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Hybridization of Cloned *Rhodopseudomonas capsulata* Photosynthesis Genes with DNA from Other Photosynthetic Bacteria

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The homology of *Rhodopseudomonas capsulata* DNA segments carrying photosynthesis genes with sequences present in total DNA from certain other photosynthetic and non-photosynthetic bacterial species was determined by hybridization. *R. capsulata* DNA fragments that carry loci for production of peptide components of the photosynthetic reaction center and light-harvesting I antenna complex were found to hybridize to DNA from some photosynthetic species. However, fragments that carry carotenoid or bacteriochlorophyll biosynthesis genes showed either weak or undetectable heterospecific hybridization under the conditions employed.

DNA-DNA and DNA-RNA hybridizations have been widely used to determine the extent of sequence similarity between genes that encode homologous functions in different organisms. Generally, use of these procedures assumes that those organisms most closely related will show the greatest similarity in the sequence of functionally corresponding genes. Thus, mRNA from *Bacillus subtilis* does not hybridize with *trp* genes from *Escherichia coli*, whereas mRNAs from the more closely related *Salmonella typhimurium*, *Serratia marcescens*, and *Shigella dysenteriae* have been found to hybridize under the conditions employed (9). Specific evolutionary conservation among tRNA and rRNA genes has been inferred from studies in which heterospecific hybridization of these RNAs was compared with hybridization of total mRNA: mRNA hybridized poorly with heterologous DNA whereas rRNA and tRNA hybridized significantly better (4, 14, 21). However, conservation of sequence has also been noted for some nitrogenase genes (20, 27) and for the gene encoding the translational elongation factor Tu (12) between species whose ancestors are believed to have diverged from each other 10^9 or more years ago.

The *Rhodospirillaceae* and *Chromatiaceae* (purple photosynthetic bacteria) (25) are members of a large group of diverse organisms that can transduce light energy to energy of chemical bonds. Their photosynthetic process differs from that of cyanobacteria and higher plants, among other ways, in that water is not used as an electron donor and oxygen is not produced (24, 25). Although the metabolic and morphological characteristics of known species of photosynthetic bacteria vary greatly, they contain remarkably similar types of photopigments (24, 25, 28). For example, 34 of 38 species of purple photosynthetic bacteria synthesize bacteriochlorophyll a_p as their primary light-absorbing pigment; although a greater variety of carotenoid pigments exists, this variation involves relatively minor modifications of the common C-40 precursor neurosporene (24, 25, 28). Neurosporene itself is the product of a series of biosynthetic reactions beginning with the citric acid cycle intermediate acetyl-CoA (28). However, despite the similar photosynthetic phenotype of these species, analysis of their 16S rRNA sequences has suggested that they are only distantly related (13). Stackebrandt and Woese (32) have proposed that some species of photosynthetic bacteria are phylogenetically more closely related to *E. coli*, *Paracoccus denitrificans*, or *Agrobacterium tumefaciens* than to each other.

Comparative biochemical data have been interpreted as indicating that there was a unicentric origin of photosynthesis before the appearance of significant amounts of free oxygen in the earth's atmosphere, more than 2×10^9 years ago (5, 29, 32, 33). If such interpretations are correct, then ancestors of contemporary photosynthetic bacteria diverged from each other more than 10^9 years ago. The conservation of photosynthetic physiology and photopigments in such organisms could be explained by independent evolution of species in response to very similar environmental selective pressures. However, repeated interspecies transfer of photosynthesis genes is also an attractive hypothesis to account

TABLE 1. Bacterial strains

Strain	Representative % G + C of genome	Source or reference
1. *Escherichia coli* K-12	50–51	This laboratory
2. *Pseudomonas aeruginosa* neotype	67	ATCC[a]
3. *Chromatium vinosum* D	61.3–66.3	3
4. *Rhodospirillum rubrum* 1.1.1	63.8–65.8	3
5. *R. tenue* LA	64.8	3
6. *Rhodopseudomonas viridis* NTHC133	66.3–71.4	3
7. *R. palustris* Bloomington	64.8–66.3	3
8. *R. gelatinosa* Rg1	70.5–72.4	3
9. *R. sphaeroides* 2.4.1	68.4–69.9	3
10. *R. capsulata* B10	65.5–66.8	3

[a] American Type Culture Collection, Rockville, Md.

for the functional similarity of their products. Bacterial genes (or clusters of genes) can be transferred between distantly related species through plasmid conjugation, phage transduction, or genetic transformation (7). This has been shown most extensively for plasmid-borne resistance to antibiotics and for other traits that provide the host organism with a biological advantage (7).

