Numerical Study of 60 Strains of *Serratia*

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SUMMARY

A numerical study of 60 strains of *Serratia* showed three phenon. Phenon A included 51 strains corresponding to the usual description of *Serratia marcescens*. Phenon B included five strains characterized by their fermentation pattern, positive malonate test and halotolerance. Phenon C included three aerogenic, cold-tolerant strains resembling pattern 2 of Fulton, Forney & Leifson (1959). One strain did not fall into any of these phenon. All strains of human origin fell into phenon A. This phenon could be subdivided into two smaller phenon, one composed of haemolytic and multi-resistant nosocomial strains. A hypothetical median organism for phenon A is described.

INTRODUCTION

Over the last 20 years the taxonomy of the *Serratia* group has been drastically simplified. In the 4th edition of *Bergey's Manual* (1934) 27 species of *Serratia* were listed, whilst in the 7th edition (1957) only five species were retained. Ewing, Davis & Johnson (1962) suggested that all *Serratia* species could be described as a single species (*Serratia marcescens*) with one variety (*S. marcescens* var. *kiliensis*). Martinec & Kocur (1960, 1961 *a, b, c*) agreed with this conclusion.

Colwell & Mandel (1965) subjected 33 strains of *Serratia* to Adansonian analysis and determined their deoxyribonucleic acid base composition. They concluded that there was only a single species in the genus *Serratia*. However, four strains differed from the homogeneous *Serratia marcescens* species group.

In our laboratory, some red pigmented isolates proved to differ from the present description of *Serratia marcescens*. A numerical study was then carried out on 60 strains of *Serratia* isolated from various sources.

METHODS

Strains used. A total of 60 strains (Table 1) was used in the study. Strains were maintained on nutrient agar (meat extract, 3 g; yeast extract, 3 g; sodium chloride, 5 g; Difco Bacto-peptone, 10 g; agar, 15 g; and distilled water, 1000 ml; pH 7.4).

Data collection and coding. A number of morphological, cultural and biochemical tests including tests of ecological significance (e.g. growth at 5 °C and 40 °C, halotolerance, susceptibility to nine antibiotics) was applied. All tests (Grimont, 1969) were at 30 °C unless otherwise stated.

The following invariant characters were discarded: Gram-negative straight rods with rounded ends; not capsulated; peritrichous when motile; growth on nutrient agar at room temperature, 30 °C, 37 °C; growth in alkaline broth (pH 9.2) in 1 day; Christensen's citrate medium alkalized; Kovacs' oxidase test negative; aerobic and anaerobic growth; catalase

