Deoxyribonucleic Acid Base Compositions of Phototrophic Bacteria

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The deoxyribonucleic acids of 185 strains of phototrophic bacteria (47 strains of *Rhodospirillaceae*, 104 strains of *Chromatiaceae*, and 34 strains of *Chlorobiaceae*) have been examined by cesium chloride density gradient centrifugation. The calculated guanine plus cytosine moles percentages are given, and the taxonomic implications are described.

Vanyushin and Belozersky (26) provided the first data obtained by chemical analysis on the base composition of the deoxyribonucleic acid (DNA) of a *Chromatium* sp. and a *Chlorobium thiosulfatophilum* strain. Marmur and Doty (9) and Schildkraut et al. (21) applied thermal denaturation and CsCl buoyant density measurements, respectively, in a survey of the DNA base composition of a larger number of bacteria, including *Rhodospirillum rubrum* as a phototrophic bacterium. Further data were supplied by Marmur et al. (10) for *Chromatium* sp. and *C. thiosulfatophilum*, and by Mandel et al. (6) for the genus *Chlorobium*, Suyama and Gibson (22) and Vanyushin et al. (27). All of these previously reported data were summarized in Table 4.

The present study provides the data on 185 strains of the phototrophic (photosynthetic) bacteria, probably representing the majority of strains at present maintained in pure cultures.

MATERIALS AND METHODS

Bacterial strains. Strains 1.1.5., 1.1.12., 2.1.10., 2.1.35. [American Type Culture Collection (ATCC) 17006], 2.1.36., 2.2.6., 2.2.10., 2.2.14., 2.3.10. (ATCC 17020), 2.3.12. (ATCC 17021), 2.3.14. (ATCC 17022), 2.4.10., 2.4.12., and 2.4.16. came from the collection of C. B. van Niel and were grown at Amherst, Mass. Strains S 1360, B-1, GH, "Norway," "Lascelles," and *Chromatium* "1" were provided as harvested cells by Germaine Cohen-Bazire and R. Y. Stanier. Strains "Connecticut," KG 25, SL 1, and "S" (ATCC 14031) were provided as harvested cells by W. R.

Sistrom. Strains G 1, G 2, G 3, G 4, G 5, G 6, G 7, G 8, G 9, and Norwegian Technical University Collection of Microorganisms (NTHC) 132 were sent by K. E. Eimhjellen and grown at Houston, Tex. Strains F (ATCC 19567), 3764, 3/1, 8/2, 38/2, and 40a/5 were sent by G. Drews and grown at Houston, Tex. S. F. Conti gave us cells of strain "2" of *Chloropseudomonas ethylica*; R. C. Fuller, *Chromatium* strain D (ATCC 17899); and D. S. Hoare, strain ATCC 17100. All other strains (designated by four ciphers) as well as strains Eik/Lasc., T/Lasc., National Collection of Industrial Bacteria (NCIB) 8327, NCIB 8346, NCIB 8347, N 1 ("Moscow"; kindly supplied by E. N. Kondratieva), and SK-413 (kindly supplied by V. M. Gorlenko) were grown at Göttingen or Woods Hole, Mass., and are now kept in the Sammlung für Mikroorganismen Göttingen (SMG), Institut für Mikrobiologie, Göttingen.

Media and cultivation. Two species of *Rhodospirillaceae*, *Rhodomicrobium vannielii* and *Rhodopseudomonas acidophila*, contributed by N. Pfennig were grown anaerobically in 100-ml screw-cap bottles at 50 to 100 ft-c and an incubation temperature at 25C in the following medium (per liter): KH_2PO_4 , 0.5 g; NH_4Cl , 0.5 g; $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$, 0.4 g; NaCl , 0.4 g; $\text{CaCl}_2 \cdot 2\text{H}_2\text{O}$, 0.05 g; disodium succinate, 1.5 g; trace element solution of Pfennig and Lippert (18), 10 ml; pH 5.8. All other strains of *Rhodospirillaceae* were cultivated as described by Pfennig (12).