Genes whose products are necessary for photosynthesis have been genetically mapped in two closely related species of photosynthetic bacteria (*Rhodopseudomonas sphaeroides* and *Rhodopseudomonas capsulata*); in both species the genes are grouped relatively closely (19, 23). Such an arrangement would facilitate interspecies transfer of photosynthesis genes en masse, as has been demonstrated in the laboratory with *R. capsulata* (19). Purified protein-pigment complexes from *R. sphaeroides* are capable of light-driven electron transport in concert with mitochondrial membrane electron carriers when combined in vitro (22), implying that non-photosynthetic organisms could potentially become photosynthetic by the acquisition of photosynthesis genes. Ambler and co-workers (2) have interpreted cytochrome *c* sequence analyses as indicating the occurrence of interspecies transfer of cytochrome *c* genes between photosynthetic as well as other bacteria. Alternatively, Dickerson (10) and Woese et al. (35) have argued that cytochrome *c* and 16S rRNA sequence data are consistent with interspecies transfer of those genes occurring relatively rarely, if at all.

If the phenotypic similarities found between species of photosynthetic bacteria result from parallel evolution of the photosynthesis genes in response to environmental pressures, one would expect considerable DNA sequence drift to have occurred subsequent to divergence of these species. Interspecies hybridization of total DNA between *R. capsulata* and *R. sphaeroides* species showed 11 to 28% of the homology seen in self-hybridizations, whereas intraspecies hybridization yielded 62 to 77% (8). The rate of DNA sequence change of invertebrate and vertebrate genes has been estimated to be about 0.1 to 1.0% in 10^6 years (6, 16). Such genetic drift could be secondary to degeneracy of the genetic code or due in part to the substitution of codons for chemically similar amino acids; alternatively, different mechanisms for accomplishing the same function could have evolved (11). In contrast, if the observed phenotypic similarities between photosynthetic bacteria result from preservation of the structural similarity of photosynthesis genes over an extended period of time by repeated lateral gene transfer, then there might exist considerable DNA sequence similarity between the photosynthesis genes of different species. It should be noted that both processes may have played a role to a greater or lesser extent, depending upon the species in question.

To assess the phylogenetic relatedness of photosynthesis genes, we hybridized cloned DNA fragments from *R. capsulata*, containing genes essential for photosynthesis, with DNA extracted from several genera of purple photosynthetic bacteria. Table 1 lists the bacterial strains used. Total DNA was isolated from each species, a sample of each was digested with *Bam*HI restriction endonuclease, and the resulting fragments were separated by gel electrophoresis as described in the legend to Fig. 2. After transfer and covalent coupling of the DNA fragments to paper, hybridizations were performed under conditions that allow as much as 23% mismatch (15) (assuming an average guanosine plus cytosine content of 66% for the *R. capsulata* genome [25]).

Figure 1 shows the correlation between the physical and genetic maps of the photosynthesis region of the genome of *R. capsulata*, as reported by Taylor et al. (34). The DNA fragments used as hybridization probes are designated EB2, *Eco* H, *Bam* G, *Bam* H, *Bam* E, *Bam* I, *Bam* D, and *Eco* F. Together, they contain at least 15 genes whose products affect the photosynthetic phenotype. All fragments have been shown to carry genes coding for enzymes involved in carotenoid (*crt*) or bacteriochlorophyll *a* (*bch*) biosynthesis except for fragments EB2 and *Eco* F. The latter two fragments carry loci that, when mutated, result in aberrant production of peptide components of the photosynthetic reaction center and the light-harvesting I