Table 1. *Strains of Serratia used in the numerical study*

No.	Original name and no.	Source	Pigment
1	<i>Serratia</i> 1-65 (LM)*	Blood	Red
2	<i>Serratia</i> 12-65 (LM)	Baker's dough	Red
3	<i>Serratia</i> 17-65 (LM)	Pus	None
4	<i>Serratia</i> 18-65 (LM)	Urine	None
5	<i>Serratia</i> 23-65 (LM)	Sputum	Red
6	<i>Serratia</i> 2-66 (LM)	Urine	None
7	<i>Serratia</i> 4-66 (LM)	Pus	None
8	<i>Serratia</i> 7-66 (LM)	—	Red
9	<i>Serratia</i> 10-66 (LM)	Sausage	None
10	<i>Serratia</i> 11-66 (LM)	Sputum	None
11	<i>Serratia</i> 15-66 (LM)	Bone marrow	None
12	<i>Serratia</i> 19-66 (LM)	Blood	None
13	<i>Serratia</i> 24-66 (LM)	Urine	None
14	<i>Serratia</i> 25-66 (LM)	Blood	None
15	<i>Serratia</i> 26-66 (LM)	Urine	Red
16	<i>Serratia</i> 72 (B)*	Pig	Red
17	<i>S. plymuthicum</i> 80 (B)	Urine	Red
18	<i>S. anolia</i> 82 (B)	Stool	Red
19	<i>S. marcescens</i> 83 (B)	Urine	Red
20	<i>S. plymuthicum</i> 90 (B)	Pig	Red
21	New species close to <i>S. marinorubra</i> 232 (B)	Cow's-milk	Red
22	<i>S. kiliensis</i> 658 (B)	Sea-water	Red
23	<i>S. kiliensis</i> 782 (B)	Animal	Red
24	<i>S. kiliensis</i> 1694 (B)	Animal	Red
25	<i>S. marcescens</i> 2029 (B)	Human	Red
26	<i>S. marcescens</i> 2030 (B)	Human	Red
27	<i>S. marcescens</i> 2032 (B)	Human	Red
28	<i>S. marcescens</i> 2034 (B)	Human	Red
29	<i>S. marcescens</i> 2187 (B)	Human	Red
30	<i>S. plymuthicum</i> 2869 (B)	Human	Red
31	<i>S. plymuthicum</i> 3923 (B)	Sea-water	Red
32	<i>S. marcescens</i> 2924 (B)	Sea-water	Red
33	<i>S. plymuthicum</i> 3617 (B)	Sea-water	Red
34	<i>S. plymuthicum</i> 3736 (B)	—	Red
35	<i>S. marcescens</i> 3830 (B)	Sea-water	Red
36	Santé Navale† (Bordeaux)	Cultivated mushroom	Red
37	Santé Navale (Bordeaux)	Cultivated mushroom	Red
38	Santé Navale (Bordeaux)	Cultivated mushroom	None
39	Santé Navale (Bordeaux)	Cultivated mushroom	Red
40	Université II (Bordeaux)	Human	None
41	Université II (Bordeaux)	Blood	None
42	Université II (Bordeaux)	Human	None
43	Université II (Bordeaux)	—	None
44	Strain 'Mar...' (DR)*	Throat	Red
45	Strain 'Arb...' (DR)	Urine	None
46	Strain 'C/D' (DR)	Urine	None
47	Strain 'And...' (DR)	Pus	None
48	Strain 'Per...' (DR)	Blood	None
49	Strain 'Bay...' (DR)	Urine	None
50	Strain 'C/B' (DR)	Urine	None
51	Strain 'Dab...' (DR)	Urine	None
52	Strain 'Cha...' (DR)	Urine	None
53	Strain 'Deb...' (DR)	Urine	None
54	Strain 'Beg...' (DR)	Urine	None
55	Strain 'Ben...' (DR)	Urine	None
56	Strain 'Arb...' (DR)	Urine	None
57	Strain 'Eve...' (DR)	Blood	None
58	Strain 'Bon...' (DR)	Urine	None
59	Strain 'Cou...' (DR)	Bone marrow	None
60	Strain 'Das...' (DR)	Urine	None

* LM = Professor Le Minor, Institut Pasteur, Paris. B = Professor Brisou, University of Poitiers.
DR = Professor Dulong de Rosnay, Hôpital Pellegrin, Bordeaux.

† Strains 'Santé Navale' have been isolated in Dr Desnues' laboratory.

positive; nitrate reduction positive (nitrate broth, Griess' method); reduction of triphenyl-tetrazolium chloride; fermentation of glucose (Hugh & Leifson's method); peptone water with Durham tube and carbohydrate or polyalcohol: acid from galactose (3 days), fructose, mannose, sucrose, trehalose, glycerol (3 days), mannitol, inositol, salicin (2 days), no acid from dulcitol; beta-galactosidase present; no gas produced when inositol is fermented; lysine decarboxylase (Falkow's medium without peptone); DNase positive (strongly or weakly); no production of indol (peptone water); no splitting of urea (Stuart's medium); no tryptophan deaminase; no arginine dihydrolase.

