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Aerobic anoxygenic phototrophic bacteria and their roles in marine ecosystems

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Abstract **Aerobic anoxygenic phototrophic bacteria (AAPB) are characterized by the following physiological and ecological features. A mother AAPB cell can unusually divide into 3 daughter cells and looks like a "Y" during the division. AAPB cells sometimes adhere together forming a free-floating population. Most of the known AAPB species are obligately aerobic. Bacteriochlorophyll a (BChl a) is the only photosynthetic pigment in AAPB, and the number of BChl a molecules in an AAPB cell is much less than that in an anaerobic phototrophic bacterial cell, while the accessorial pigments carotenoids in AAPB are abundant in concentration and diverse in species. In addition to the common magnesium containing BChl a, a zinc-containing BChla was also seen in AAPB. AAPB have light harvesting complex Ⅰ but usually lack light harvesting complex Ⅱ. Although AAPB featur in photosynthesis, their growth is not necessarily light- dependent. There is a mechanism controlling the photosynthesis approach. AAPB are widely distributed in marine environments especially in oligotrophic oceans accounting for a substantial portion of the total biomass and playing a unique role in the cycle of carbon and other biogenic elements. Besides the contribution to primary production, AAPB also have great potentials in bioremediation of polluted environments. Studies on AAPB would be of great value in understanding the evolution of photosynthesis and the structure and function of marine ecosystems.**

Keywords: aerobic anoxygenic phototrophic bacteria (AAPB), bacterial chlorophyll, microbes, marine ecosystem.

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Covering 71% of the surface of the earth, the ocean is the biggest carbon reservoir in the world and plays a crucial role in global carbon cycling. Oxygenic photosynthesis of phytoplankton has been known to be the mechanism for forming primary production in the sea for many years, but anoxygenic photosynthesis has been ignored. In fact, there are two anoxygenic phototrophic approaches existing in marine bacteria. One is the anaerobic anoxygenic photosynthesis, the other is aerobic anoxygenic photosynthesis. The latter by aerobic anoxyenic phototrophic bacteria (AAPB) is particularly of ecological significance in the global carbon cycling given the vast aerobic area of the ocean. AAPB were discovered 20 years ago[1], but did not draw much attention until recently. Now, many physiological and ecological features of AAPB have been brought to light. For example, AAPB are obligately aerobic, photosynthetic but not completely light dependent[2,3]. The cellular content of bacterial chlorophyll a (BChl a) of AAPB is much lower than that of anaerobic phototrophic bacteria. AAPB contain diverse carotenoids. Some AAPB species even possess a unique zinc containing BChl a[4]. The ratio of BChl a to phytoplankton chlorophyll a (Chl a) can be up to 10% in the oceanic water, occupying 11% of the total microbial biomass[5]. AAPB are present in the whole euphotic zone of the oceans over the world. The recognition of the ecological significance of AAPB in terms of carbon fixation actually implies that we have to reconsider and reevaluate the current models and budgets of ocean carbon cycling based on the data from oxygenic photosynthesis[6]. AAPB represent a function-unknown cluster of marine microbes that might be of crucial importance to the understanding of ocean carbon cycling[5]. In this review, the authors summarized the recent pro- gress and study trends in the physiological and ecologi- cal features and the roles of AAPB in the marine ecosystems.

1 Cellular feature

All the known AAPB have gram-negative cell walls[3]. The most seen AAPB cells are cylinder-shaped, with cilia and flagella (Fig. 1). AAPB cells are usually 1.2 μm in length, 0.7 μm in diameter and 0.5 μm^3 in cell volume, 0.5 pg in wet weight, 0.05 pg in dry weight. And the ratio of BChl a to dry cell weight is 2.4 μmol/g and cellular BChl a content is 1.2×10^{-19} mol[5]. Three types of cell division are seen in AAPB: 2 daughter-cell division, 4 daughter-cell division and the unusual 3 daughter-cell division (Y cell division). Sometimes, 5—10 AAPB cells adhere together and form a free-floating population[3]. AAPB isolated from natural water usually look pink or orange.