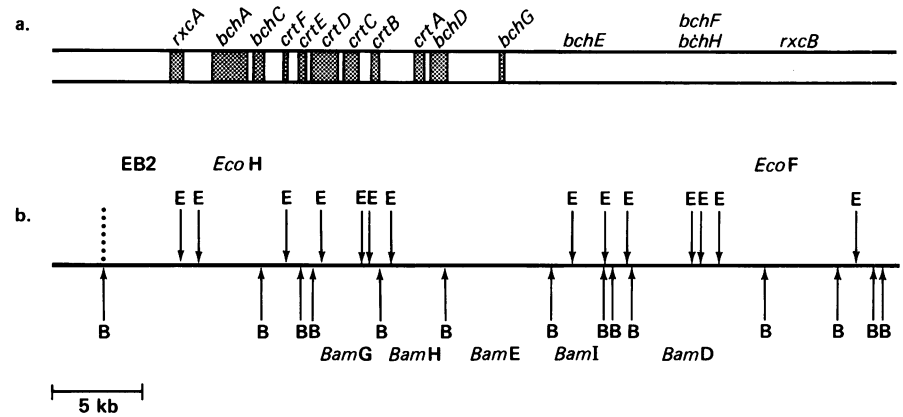

FIG. 1. Genetic (a) and physical (b) maps of the photosynthesis region of *R. capsulata*, drawn to scale. The number refers to distance in kb. The *crt* genes are necessary for production of carotenoid biosynthetic enzymes, the *bch* genes encode products involved in bacteriochlorophyll *a* biosynthesis, and the *rxc* loci are essential for production of reaction center and light-harvesting I antenna complex polypeptides. Restriction endonuclease sites are indicated by arrows: E, *Eco*RI; B, *Bam*HI. Figure taken from Taylor et al. (34).

antenna complex (34). The fragments were each purified from plasmid DNA cloning vectors and radioactively labeled for use in hybridizations, as detailed in the legend to Fig. 2.

Autoradiograms resulting from hybridization experiments are shown in Fig. 2. Because of the low stringency of the hybridization conditions used in these experiments, a background of nonspecific hybridization was usually observed. An autoradiogram resulting from hybridization with the 4.6-kilobase (kb) EB2 fragment is presented in Fig. 2a. As expected, there was strong binding of the probe to a position on the blot corresponding to the 9.3-kb fragment contiguous with EB2 (see Fig. 1) in the lane containing *Bam*HI-digested *R. capsulata* DNA. Unlike most of the other fragments tested, EB2 hybridized quite strongly to DNA from species other than *R. capsulata*, namely, *Rhodospirillum rubrum* and *Chromatium vinosum*. Although the intensity of the bands indicates DNA sequence homology within the fragments, variation in the size of the hybridizing fragments shows that sequence polymorphism exists within the homologous regions. The size of the hybridizing fragment from *R. rubrum* is approximately 2.1 kb and that from *C. vinosum* is approximately 4.5 kb. It was also observed that there was weak hybridization of EB2 to DNA fragments from *Rhodopseudomonas palustris*, *Rhodopseudomonas viridis*, and *Rhodospirillum tenue*.

The hybridization results shown in Fig. 2 are summarized in Table 2. A clear band, separate from the high-molecular-weight smear often observed, was the requirement for the designation of weak (+/−) hybridization. The intensities were judged relative to the strength of the *R. capsulata* band(s) in the same autoradiogram as observed by eye; therefore, the designations are semiquantitative at best.

The hybridization with the *Eco* F fragment as probe is of special interest. It was expected that this probe would bind to three fragments (ca. 7.5, 4.0, and 2.2 kb in size; see Fig. 1) resulting from *Bam*HI digestion of *R. capsulata* DNA. However, in addition to the expected bands, two strongly hybridizing fragments (ca. 7.0 and 6.3 kb) were observed. Since the same blot was used to hybridize with *Bam* D and other probes and since the expected number of bands was found in those experiments, the extra bands seen in the *Eco* F fragment hybridization could not have resulted from partial digestion of the *R. capsulata* DNA before coupling to the paper. We conclude that there must be DNA sequences in *R. capsulata*, in addition to those shown in Fig. 1, that are homologous to the *Eco* F fragment.

