by the cell suspensions were carried out in 10-mL medical syringes in the light (1000 lx) and in the dark. To create aerobic conditions, the syringes were filled with 5 mL of the medium and 5 mL of the air as the gas phase. Reaction was started by addition of acetate (5 mM, 0.02 MBq) and was stopped after a relevant time interval by filtering of 1 mL of the cell suspension through nitrocellulose filters (0.45 μm). The filteres were dried and analized on a LKB RacBeta 1127 scintillation counter.

Determination of the enzymatic activity. The activity of the enzymes of the tricarboxylic acid (TCA) cycle and the glyoxylate bypass was determined at the late exponential phase of growth. The cells were separated from the medium by centrifugation, washed with potassium phosphate buffer, pH 7.8, and disrupted by sonication (22 kHz, 3 min). After centrifugation (36000 *g*, 20 min), the supernatant was used for enzyme activity determination. The activity of the tricarboxylic acid (TCA) cycle and the glyoxylate bypass enzymes was determined using the standard techniques [10].

Oxydase activity. Oxydase activity in the cell suspension was measured as oxygen absorption using a closed Clark Pt electrode. *N*,*N*,*N*,*N*,-tetramethyl-*p*-phenilenediamine (TMPD, 100 μM) with 5 mM of sodium ascorbate was used as the donor of electrons. One polarographic cell contained 1–3 mg of protein per 1 mL.

Differential cytochrome spectra. Differential cytochrome spectra of the cells grown under aerobic conditions in the dark were registered in the cell-free extracts using a Hitachi 200-20 spectrofotometer.

Bacteriochlorophyll synthesis. Bacteriochlorophyll was determined in acetone–methanol cell extracts at 765 nm [11]. The protein content in the cells and cell-free extracts was measured by the Lowry method.

RESULTS

Growth of the cells and bacteriochlorophyll synthesis under aerobic and anaerobic conditions in the light and in the dark. Comparative study of bacterial growth on acetate showed that the yield of *Rba. sphaeroides* under aerobic conditions in the dark was three times lower than under anaerobic conditions in the light. The yield of the *Rbc. bogoriensis* cells under aerobic conditions in the dark was only one-third lower than that of the cultures grown under anaerobic conditions in the light. *Rna. thiooxidans* grew only in the presence of oxygen. Under aerobic conditions, light was shown to stimulate the growth of all three cultures (Table 1).

The presence of oxygen in the medium is the main factor regulating the formation of a photosynthetic apparatus in most purple phototrophic bacteria. Similar to other anaerobic anoxygenic bacteria, oxygen suppressed bacteriochlorophyll synthesis in *Rba. sphaeroides* and *Rbc. bogoriensis* (Table 1). While *Rna. thiooxidans* was unable to grow under anaerobic conditions, the level of bacteriochlorophyll synthesis

Table 2. Acetate assimilation by the *Rba. sphaeroides, Rba. bogoriensis*, and *Rna. thiooxidans* cells grown under various conditions (nmol/mg protein per min)

Experimental variant	Growth conditions				
	Rba. sphaeroides		*Rbc. bogoriensis*		*Rna. thiooxidans*
	Anaerobic, light	Aerobic, dark	Anaerobic, light	Aerobic, dark	Aerobic, dark
Anaerobic, light	14.1	3.8	46.0	39.5	–
Aerobic, light	19.6	6.3	49.7	51.6	7.7
Aerobic, dark	17.3	4.2	10.7	17.6	5.2

Rna. thiooxidans did not assimilate acetate anaerobically in the light.

Table 3. Inhibition of acetate assimilation by fluoroacetate in *Rba. sphaeroides*, *Rba. bogoriensis*, and *Rna. thiooxidans* (% of inhibition)

Experimental variant	Growth conditions				
	Rba. sphaeroides		*Rbc. bogoriensis*		*Rna. thiooxidans*
	Anaerobic, light	Aerobic, dark	Anaerobic, light	Aerobic, dark	Aerobic, dark
Anaerobic, light	40	16	38	41	–
Aerobic, light	49	48	40	67	46
Aerobic, dark	84	71	63	66	46

Rna. thiooxidans did not assimilate acetate anaerobically in the light.