Species of *Chromatiaceae* and *Chlorobiaceae* were grown as described by Pfennig (12) and Pfennig and Lippert (18). For strains of marine

origin, the medium was supplemented with 1 to 3% NaCl.

DNA isolation. Washed cells were lysed by the addition of sodium dodecyl sulfate to a final concentration of 2% (w/v). Initial steps of deproteinization were accomplished by mixing the lysate with an equal volume of cold phenol saturated with saline-ethylenediamine-tetraacetic acid (EDTA) buffer (0.15 M NaCl, 0.1 M sodium ethylenediaminetetraacetate) adjusted to pH 8.0. Phases were separated by centrifugation at $5,000 \times g$ at 5°C, and the nucleic acids precipitated from the upper aqueous phase by the addition of 2 volumes of 95% ethanol. Further purification was by the method of Marmur (8). Samples were stored in 0.15 M NaCl containing 0.015 M sodium citrate, (pH 7.0) at 5°C over CHCl_3 .

DNA base composition. The buoyant density in neutral CsCl of each sample was determined at least twice in Spinco model E ultracentrifuges operating at 44,770 and at 42,040 rev/min at 25°C. Centrifugation was for 20 to 22 hr at the higher speed and for 23 to 24 hr at the lower speed. Specific details of operation and calculation of buoyant densities and moles per cent guanine plus cytosine (% GC) have been given (7). All densities were calculated by comparison with reference DNA of bacteriophage 2C ($1.7420 \pm 0.0004 \text{ g/cm}^3$), which is relative to the primary reference of DNA of *Escherichia coli* ($\rho = 1.7100$; 51.0 moles % GC).

RESULTS

The buoyant density measurements and the calculated moles % GC are shown in Tables 1 to 3.

The arrangement of the strains into species, genera, and families is based on their phenetic (morphological, physiological, and biochemical) characteristics, as suggested for the 8th edition of *Bergey's Manual*. In the case of the *Rhodospirillaceae*, van Neil's classification (25; *Bergey's Manual*, 7th ed., p. 35-67) is maintained. The *Chromatiaceae* and *Chlorobiaceae* were rearranged on the basis of pure-culture studies as proposed by Pfennig (13). The following recently described species have been included: *Rhodospirillum tenue* (15), *Rhodopseudomonas acidophila* (16), *Ectothiorhodospira mobilis* (11, 23), *E. shaposhnikovii* (1), *E. halophila*; *Chromatium buderii* (24), *Thiocapsa pfennigii* (3), *Chlorobium vibrioforme* (11, 13), *C. phaeobacteroides* (14), *C. phaeovibrioides* (14), and *Prosthecochloris aestuarii* (4).

DISCUSSION

Rhodospirillaceae. Among the *Rhodospirillaceae* bacteria (Table 1), the DNA base contents of the following species lie within exclusive ranges: (i) *Rhodomicrobium vannielii*, 62 to 64 moles % GC; (ii) *Rhodopseudomonas palustris*, *R. acidophila*, *R. capsulata*, and all five *Rhodospirillum* species, 63 to 67 moles % GC; (iii) *Rhodopseudomonas viridis*, 66 to 68 moles % GC; (iv) *Rhodopseudomonas sphaeroides*, 68 to 70 moles % GC; (v) *Rhodopseudomonas gelatinosa*, 71 to 72 moles % GC.

As a comparison with previous measurements, Table 4 shows that the GC values are close to those found in this study.

Chromatiaceae. The following "large-celled" *Chromatiaceae* bacteria (Table 2), *Thiospirillum jenense*, *Chromatium okenii*, *C. weissei*, and *C. warmingii*, are characterized by GC contents ranging from 45 to 60 moles %. The large-celled *C. buderii* and the following "small-celled" group are characterized by 61 to 63 moles % GC: *Ectothiorhodospira shaposhnikovii*, *C. minus*, and *Thiocystis* (formerly *Thiothece*) *gelatinosa*.