The following 55 tests remained in the numerical study: motility; size of colony, surface (S or M); pigment formation on egg yolk agar, nutrient agar, Brain Heart Infusion agar; pellicle and ring in nutrient broth; growth at 5 °C and at 40 °C; growth in broth with NaCl 6.5 % and 7.5 %; growth in KCN medium; growth in presence of Brilliant Green 1/200 000, Crystal Violet 1/100 000, thallium acetate 1/5000; growth on Simmons's citrate; malonate broth becoming alkaline; carbohydrate fermentation: xylose, arabinose, rhamnose, galactose (quantitative result only), maltose, lactose (and ONPG test with and without prior induction), cellobiose, raffinose, glycerol (quantitative result only), sorbitol, adonitol, soluble starch, salicin (quantitative result only), aesculin hydrolysis, methyl-red reaction, gas in glucose; H₂S production (paper strip); gelatin (Frazier) and casein hydrolysis, coagulated serum liquefaction; decarboxylase reactions with ornithine, asparagine, histidine; haemolysis (horse blood); DNase (quantitative result only); lecithinase (lecithin agar); Tween-esterase; resistance to the following antibiotics: ampicillin, streptomycin, kanamycin, chloramphenicol, erythromycin, tetracycline, colistin, nalidixic acid, gentamycin.

Multi-state characters were turned into several two-state characters and were encoded following the non-additive procedure (Sneath, 1957) and using Adansonian principles.

Computation of similarities. For estimating overall similarity, the Jaccard-Sneath coefficient (Sneath, 1957) excluding negative matches was used. A program for computation of similarities was written in Fortran IV and data were processed through an IBM 360/44 machine.

Cluster analysis. Two clustering methods were used: the single linkage method (Sneath, 1957) and the weighted pair group method (Sokal & Sneath, 1963). Dendrograms were constructed from the results of the clustering procedures.

Taxometric maps were designed following two methods. The first one is Carmichael & Sneath's (1969): clusters are represented by circles whose diameter is the same as the distance between the two most distant points in the cluster. The distance between the closest neighbours in two clusters is represented by a line connecting the margins of the two circles. The second method is modified from Lysenko & Sneath (1959): a cluster is represented by a circle whose diameter is the same as the complement of the mean intragroup similarity. Centre to centre distance between two circles is the complement of the mean intergroup similarity.

For the largest phenon a hypothetical median organism was calculated according to the method of Liston, Wiebe & Colwell (1963): the mean number (n) of positive characters occurring in the phenon is determined and characters are ranked according to their frequency of occurrence. The median organism will possess the characters which occur in most of the strains in the phenon, i.e. the n most frequent characters.

RESULTS

The dendrograms obtained from the single linkage method and from the weighted pair group method are given respectively in Fig. 1 and Fig. 2. Both are roughly similar. As can be seen, 59 organisms fell into three phenon while one strain was distinct from them. For convenience, the phenon were called A, B and C. Phenon A contains 51 strains, phenon B

Fig. 1. Dendrogram constructed by the single linkage method.

contains five strains, while phenon C contains only three strains. Strain 38 stood apart from all three phenon. The homogeneity of these clusters was checked by calculating mean intragroup similarities. Relationships between clusters were evaluated by calculation of mean intergroup similarities. Mean *S* values (mean similarities) are given in Table 2.

Fig. 2. Dendrogram constructed by the weighted pair group method.

The homogeneity and individuality of the three phena are illustrated by two taxometric maps (Fig. 3*a, b*). Fig. 3(*a*) was constructed by taking into account the extreme distances (largest distance within a phenon, shortest between phena) following Carmichael & Sneath (1969). Fig. 3(*b*) was constructed using average distances ($1 - S$). Both maps, although

Fig. 3. Taxometric maps constructed by the methods of (a) Carmichael & Sneath (1969) and (b) Lysenko & Sneath (1959) modified.

Table 2. *Intra- and intergroup mean S values*

A	0.75		
B	0.47	0.83	
C	0.54	0.57	0.77
38	0.49	0.55	0.61
	A	B	C

based on different methods, give the same overall results. They are useful in interpreting the dendrograms.

The average of the mean intergroup distances (mean $1 - S$) is 0.46. One can say that the centres of phena A, B, C and strain 38 are roughly equidistant and delimit a tetrahedron with sides 0.46 ± 0.07 units long. The most useful characters for differentiation of phena A, B, C and strain 38 are listed in Table 3.