by these bacteria under aerobic conditions in the dark was close to that *Rba. sphaeroides* and *Rbc. bogoriensis*.. However, the synthesis of the pigment in *Rna. thiooxidans* was observed only under aerobic conditions in the dark and was suppressed by the light. This may be explained as an effect of the circadian rhythm of the growth of these bacteria in their natural environment. Bacteriochlorophyll synthesis occurs in the night in the absence of light. During the day bacteriochlorophyll synthesis is suppressed by the light, and the pigment synthesized during the night is destroyed. Residual quantities of bacteriochlorophyll in *Rba. sphaeroides, Rbc. bogoriensis*, and *Rna. thiooxidans* grown under aerobic conditions in the dark were probably sufficient to stimulate the growth of these cultures in the light (Table 1).

Acetate assimilation. *Rba. sphaeroides, Rbc. bogoriensis*, and *Rna. thiooxidans* are photoheterotrophs and may use for their growth a wide range of organic substrates including acetate [3, 7, 9]. In *Rba. sphaeroides* grown on the medium with acetate, assimilation of the labeled acetate occurred both under anaerobic conditions (in the light) and under aerobic conditions (in the light and in the dark). However, the degree of acetate fixation depended both on the growth and experimental conditions (Table 2). Acetate assimilation was significantly higher in the light-grown cells than in the cells grown in the dark. In the cells grown aerobically, acetate fixation was stimulated by light and increased by 10–50%, irrespective of the growth conditions. Unlike *Rha. sphaeroides*, aceate assimilation by *Rbc. bogoriensis* in the light under anaerobic and aerobic conditions was much less dependent on the growth conditions. The rate of aerobic acetate fixation increased significantly in the light (three- to fivefold) irrespective of the growth conditions. Since *Rna. thiooxidans* did not grow under anaerobic conditions in the light, these bacteria assimilated acetate only under aerobic conditions. However, in these bacteria aerobic acetate assimilation increased in the light by 50%, suggesting their capability for photosynthesis. Fluoroacetate is a known specific inhibitor of the aconitase activity in the TCA cycle. In *Rba. sphaeroides* and *Rbc. bogoriensis*, irrespective of the growth conditions, the effect of fluoroacetate on acetate assimilation increased significantly under aerobic conditions in the dark (Table 3). The level of the inhibiting effect of fluoroacetate did not depend on the light during the experiment (Table 3).

Activity of the enzymes of the tricarboxylic acid cycle. Activity of almost all TCA cycle enzymes in the *Rba. sphaeroides* cells grown under aerobic conditions in the dark was significantly higher than that of the cells grown anaerobically in the light (Table 4). In *Rbc. bogoriensis* grown aerobically, the activity of most TCA cycle enzymes either decreased or remained unchanged. In *Rna. thooxidans*, the activity of the TCA cycle enzymes was comparable to that of *Rba. shaeroides* and *Rbc. bogoriensis* and was sufficient

Table 4. Activity of the TCA cycle and glyoxylate bypass enzymes in *Rba. sphaeroides, Rba. bogoriensis,* and *Rna. thiooxidans* grown in the presence of acetate under various conditions (nmol/min per mg protein)

Enzyme	Growth conditions				
	Rba. sphaeroides		*Rbc. bogoriensis*		*Rna. thiooxidans*
	Anaerobic, light	Aerobic, dark	Anaerobic, light	Aerobic, dark	Aerobic, dark
Citrate synthase	39.5	189.1	53.4	10.6	37.0
Aconitase	217.1	388.3	21.8	25.2	265.3
Isocitrate dehydrogenase	100.6	429.3	110.7	15.6	118.1
2-Oxoglutarare dehydrogenase	21.8	0.8	7.6	4.0	2.2
Succinate dehydrogenase	18.9	73.2	5.6	5.5	11.5
Fumarate hydratase	165.0	1345.2	85.7	41.3	440.0
Malate dehydrogenase	517.1	1600.1	1073.3	483.6	685.7
Isocitrate lyase	0.0	0.0	16.0	15.4	0.0
Malate synthase	23.3	42.8	1.3	4.1	29.1

to provide for efficient growth of the cells under aerobic conditions.

Cytochrome content. All studied organisms (if grown under aerobic conditions in the dark) were able to synthesize cytochrome aa_3 as the terminal cytochrome *c* oxidase. However, unlike *Rba. sphaeroides* and *Rbc. bogoriensis, Rna. thiooxidans* was characterized by an enhanced level of cytochrome aa_3 (Fig. 1).