The majority of strains, including the most common species, *Chromatium vinosum*, *C. violascens*, *Thiocystis violacea*, *Thiocapsa roseopersicina* (syn. *T. florida*), and the gas vacuole-containing genera, *Lamprocystis*, *Thiodictyon*, and *Amoebobacter*, cover the range between 63 and 66 moles % GC. The species with the highest GC content are *E. mobilis*, *E. halophila*, *C. gracile*, and *Thiocapsa pfennigii* with 67 to 70 moles % GC.

The rather wide variations of GC contents found within the physiologically, morphologically, and biochemically well defined species, *Rhodopseudomonas viridis*, *R. acidophila*, *Chromatium vinosum*, *C. violascens*, and *C. warmingii*, are surprising, but of themselves do not sufficiently justify a subdivision of these species. In the case of *C. minus*, only two strains are in pure culture. Both contain bacteriochlorophyll *a* and okenone as the main carotenoid. The range of utilization of H donors is similar, and they are of the same size (2 μm wide). The large and significant difference of 10% GC contents in their DNA species suggests that they are not closely related. We prefer to adopt the conservative position of postponement of a formal taxonomic separation until sufficient phenotypic differences can be determined for a species distinction.

Eleven of the 20 *Chromatium vinosum* strains were isolated from marine or other saline environments, as were 3 of the 7 *C.*

TABLE 1. DNA-CsCl buoyant densities and base compositions of *Rhodospirillaceae* species

Species	Strain	DNA buoyant density (g/cm ³) ^a	Moles % GC
<i>Rhodospirillum rubrum</i>	1.1.12	1.7225	63.8
	9960	1.7235	64.8
	1.1.5 (ATCC 17033)	1.724	65.3
	6461	1.724	65.3
	2461	1.7245	65.8
<i>R. tenue</i>	2761 (ATCC 25093) ^b	1.7235	64.8
<i>R. fulvum</i>	3060	1.723	64.3
	S1360	1.723	64.3
	1360 ^b	1.724	65.3
<i>R. molischianum</i>	S (ATCC 14031) ^b	1.7205	61.7
	B - 1	1.722	63.2
	6960	1.7235	64.8
<i>R. photometricum</i>	NTHC 132 ^b	1.7245	65.8
<i>Rhodopseudomonas palustris</i>	1850	1.7235	64.8
	GH	1.7235	64.8
	1350	1.7245	65.8
	2.1.36	1.725	66.3
	2.1.10	1.725	66.3
	2.1.35 (ATCC 17006)	1.725	66.3
	6951	1.725	66.3
<i>R. viridis</i>	9351	1.725	66.3
	G7	1.7255	66.8
	40a/5	1.7255	66.8
	G1	1.726	67.3
	38/2	1.726	67.3
	G9	1.726	67.3
	8/2	1.726	67.3
	Norway	1.726	67.3
	G4	1.7265	67.9
	G8	1.7265	67.9
	G5	1.7265	67.9
	Lascelles	1.7265	67.9
	2450	1.7265	67.9
	F (ATCC 19567) ^b	1.727	68.4
	G2	1.727	68.4
	G3	1.727	68.4
	G6	1.727	68.4
	2750	1.730	71.4
<i>R. acidophila</i>	3251	1.721	62.2
	7150	1.721	62.2
	2751	1.7215	62.8
	3250	1.722	63.3
	7750	1.723	64.3
	7250	1.724	65.3
	7050 (ATCC 25092) ^b	1.724	65.3
	7550	1.7255	66.8

TABLE 1. (Continued)