Table 3. *Interphenon differentiating characteristics*

	Phena			
	A	B	C	38
Pigment production	22*	5*	2*	0*
Growth at 5 °C	0	0	3	1
Growth at 40 °C	36	0	0	1
NaCl 6.5 % (1 day)	0	5	0	0
NaCl 7.5 %	0	4	0	0
Gas from glucose	0	0	3	0
Acid from:				
Adonitol (1 day)	0	5	0	0
Adonitol (3 days)	51	5	0	1
Arabinose	0	5	3	1
Cellobiose (1 day)	0	5	2	1
Cellobiose (3 days)	5	5	2	1
Glycerol: pH 5.8 in 1 day	50	0	2	0
pH 5.8 in 3 days	50	0	3	1
pH 6.4 to 6.7 in 3 days	1	5	0	0
Lactose (1 day)	0	5	0	0
Raffinose (1 day)	0	5	3	1
Raffinose (2 days)	1	5	3	1
Rhamnose	0	0	0	1
Sorbitol	49	0	3	1
Xylose	0	5	3	1
Ornithine decarboxylase	49	0	1	1
Casein hydrolysed (1 day)	40	0	1	0
(3 days)	46	0	2	0
(5 days)	48	1	3	0
Lecithin-agar	48	5	3	0
Tween 80	51	5	3	0
Malonate	0	5	0	0
Haemolysis (horse blood, 1 day)	9	0	0	0
Growth on thallium acetate	50	3	0	0
Growth on tetracycline 5 µg/ml	45	0	0	0

* No. of positive strains.

Phenon A. Strains of this phenon did not ferment pentoses, raffinose and rhamnose. Gas was not produced during fermentation of sugars. A very tiny bubble of gas could be seen irregularly and was not taken into account. Most strains fermented sorbitol and possessed ornithine decarboxylase. Malonate broth did not become alkaline. Most strains were tetracycline resistant. All human strains (42) fell into phenon A. The other sources were as follows: four strains isolated from animals, three isolated from sea-water, one from food and one of unknown origin.

A hypothetical median organism for phenon A, calculated according to Liston *et al.* (1963), possesses the following characters: motile; colony 2 to 5 mm; S colony form; pigment production on egg-yolk agar; ring in broth, no pellicle; growth at 40 °C but not at 5 °C; growth in NaCl 6.5 % (2 days) but not in NaCl 7.5 %; growth in KCN medium; growth on Crystal Violet 1/100000; growth on thallium acetate 1/5000 (2 days); growth on Simmons's citrate; malonate broth negative; fermentation of galactose (1 day), maltose, glycerol (1 day), sorbitol, adonitol (3 days), soluble starch, salicin (1 day); no fermentation of xylose, arabinose, rhamnose, cellobiose, raffinose, lactose (1 day); gas not produced from glucose; beta-galactosidase may be inducible or constitutive; aesculin hydrolysed; methyl-

red reaction negative; H_2S not produced; gelatin hydrolysed (1 day); coagulated serum liquefied in less than 5 days; casein hydrolysed (1 day); decarboxylation of ornithine, asparagine, histidine; hot-cold haemolysis of horse blood (not in 1 day at 30 °C); DNase positive (1 day); precipitation around colony on lecithin agar; precipitation around colony on Tween 80 agar (1 day); minimal inhibitory concentrations with the following antibiotics: ampicillin (over 5 µg/ml), streptomycin (over 100 µg/ml), kanamycin (less than 5 µg/ml), chloramphenicol (5 to 15 µg/ml), erythromycin (over 50 µg/ml), tetracycline (over 5 µg/ml), colistin (over 100 µg/ml), nalidixic acid (less than 5 µg/ml), gentamycin (0.1 to 1 µg/ml). The similarity coefficients between the hypothetical organism and every organism of phenon A were calculated. *S* values ranged from 0.97 (strain 5) to 0.63 (strain 4). All but one strain showed similarities to the median > 0.70. Forty-four strains showed *S* values ≥ 0.80, and 18 strains ≥ 0.90. Strain 4, having a low similarity with the median organism seems misplaced in phenon A.

On both dendrograms, two subgroups, referred to as A_1 and A_2 , are distinguishable within phenon A, but their memberships differ somewhat between the two dendrograms.