Clearly the DNA sequence of the photosynthesis gene cluster of *R. capsulata* is not shared by any of the species tested in this study. Although these data make it unlikely that evolutionarily recent lateral transfer of photosynthesis genes en masse is reponsible for the observed similarities in pigments of purple photosynthetic bacteria, the possibility of widespread transfer of photosynthesis genes at a time in the relatively distant past cannot be ruled out. The comparatively strong homology seen between the *R. capsulata* probes and DNA from *C. vinosum* and *R. rubrum* was surprising, because *R. capsulata* seems to be more closely related to *R. sphaeroides* than to other photosynthetic bacteria, based on 16S rRNA and cytochrome *c* sequence comparisons (10, 32). The homologies that we have observed could be the result of

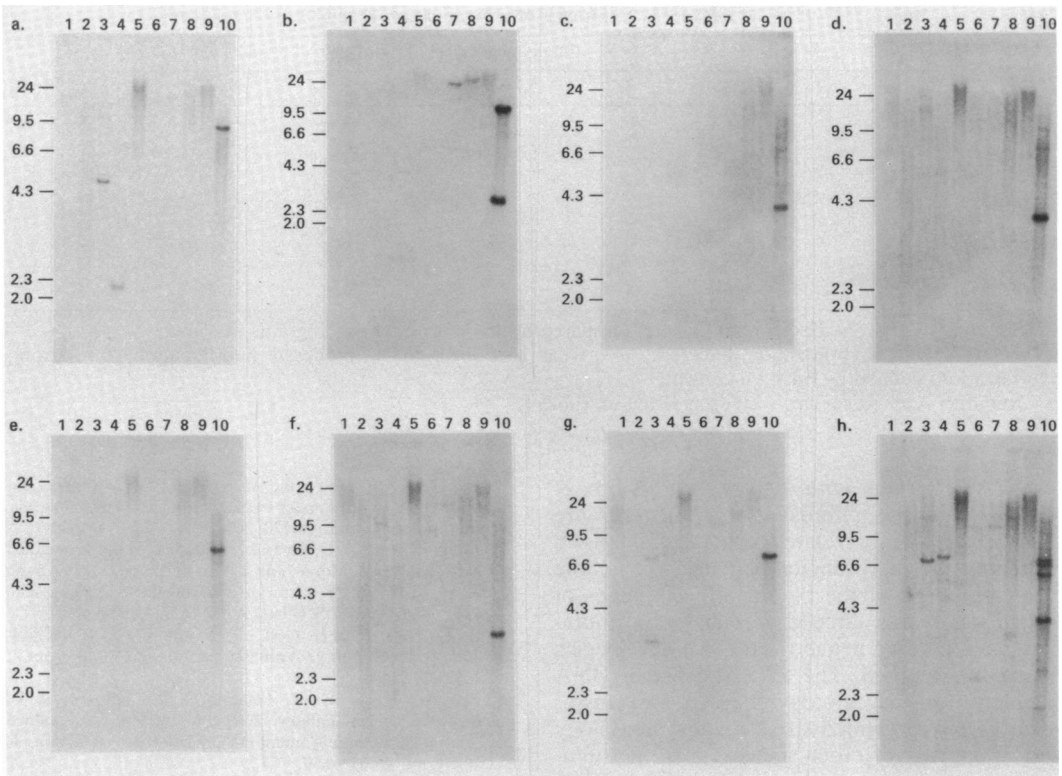

FIG. 2. Autoradiograms of hybridizations between *R. capsulata* DNA fragments EB2 (a), *Eco* H (b), *Bam* G (c), *Bam* H (d), *Bam* E (e), *Bam* I (f), *Bam* D (g), *Eco* F (h), and DNA from several genera of bacteria. The numbers above the lanes indicate the species, as listed in Table 1, from which the DNA in each lane was isolated. *E. coli* and *Pseudomonas aeruginosa* were grown at 37°C in shaking Erlenmeyer flasks containing nutrient broth. The photosynthetic bacteria were grown photosynthetically (anaerobically) as described previously (3). Cells were harvested by centrifugation and stored as frozen paste at −20°C before extraction of DNA as described by Marmur (18). Samples of DNA (5 to 10 μg) were digested in 20 μl for 24 h, with 16 U of *Bam*HI as recommended by the supplier (Bethesda Research Laboratories). The digested samples were subjected to electrophoresis in horizontal 0.7% agarose gels with Loening buffer (30), for 16 h at 30 V. The separated DNA fragments were then blotted (31) onto activated 2-aminothiophenol-derivatized Schleicher & Schuell 589 paper (1). The fragments used as probes were purified from recombinant plasmids by restriction endonuclease digestion, electrophoresis, and electroelution of the desired fragment into a dialysis bag (30). Purified fragments were radioactively labeled with ^{32}P by nick-translation (17) to a specific activity of about 10^8 cpm/μg. Prehybridizations and hybridizations were performed in sealed plastic bags, with 25 μl of solution per 1 cm^2 of paper. The prehybridization solution consisted of 5× SSPE buffer (17), 0.3% sodium dodecyl sulfate, 50% deionized formamide, and 100 μg of denatured, sonicated calf thymus DNA per ml. The hybridization solution was identical except that it contained approximately 10^6 cpm of radioactively labeled probe. Hybridizations were performed at 42°C for 16 to 24 h and filters were then washed three times for 7 min each with 200 ml of 2× SSPE and 0.2% sodium dodecyl sulfate at 45°C with agitation. Washed filters were covered in plastic wrap and exposed to preflashed Kodak XAR-5 film at −76°C in a film cassette with an intensifying screen (Du Pont Cronex Lightning Plus). The numbers indicate the size (in kb) of molecular weight markers and the position to which they migrated after electrophoresis.