Species	Strains	DNA buoyant density (g/cm ³) ^a	Moles % GC
<i>R. gelatinosa</i>	3/1	1.7295	70.5
	2150	1.730	71.4
	2.2.10	1.731	72.4
	2.2.6	1.731	72.4
	2.2.14	1.731	72.4
<i>R. capsulata</i>	3764	1.724	65.3
	2.3.14 (ATCC 17022)	1.725	66.3
	2.3.10 (ATCC 17020)	1.725	66.3
	6950	1.725	66.3
	2.3.12 (ATCC 17021)	1.7255	66.8
<i>R. sphaeroides</i>	2.4.12	1.727	68.4
	2.4.16	1.7275	68.9
	2.4.10	1.7285	69.9
<i>Rhodomicrobium vannielii</i>	Connecticut	1.7205	61.8
	KG25	1.721	62.3
	9255	1.7215	62.8
	ATCC 17100 ^b	1.7215	62.8
	2455	1.7218	63.1
	7256	1.722	63.3
	2155	1.722	63.3
	7255	1.7225	63.8

^aMean of at least two analyses.^bType or proposed neotype strain (19).

violascens, 5 of the 8 isolates of *Thiocystis violacea*, and 2 of the 9 *Thiocapsa roseopersicina* strains. Within these species no congruent grouping according to salinity requirement and GC values resulted, and it is only the range of GC determinations which provides a suspicion that these nomenspecies eventually may be subdivided.

Chlorobiaceae. The *Chlorobiaceae* bacteria (Table 3) are characterized by the rather narrow range between 48.5 and 58.1 moles % GC. Since the study of the genus *Chlorobium* by Mandel et al. (6), new species and new considerations have developed. A careful reinvestigation showed that in the genus *Chlorobium* there exist two morphological types, a straight rod and a curved rod. Pelsh (11) had already proposed the name *C. vibrioforme* for the curved type. *C. vibrioforme* is further characterized by bacteriochlorophyll *d* and a definite NaCl requirement. The thiosulfate-nonutilizing, straight, green rods of the genus *Chlorobium* form the species *C. limicola*. It is interesting

that all of these contain bacteriochlorophyll *c* and show a GC value of 51.0 to 52.0 moles %. Since, however, in the group of the thiosulfate-utilizing, straight rods, GC values of 52.5 to 58.1 moles % and bacteriochlorophylls *c* and *d* (only strain NCIB 8327) occur, we do not think that a separation of *C. limicola* and *C. thiosulfatophilum* (5) on the basis of thiosulfate utilization alone can be maintained. We prefer to consider the thiosulfate-utilizing forms, probably different only by the possession of the enzyme thiosulfate reductase, as subspecies (*formae*) of the thiosulfate-nonutilizing species. This is also supported by the fact that in *C. vibrioforme* the strain 1930 (also characterized by bacteriochlorophyll *d* and NaCl requirement) also utilizes thiosulfate.

The group of the brown chlorobia, *Chlorobium phaeobacteroides* and *C. phaeovibrioides*, is characterized by well defined GC values with little variations.

General observations. In examining this very large number of DNA samples, we did not encounter any "satellite" species of DNA as

TABLE 2. DNA-CsCl buoyant densities and base compositions of Chromatiaceae species

Species	Strain	DNA buoyant density (g/cm ³) ^a	Moles % GC
<i>Ectothiorhodospira mobilis</i>	8112 ^b	1.726	67.3
	8113	1.726	67.3
	8815	1.727	68.4
	8115	1.7285	69.9
<i>E. shaposhnikovii</i>	N1 (Moscow) ^b	1.721	62.3
<i>E. halophila</i>	SL1 ^b	1.727	68.4
<i>Thiospirillum jenense</i>	1112	1.7045	45.5
<i>Chromatium okenii</i>	6511 (ATCC 17094)	1.707	48.0
	1811	1.708	49.0
	1111 ^b	1.709	50.0
<i>C. weissei</i>	6211	1.707	48.0
	2111 ^b	1.707	48.0
	1812	1.709	50.0
<i>C. warmingii</i>	6511 (ATCC 14959) ^b	1.714	55.1
	1113	1.7155	56.6
	1311	1.719	60.2
<i>C. buderi</i>	8111 ^b	1.721	62.2
	8812	1.7215	62.8
	8813	1.7215	62.8
<i>C. minus</i>	1211 ^b	1.711	52.0
	3113	1.721	62.2
<i>C. vinosum</i>	1312	1.720	61.3
	1611	1.722	63.3
	9411	1.722	63.3
	8511	1.722	63.3
	8211	1.7225	63.8
	8011	1.7225	63.8
	9011	1.7225	63.8
	9511	1.7225	63.8
	8417	1.7225	63.8
	D (ATCC 17899) ^b	1.723	64.3
	8411	1.7235	64.8
	6712	1.724	65.3
	9611	1.724	65.3
	Eik/Lasc.	1.724	65.3
	6412 (ATCC 17095)	1.724	65.3
	2811	1.724	65.3
	8212	1.724	65.3
	8711	1.724	65.3
	8214	1.7245	65.8
	6411	1.725	66.3