Oxidase activity. Oxygen utilization using the TMPD + ascorbate pair as the donor of electrons was used to characterize the oxidase activity of the studied bacterial cells. All studied organisms demonstrated relatively high oxidase activity, irrespective of the growth conditions (Table 5). The values of the oxidase activity for *Rba. sphaeroides* and *Rbc. bogoriensis* grown under anaerobic conditions in the light or under aerobic conditions in the dark did not change significantly. Oxidase activity of *Rna. thiooxidans* was comparable with that of *Rba. sphaeroides* or *Rbc. bogoriensis*.

DISCUSSION

All studied anoxygenic phototrophic bacteria were able to grow aerobically in the dark (Table 1). The main factor which regulated the synthesis of the photosynthetic pigments and development of the photosynthetic apparatus in these bacteria was the presence of oxygen. In *Rba. sphaeroides* and *Rbc. bogoriensis* grown aerobically, synthesis of bacteriochlorophyll was suppressed almost completely, as is typical of all nonsulfur purple bacteria [3]. This evolutionary fixed property allows anaerobic anoxygenic phototrophs to grow chemotrophically under aerobic conditions in the light, since under these conditions high concentrations of chlorophyll result in accumulation of the highly toxic triplet form of bacteriochlorophyll and of singlet oxygen [12]. In *Rna. thiooxidans*, which lost the ability to grow under anaerobic conditions, the level of bacteriochlorophyll synthesis in the dark under aerobic conditions was the same as in *Rba. sphaeroides* and *Rbc. bogoriensis*. However, in *Rna. thiooxidans* synthesis of the pigment occurred only under aerobic conditions in the dark, making it possible to prevent accumulation of the toxic forms of bacteriochlorophyll and singlet oxygen. However, residual concentration of bacteriochlorophyll in *Rba. sphaeroides, Rbc. bogoriensis*, and *Rna. thiooxidans* grown aerobically in the dark was presumably enough for the stimulation of the growth and of acetate assimilation under aerobic conditions in the light (Tables 1, 2).

Table 5. Oxidase activity of *Rba. sphaeroides, Rbc. bogoriensis*, and *Rna. thiooxidans* grown under various conditions in the medium containing acetate (nM/min per mg of the protein)

Growth conditions	*Rba. sphaeroides*	*Rbc. bogoriensis*	*Rna. thiooxidans*
Anaerobic, light	35.4	79.2	No growth
Aerobic, dark	44.9	102.0	60.3

The results obtained in the studies of acetate assimilation reflect the degree of adaptation of the studied bacteria to aerobic growth in the dark. Thus, the capacity of *Rba. sphaeroides* for assimilation of carbon from acetate decreased drastically during growth under aerobic conditions in the dark. *Rbc. bogoriensis* and *Rna. thiooxidans* did not show such a decrease, indicating an evolutionary fixed adaptation of these bacteria to growth under aerobic conditions (Table 2).

The same conclusions could be made based on the analysis of the TCA cycle enzymes activity in the studied organisms (Table 4). In anoxygenic photoheterotrophs that are able to grow both aerobically and