lateral gene transfer, although other explanations exist.

The small degree of intergeneric relatedness of photosynthesis genes implied by the hybridizations performed in this study contrasts with results obtained by Riley and Anilionis with metabolic genes of enteric bacteria (26). Those authors used as probes fragments of *E. coli* DNA bearing *lac*, *thy*, *tna*, *trp*, and phage λ genes in hybridizations with DNA from bacteria of the genera *Citrobacter*, *Enterobacter*, *Erwinia*, *Klebsiella*, *Proteus*, *Salmonella*, and *Shigella*. Hybridization was observed with all species and for all probes except for phage λ DNA, which did not hybridize with four of the nine species tested (26).

The extremely weak hybridization that we observed with the majority of the fragments

TABLE 2. Summary of hybridization results

Probe[a]	Intensity of hybridization[b]									
	1[c]	2	3	4	5	6	7	8	9	10
EB2 (a)	−	−	+	+	+/−	−	+/−	−	−	++
Eco H (b)	−	−	+/−	+/−	+/−	+/−	+/−	+/−	+/−	++
Bam G (c)	−	−	−	−	−	−	−	−	−	++
Bam H (d)	−	−	+/−	+/−	−	−	−	−	−	++
Bam E (e)	−	−	+/−	−	−	−	+/−	+/−	−	++
Bam I (f)	−	−	+/−	−	−	+/−	+/−	−	−	++
Bam D (g)	−	−	+/−	+/−	−	+/−	+/−	+/−	−	++
Eco F (h)	−	−	+	+	+/−	+/−	+/−	+/−	−	++

[a] See Fig. 1 for probe descriptions. Letters in parentheses refer to autoradiograms in Fig. 2.
[b] −, No specific hybridization detected; +/−, weak hybridization; +, moderate hybridization; ++, strong hybridization, defined by positive control.
[c] Numbers refer to species tested, as listed in Table 1.

tested is congruent with the proposal of Fox et al. (13) that the photosynthetic bacteria are relatively distantly related organisms derived from an extremely ancient lineage. Thus, the DNA sequence of the photosynthesis genes of *R. capsulata* has undergone substantial mutation since its divergence from the other species we have examined. The EB2 and *Eco* F DNA fragments of the photosynthesis gene cluster seem to have retained the strongest homology with fragments of other species; this may indicate that there are more constraints on DNA sequence variability within genes carried by these fragments. Although both EB2 and *Eco* F bear *rxc* loci, these fragments probably contain other, heretofore undescribed genes. It is clear from this and other studies (4, 26) that the rates at which different portions of a genome evolve are not constant.

Although the photosynthetic bacteria have appeared to be closely related to each other based upon phenotypic criteria, evidently due to selective pressures in the environment from which they were isolated, the experiments reported here indicate that there is great genetic diversity of even the photosynthesis genes within this group of organisms. It is anticipated that more detailed studies will elucidate the nature of the DNA homologies that we have observed and perhaps provide information about the processes that have resulted in conservation of those DNA sequences.

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