TABLE 2. (Continued)

Species	Strain	DNA buoyant density (g/cm ³) ^a	Moles % GC
<i>C. violascens</i>	T/Lasc.	1.7205	61.8
	1313	1.721	62.2
	6111 (ATCC 17096) ^b	1.721	62.2
	8313	1.7225	63.8
	8314	1.7225	63.8
	3311	1.723	64.3
<i>C. gracile</i>	"1"	1.7275	68.9
	8611 ^b	1.7285	69.9
	8911	1.729	70.4
<i>Thiocystis violacea</i>	8213	1.7215	63.8
	8311	1.7215	62.8
	2711 ^b	1.7218	63.1
	8512	1.722	63.3
	8814	1.722	63.3
	8012	1.723	64.3
	9312	1.723	64.3
	2311	1.7235	64.8
<i>T. gelatinosa</i>	7311	1.7265	67.9
	2611 ^b	1.720	61.3
<i>Thiocapsa roseopersicina</i> (syn. <i>Thiocapsa floridana</i>)	8318	1.722	63.3
	8811	1.7225	63.8
	1813	1.723	64.3
	NCIB 8347 (ATCC 19599)	1.723	64.3
	6311 (ATCC 19129)	1.7235	64.8
	1711 ^b	1.724	65.3
	9412	1.724	65.3
	6612	1.7245	65.8
<i>T. pfennigii</i>	9314	1.725	66.3
	8013	1.728	69.4
	9111	1.728	69.4
<i>Lamprocystis roseopersicina</i>	8816	1.7285	69.9
	3012 ^b	1.7225	63.8
	3112	1.723	64.3
<i>Thiodictyon elegans</i>	3011	1.724	65.3
	3111 ^b	1.725	66.3
<i>T. bacillosum</i> (syn. <i>Amoebobacter bacillosus</i>)	1814 ^b	1.725	66.3
<i>Amoebobacter roseus</i> (syn. <i>Rhodotherce conspicua</i>)	6611 ^b	1.723	64.3
<i>A. pendens</i> (syn. <i>Rhodotherce pendens</i>)	1314 ^b	1.724	65.3

^aMean of at least two analyses.^bType or neotype strain (19).

TABLE 3. *DNA-CsCl* buoyant densities and base compositions of *Chlorobiaceae* species