anaerobically, the TCA cycle has several functions. Under anaerobic conditions in the light, the organic compounds that are oxidized via the TCA cycle act as carbon sources and reducers for the biosynthetic processes within the cell. ATP is synthesized by photosynthetic phosphorylation. Under aerobic conditions in the dark, the TCA cycle plays a bioenergetical function as well. During acetate oxidation in the dark, ATP is mainly supplied by oxidative phosphorylation in the respiratory electron transfer chain. The reducers for this respiratory chain are supplied by the redox reactions of the TCA cycle. Thus, the working load of the TCA cycle reactions under aerobic conditions in the dark must increase signifiacntly. In accord with this suggestion, the activity of almost all TCA cycle enzymes in *Rba. sphaeroides* grown aerobically in the dark increased significantly compared to the cells grown anaerobically in the light. This finding was confirmed by the fact that the sensitivity of acetate assimilation towards the action of the specific TCA cycle inhibitor, fluoroacetate, also increased (Table 3). In *Rbc. bogoriensis*, regulation of the TCA cycle enzymes synthesis during the transition from photoheterotrophic to chemoorganotrophic metabolism was less pronounced. In *Rbc. bogoriensis* grown aerobically, the synthesis of the TCA cycle enzymes either decreased or remained unchanged, this being presumably caused by the better adaptation of the *Rbc. bogoriensis* cells to aerobic growth in the dark (Table 1). The yield of the *Rba. sphaeroides* cells grown aerobically in the dark was three times lower than that of the cells grown anaerobically in the light. The yield of the *Rbc. bogoriensis* cells in the dark under aerobic conditions was only one-third lower than that of the cells grown anaerobically in the light. *Rna. thiooxidans* grew only in the presence of oxygen in the medium. All studied bacteria possessed high oxidase activity irrespective of the growth conditions (Table 5). Importantly, the oxidase activity of *Rba. sphaeroides* and *Rbc. bogoriensis* did not change significantly during their transition from anaerobic photoorganotrophic to aerobic chemoorganotrophic growth conditions. Therefore, the presence of a respiratory chain in the cells grown anaerobically in the light makes it possible to substitute rapidly the ATP synthesis using the photosynthetic electron transfer chain by the ATP synthesis using the respiratory electron transfer chain. However, in *Rba. sphaeroides* and *Rbc. bogoriensis*, in addition to the cbb_3 cytochrome oxidase which functions as the oxidase in the light-grown cells, under aerobic conditions in the dark the aa_3 cytochrome oxidase was synthesized, which enhanced the ATP generation effeciency by its respiratory chain [13, 14]. *Rna. thiooxidans* grew only in the dark under aerobic conditions and possessed the respiratory chain [15] with cytochrome aa_3 as the terminal cytochrome oxidase (Fig. 1) as many obligate aerobic chemoorganotrophs.