2 Physiological and ecological characteristics of AAPB

(ⅰ) AAPB are obligately aerobic bacteria except for *Roseobacter denitrificans* which can use nitrite or trimethylamine N-oxide as an electron accepter for photosynthesis under anaerobic conditions[7]. The reason that AAPB depend on oxygen for photosynthesis is most likely that the protein environment of the photosynthesis reaction center (RC) primary acceptor Q_A produces a high midpoint potential, which results in nearly complete reduction of Q_A under anaerobic conditions, preventing light driven charge separation; or reduction of the photosynthetic apparatus electron transfer components

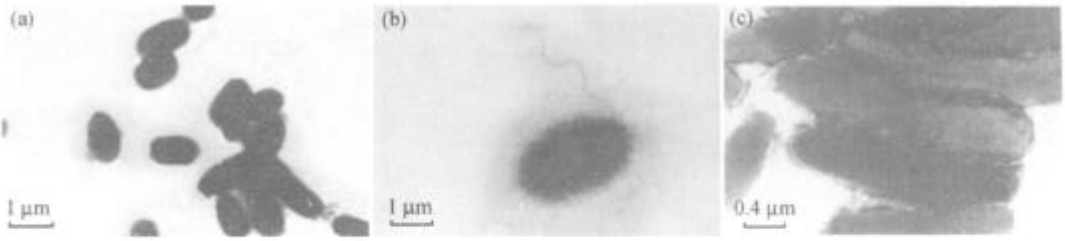

Fig. 1. AAPB isolated from the East China Sea. (a) A group of cells; (b) a cell with a flagellum; (c) cells under division.

interferes the photosynthetic electron transfer and results in photo- reduction of the double bond C==C at the 3,4-positon of spheroidenone. Any way, it is related to the protein environment of RC Q_A and light regulation of BChl a synthesis[3, 8].

(ii) Although AAPB feature in photosynthesis, their growth is not necessarily light-dependent. There is a mechanism controlling the photosynthesis approach[9]. AAPB actually grow best when organic substrates are available. Organic carbon rather than inorganic carbon is used as the carbon and energy sources. For anaerobic purple bacteria, light is the major energy (ATP) source during anaerobic photoheterotrophic growth, and organic compounds are the substrates oxidized to produce reducing power and intermediates for biosynthetic anabolism[3]. For anaerobic phototrophic bacteria, biosynthesis of Bchla is inhibited by strong light but stimulated by weak light. In contrast, for AAPB, light intensity lower than 20 $\mu E \cdot m^{-2} \cdot s^{-1}$ would strongly inhibit their synthesis of BChl a[10].

(iii) Unlike anaerobic phototrophic bacteria that have several species of photosynthetic pigments, such as bacteriochlorophyll a, b, c, d, e, f, etc., AAPB contain only bacteriochlorophyll a. As BChl a is incorporated in the pigment-protein complex, its *in vivo* absorption peaks are in the near infrared region from 800 to 870 nm, but the absorption peaks of the extracts in organic solvent are at 370 —390 nm and 770 nm[11]. The number of BChl a molecules in an AAPB cell is much less than that in an anaerobic phototrophic bacterial cell. Most AAPB BChl a contain a magnesium atom, but a zinc-containing BChl a was found in the *Acidiphilium rubrum*[4]. Since all natural chlorophylls were thought to be derived from the Mg-containing porphyrin. The discovery of Zn-containing bacteriochlorophyll may suggest the existence of other kinds of unknown bacteriochlorophyll[3].

(iv) Abundant accessory pigments. The content of photosynthetic pigments in AAPB is low, while the accessorial pigments carotenoids in AAPB are abundant in concentration and diverse in species. So far more than 20 carotenoids have been found, including β-carotene, spirilloxanthin, bacteriorubixanthinal, zeaxanthin, adonixanthin, caloxanthin, nostoxanthin, erythroxanthin, etc. The molar ratio of BChl a to carotenoid in AAPB cells ranges from 1∶8 to 1∶10[12]. These polar carotenoids are associated with light harvesting-light reaction center complex (LH Ⅰ - RC), transferring light energy to the BChl a molecules. The high polarity of a carotenoid molecule does not interfere with the function of LH[3].