Species	Strain	DNA buoyant density (g/cm ³) ^a	Moles % GC
<i>Chloropseudomonas ethylica</i>	2	1.714	55.1
<i>Chlorobium limicola</i>	6330 (Gillr.) ^b	1.710	51.0
	1330 (Kl.-K.)	1.7105	51.5
	1830 (Zeul.)	1.7105	51.5
	1230 (Rey.)	1.711	52.0
	9330	1.711	52.0
<i>C. limicola</i> f. <i>thiosulfatophilum</i>	6430 (Golf P.)	1.7115	52.5
	1630 (Lune.)	1.7115	52.5
	NCIB 8346	1.715	56.1
	NCIB 8327	1.7155	56.6
	Berkeley	1.7155	56.6
	3331	1.716	57.1
	2230 (Roth.)	1.7165	57.6
	6130 (Carm. R. 24)	1.7165	57.6
	6131 (Carm. R. 3)	1.717	58.1
	6230 ^b (Tassaj.)	1.717	58.1
	1430 (Fed.)	1.717	58.1
	2030 (Benn.)	1.717	58.1
<i>C. vibrioforme</i>	2630	1.711	52.0
	6030 ^b (Moss. L.)	1.7125	53.5
	9930 (Ps)	1.714	55.1
	6132 (Carm. R. 17)	1.716	57.1
<i>C. vibrioforme</i> f. <i>thiosulfatophilum</i>	1930 (Sehe.) ^b	1.7125	53.5
<i>C. phaeobacteroides</i>	2430 ^b	1.708	49.0
	2431	1.709	50.0
<i>C. phaeovibrioides</i>	2531	1.711	52.0
	2632	1.711	52.0
	2631 ^b	1.712	53.0
	2930	1.712	53.0
<i>Prosthecochloris aestuarii</i>	8530	1.709	50.0
	SK-413 ^b	1.7153	56.4
<i>Pelodictyon clathratiforme</i>	2730	1.7075	48.5
<i>P. luteolum</i> (syn. <i>P. aggregatum</i>)	2532	1.7125	53.5
	2530 ^b	1.717	58.1

^aMean of at least two analyses.^bType or neotype strain (19).

TABLE 4. DNA base composition determinations of phototrophic bacteria as given in previous publications (and not contained in Tables 1 to 3)

Species	Strain	Moles % GC	Method ^a	References
<i>Rhodospirillum rubrum</i>		63.4	i	27
	S-1 (ATCC 11170)	60	ii	9
	S-1 (ATCC 11170)	67	iii	21
	ATCC 11170	66.3	iii	22
<i>Rhodopseudomonas palustris</i>	Taniguchi	66.3	iii	22
<i>R. sphaeroides</i>	ATCC 14690	71.4 (satellite 65.5)	iii	22
<i>Ectothiorhodospira shaposhnikovii</i> (formerly <i>Rhodopseudomonas</i> sp.)		64.0	i	27; E.N. Kondratieva, personal communication
<i>Chromatium vinosum</i>	D	66.3 (satellite 54.0)	iii	22
<i>C. minutissimum</i>	Glubokoe	63.7	i	E.N. Kondratieva, personal communication
<i>Chromatium</i> sp.		63.7	i	26, 27
<i>Chromatium</i> sp.	K	64-66		10
<i>Chloropseudomonas ethylica</i>		57.2	i	27
		57.3	i	E.N. Kondratieva, personal communication
		57.6	i	27
<i>Chlorobium limicola</i>	Gilr.	50	ii	6
	Kl.-K.	51	ii	6
<i>C. limicola</i> f. <i>thiosulfatophilum</i>	Berkeley	56	ii	6
	Fed.	56	ii	6
		57.8	i	26, 27; E.N. Kondratieva, personal communication
		56-58		10
<i>C. vibrioforme</i>	Moss L.	51	ii	6
	Ps	52	ii	6

^ai, By chemical analysis; ii, by thermal denaturation; iii, by buoyant density.

have been reported by Suyama and Gibson (22). Upon original isolation, the DNA of *Rhodospirillum photometricum* displayed two bands of DNA. We were able to discern the presence of a gram-positive coccus in this culture, the DNA of which corresponded in density to that of this minor component. In two other cases, satellites were observed, but clonal reisolation of the phototroph then demonstrated only the single species of DNA which we have reported.

The DNA species of 70 nonphototrophic budding bacteria have been examined and will be reported separately (M. Mandel, P. Hirsch, and S. F. Conti, *manuscript in preparation*). The range of GC contents for the representatives of *Hyphomicrobium* and *Hyphomonas* overlap with the ranges reported here for the *Rhodospirillaceae* bacteria, some of which are also capable of budding (2, 16, 28).

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