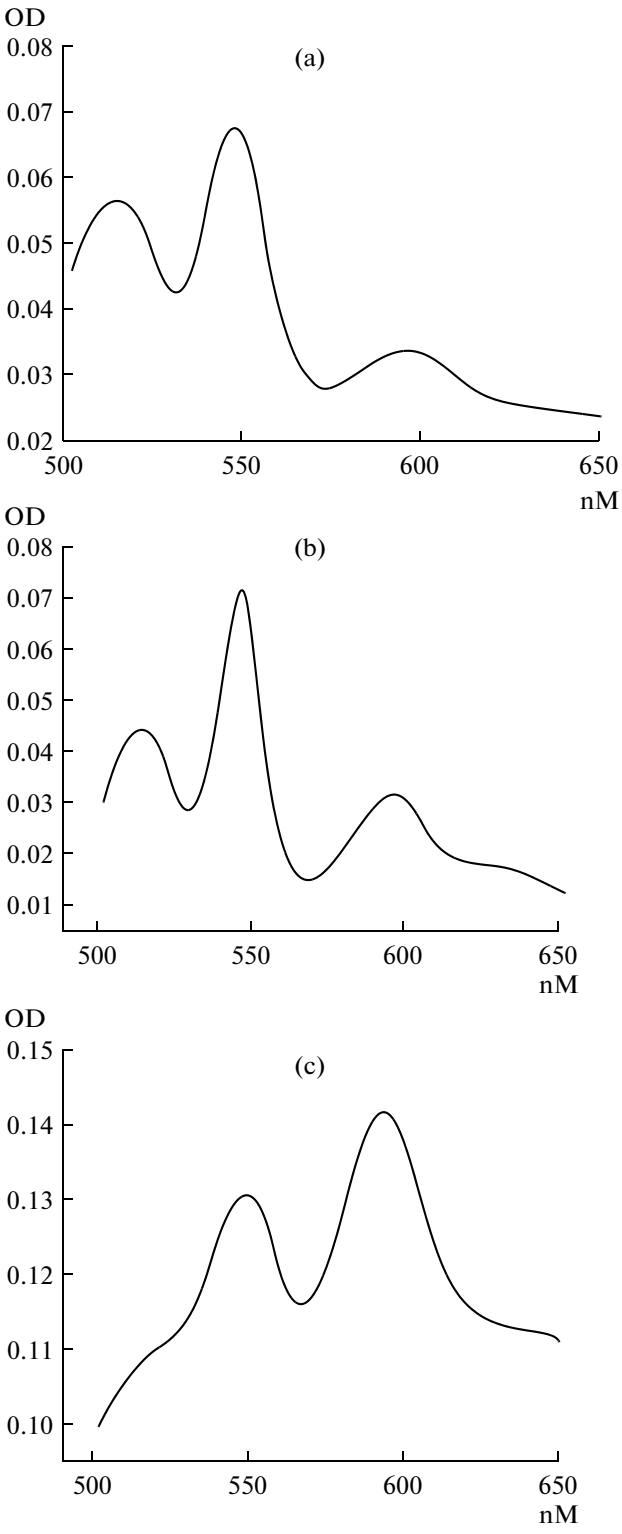

Fig. 1. Differential spectra (dithionite minus ferricyanide) of the cell-free extracts grown aerobically in the dark: *Rba. sphaeroides* (a), *Rbc. bogoriensis* (b), and *Rna. thiooxidans* (c).

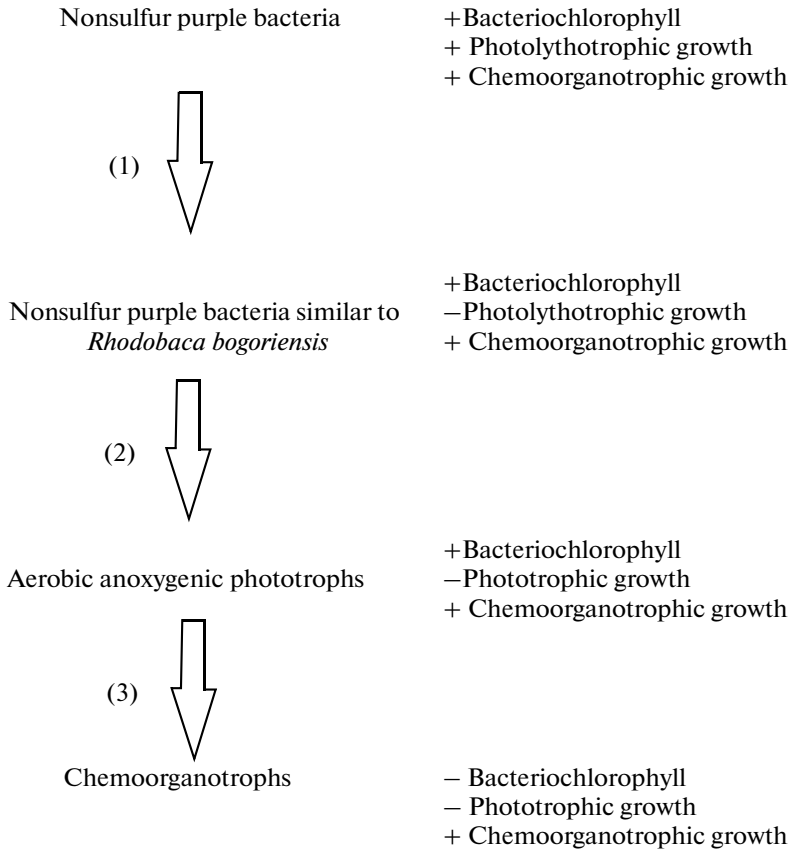

Fig. 2. Proposed path of the evolution of photoorganotrophs to chemoorganotrophs.

Thus, one could suggest the origin of modern chemoorganotrophs from anoxygenic phototrophic bacteria. Such a scheme implies the evolution from anoxygenic photoorganotrophs to aerobic chemoorganotrophs via several stages (Fig. 2). (1) When oxygen appeared in the atmosphere, anoxygenic nonsulfur purple bacteria obtained the capabilty for aerobic growth in the dark. Some representatives of this group lost their capability for CO_2 assimilation through the Calvin cycle and, therefore, for photolythotrophy, but preserved their capabilty for growth in the light (as photochemoorganothrophs). (2) At the second stage these bacteria lost the capability for phototrophic growth but preserved their capability for bacteriochlorophyll stnthesis. (3) At the third stage they lost the capability for bacteriochlorophyll synthesis and transformed to typical chemoorganotrophs.

Notably, a new physiological group of nonsulfur purple bacteria has been discovered recently, the representatives of which, while being anaerobic photoheterotrophs, preferred aerobic chemoorganotrophic growth [16]. According to their physiological characteristics, they occupy an intermediate position between the first and second evolutionary groups.

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Translated by L. Gabdrakhmanova