(v) AAPB have light harvesting complex Ⅰ (LH Ⅰ) but usually lack of light harvesting complex Ⅱ (LH Ⅱ)[5]. AAPB cannot grow on photosynthesis independently. The key enzyme of calvin cycle ribulose bisphophate carboxylase (Rubp) has not been found in any AAPB species[3,12]. But light energy can enhance the transportation and assimilation of substrate for biosynthesis. This has been verified in the continuous culture experiments with *Erythromicrobium hydrolyticum*[10]. Therefore bacteria with capability of photosynthesis are more competitive than those lack photosynthetic pigments[3]. AAPB provide us with a good material for studies toward a better understanding of photosynthetic physiology, and the origin and derive of photosynthetic apparatus.

3 Origin, phylogeny and taxonomy

Although we have known that purple nonsulfur phototrophic bacteria, which belong to α-proteobacteria, are the closest relatives of AAPB in taxonomy[13], the ancestor of AAPB and their evolutionary pathway of their photosynthesis are still unclear. Genomic analysis of the photosynthetic genes and operon organization naturally occurring in marine bacteria revealed that those phototrophic gene clusters which closely resembled one subclass of proteobacteria are never recorded in marine environments before [14]. The recent studies indicate that AAPB donot form a homogenous family in the phylogenetic trees, but are distributed among phototrophic and nonphototrophic bacteria. AAPB seem to originate from an archaic marine aerobic anoxygenic phototrophic bacterium. In adaptation to the continuously changed environments, AAPB either permanently lost their photosynthetic genes or developed a mechanism switching the photosynthesis apparatus according to the availability of substrates. This is quite similar to the situation of phylogeny of anaerobic phototrophic bacteria and forms the basis that non-photosynthetic bacteria had a photosynthetic ancestor with photosynthesis genes lost during evolution[3,15]. The dis-

covery of the phototrophic strain, JF-1, also shows that the photosynthesis may originate from the deep-sea hydrothermal vent environments and was gradually distributed to shallow waters. Anyway, the current evidence is not yet enough to come to a definite conclusion on the origin and evolution of AAPB.

AAPB usually are taxonomically classified into two marine genera: *Erythrobacter* and *Roseobacter*, and six freshwater genera: *Acidiphilium*, *Erythromicrobium*, *Erythromonas*, *Porphyrobacter*, *Roseococcus*, and *Sandaracinobacter*, while DNA-DNA hybridization, morphological and physiological evidence lead to a proposal for two marine genera: marine *Erythrobacter* and *Roseobacter*[16] and the two freshwater genera: *Erythromicrobium* and *Roseococcus*[17]. Although DNA GC contents vary substantially with different genera (GC content of *Erythrobacter* ranges from 57—60 mol%, and 70.4 mol% for *Roseococcus thiosulfatophilus*), it is not a very strict criterion for classification. Even the taxonomic importance of photosynthetic pigments is also controversial, for the differences in 16SrRNA between phototrophic and nonphototrophic spesies are small. There are two kinds of explanation on this point: If AAPB originate from a branch of anaerobic phototrophic bacteria ancestors, they may show an intermediate evolution phase between anaerobic purple phototrophic bacteria and nonphotosynthetic bacteria. Or, photosynthetic genes were obtained by nonphotosynthetic bacteria during gene transfer[18]. Because photosynthetic pigments are not only detectable but also determining on the ability and type of a species to utilize energy, BChl together with RC, LH pigment-protein complexes and electron transfer components should be taken as valid taxonomic criteria[3].

4 Ecological functions of AAPB in the ocean

So far, AAPB have been found in diverse marine environments, even in hydrothermovents; for example, the JF-1 strain can tolerate extreme salinity (100 ‰), wide range of temperature (5—42℃), and pH 5.5—10.0[19]. The most ecologically meaningful aspect is their wide distribution in the vast area of the sea. Kolber et al.[5] reported that AAPB accounts for (11.3±1.7)% of the total microbial community in the euphotic zone of the Northeastern Pacific (48° N, 128° W). The BChl a/Chl a ratio is about 0.8%. Furthermore the ratio increases to 10% in the oligotrophic area of the Northeastern Pacific (14° N, 104° W). Goericke[20] pointed out that the percentage of AAPB increases with decreasing total chlorophyll content, and thus the oceanic waters are the main habitats of AAPB[20]. Kolber et al.[5] estimated the average BChl a/ Chl a percentage over the global ocean is about 5% —10%. If this estimate is reliable, the contribution of AAPB to the total primary production will be a big impact on the current theory and knowledge, because the current understanding of marine carbon pool and the role of marine ecosystem in the global carbon cycling is based on the fact that primary production is provided by phytoplankton rather than others. Indeed, we often run into trouble with oxygen balance in modeling. That is, oxygen budgets from photosynthesis are often out of range with measurements. If AAPB are important contributors to marine organic production, then the consideration of AAPB in oxygen budgets would cause the current oxygen balance to move to the net consumption side. In the previous models, bacteria are the principal components of the heterotrophic carbon pool. When 5%—10% of the carbon in this pool are moved to the autotrophic pool, the whole carbon budget of the ocean would change greatly.

Back in 1993, Jiao and Wang[21] proposed a concept of "the structure of marine primary productivity" which gave insight into the connotation of primary productivity. In this concept, primary productivity is analyzed from the following four points of view: "the producer structure of primary productivity"—— proportions of the components in the total primary production by different primary producers; "the size structure of primary productivity"—— proportions of the components in the total primary production by different cell size classes, pico-, nano-, and net-plankton; "the production structure of primary productivity" —— the ratio of photosynthetically produced particulate organic carbon to the sum of photosynthetically produced particulate organic carbon and photosynthetically produced dissolved organic carbon; and "the functioning structure of primary productivity"—— the ra- tio of new production to the total primary production. Among which, the "producer structure" clearly pointed out that the contribution of photobacteria could be an important contributor to the total primary production, and suggested that different components should be measured separately toward a better understanding of the functions of different ecosystems. The discovery of the ecological importance of the AAPB further verified necessity and essentiality of studying the structure of primary productivity. Field investigation is the first step to understand the nature, and data from the nature are the final proof for our conclusions. Goericke et al.[20] reported that the average BChl a/Chl a ratio of the South Carlifornia coast is 1.1% in the near shore water and 0.5% in the mesotrophic shelf water and oligotrophic coastal water. This is quite different from the conclusion of Kolber et al. Obviously, wide investigations are needed for a better understanding and more convincible conclusion of the contribution of AAPB in different marine environments. Only obtaining data from the representative marine environments can the role of AAPB in the carbon cycling of the marine ecosystem be addressed.

The most common method used in AAPB study is the high performance liquid chromatography (HPLC)

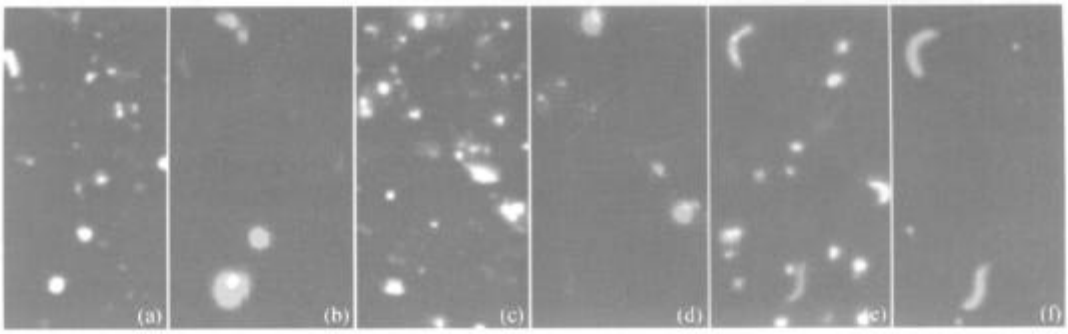

Fig. 2. DAPI stained heterotrophic bacteria ((a), (c), (e)) and aerobic anoxygenic phototrophic bacteria ((b), (d), (f)) under epifluoroscence microscopy as seen by CCD-camera with infra-red capability. (a) and (b), (c) and (d), (e) and (f) are the same samples respectively.

which is very useful in pigment separation and determination but not able to determine the percentage of AAPB in total bacteria. The recent progress in this regard is the epifluorescence microscope-infrared photography appro- ach (EFM-IRP) by the authors (Fig. 2). The EFM-IRP takes the advantage of fluorescent emissions of the BChl a of AAPB at 750—1050 nm when excited at 350—500 nm, by using an infra-red sensitive CCD camera for photograph of AAPB on an epifluorescence microscope. This approach not only enumerates AAPB and total bacteria, but also makes the different cell shapes visible. Our preliminary study showed that the AAPB in oligotrophic environments are often curved and rod in shape, and those in eutrophic environments are more round comparatively. In addition, application of flow cytometry to AAPB also turned to be feasible, which would provide rapid enumeration of both AAPB and other bacteria.

So far, our data from the China Seas showed an increasing gradient in AAPB abundance from the coastal waters to the oceanic waters, e.g. contributions of AAPB in the the Yangtze River estuary is comparable to the results by Goericke et al.[20] on the South Carlifornia coasts, but that in the Kuroshio Current area is distinctly higher. Further studies are still going on.

Besides the contribution to primary production, AAPB also have great potentials in bioremediation of polluted environments, such as decomposition of toxic organics and reduction, adsorption, precipitation and transformation of toxic heavy metals to less toxic forms[22]. AAPB are reported to be resistant to high level of Se, Pb and Mo[23]. It is also revealed recently that AAPB can reduce the high toxic telluride (Te-**IV**) to metallic tellurium (Te-0). These specific functions can be applied to bioremediation of industrial waste with heavy metal pollution as well as bioleaching of metals from ores or mining tailings with metal levels too low for smelting. For bioleaching of metal, an instance is the American copper industry. About 10% of the US copper production are from leaching by *Thiobacillus* and *Leptospirillum* species. Since native tellurium is rare and usually in tellurides of lead, copper, silver, gold and antimony and thus difficult to extract, and culture of AAPB is easy, extraction of tellurium by AAPB metallurgy is therefore promising[3].

5 Perspectives

Looking back at the history of marine microbial ecology, we can see a number of significant findings emerging one after another in the past two decades. For example, the discovery of *Synechococcus* in 1979[24], which was the No.1 abundant autotrophs known then; the discovery of *Prochlorococcus* a decade later, which not only replaced *Synechococcus* as the most abundant aerobic oxygenic phototrophs but also drew great attention from scientists to the unique photosynthesis pigments, divinylchlorophyll a, b and other unique features[25,26]. After that, archaea were proved to be not only abundant in extreme environments but also present in the vast common marine environments[27,28]. In the 1990s planktonic virus/phages were found to be extremely abundant, and their ecological role in the marine ecosystem is as consumers that can cause a substaintial loss of other unicellular microbes[29,30]. At the beginning of the 2000s the contribution of AAPB to the total marine primary production was revealed not to be neglected[5,31,32]. These new findings greatly changed our understanding and knowledge about the structures and functions of marine ecosystems and challenged the concepts and theories we have built in the past. Although marine microbes are tiny in cell size, because of their tremendous numbers and their unique ecological roles, they are actually the giant of the ocean. On small scales, they can influence living resource, on large scales, they are associated with global changes. On the other hand, the percentage of known marine microbes is estimated to account for only 10% or less of the whole[30]. Application of new techniques and new methods will result in discovery of new species and new mechanisms. Marine microbial biology and ecology has become a new frontier

of marine sciences. Progress in this area will not only promote the development of the discipline but also contribute to the practice of living resources and environmental issues.

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