With the single linkage (Fig. 1) subgroup A_1 (A_1/SL) consists of 11 strains. All were human strains. Ten of them came from the same hospital in Bordeaux. Seven were strongly haemolytic on horse blood and all were multi-resistant to antibiotics. Ten strains could grow at 40 °C. None was pigmented. With the average linkage (Fig. 2) subgroup A_1 (A_1/AL) consists of 12 strains of human origin. Eleven of them were isolated in the same hospital in Bordeaux. All could grow at 40 °C.

With the single linkage, subgroup A_2 (A_2/SL) consists of 19 strains. With the average linkage, A_2/AL consists of 28 strains. All 19 strains of A_2/SL are included in A_2/AL . The typical strain 5 was at the starting-point of the subgroup formation. As the level of clustering decreased, fewer organisms joining the cluster were pigmented. At level 0.82, A_2/AL consisted of 20 strains, 17 of which were pigmented. At level 0.75, 17/28 strains only were pigmented. At level 0.60, 22/51 strains clustered were pigmented (in phenon A).

Subgroups A_1 and A_2 are then essentially differentiated by pigmentation, susceptibility to antibiotics and haemolysis.

Phenon B. This phenon consists of five non-human strains. Three were isolated from cultivated mushrooms, one from sea-water and one from a pig. All were pigmented and fermented pentoses, raffinose, cellobiose, lactose and adonitol, but not sorbitol. Malonate broth became alkaline. They were also characterized by halotolerance, no growth at 5 °C and 40 °C, lack of ornithine decarboxylase and by susceptibility to tetracycline.

Phenon C. This phenon consists of three non-human strains. One was isolated from sea-water, one from sausage, and one was of unknown origin. Pentoses, raffinose and sorbitol were fermented but not adonitol. Gas was produced during fermentation of all sugars and polyalcohols except inositol. Growth occurred at 5 °C but not at 40 °C. All three strains were susceptible to tetracycline.

Strain 38. This aberrant strain was isolated from a cultivated mushroom. It fermented pentoses, raffinose, cellobiose, sorbitol and rhamnose. It was susceptible to tetracycline but lacked Tween-esterase. While *Serratia* strains usually have a fishy odour (like trimethylamine), this strain had an odour like soya sprouts.

Differences between phenon A were emphasized by the numerical method, but one must keep in mind that all 60 strains in this study share in common the numerous invariant characters described above (see Methods), but not included in the computer analysis. Furthermore, some tests were positive for all but one strain (atypical strain falling in phenon A): growth on KCN medium (strain 4), Simmons's citrate (strain 4), fermentation of soluble

starch (strain 25). Some tests were positive for all but two strains: fermentation of galactose (strains 49 and 51), fermentation of maltose (strains 25 and 29), DNase (doubtful for 47 and 51). Some tests were positive for all but three strains: gelatin hydrolysis (doubtful for 43, 49, 51), liquefaction of coagulated serum (strains 25, 49, 51). As can be seen (Fig. 1, 2), all of these infrequent results were given by marginal organisms of phenon A.

DISCUSSION

It appears from the present study that the concept of a single *Serratia* species is the product of an oversimplification and that at least three taxa can be recognized.

Phenon A resembles *Serratia marcescens* of Ewing *et al.* (1962) and the single phenon of Colwell & Mandel (1965) and biotype I of Bascomb, Lapage, Willcox & Curtis (1971) very closely. It also resembles pattern 1 of Fulton *et al.* (1959) except that cellobiose is not readily fermented by our strains.

Phenon B is not described by Ewing *et al.* (1962). It is different from pattern 2 of Fulton *et al.* (1959), strains of phenon B fermenting adonitol readily and being anaerogenic. Phenon B and biotype II of Bascomb *et al.* (1971) share many characteristics. However, they differ in some respects (malonate, lysine decarboxylase tests, fermentation of sorbitol).

Phenon C resembles pattern 2 of Fulton *et al.* (1959) in producing acid from the same sugars and not from adonitol, and in producing gas from glucose. It differs only in gelatin hydrolysis, but a different method was used. Strains of phenon C, if we except pigmentation, also resemble strains of *Enterobacter liquefaciens* by giving the same biochemical reactions (Edwards & Ewing, 1962) and being cold-tolerant mesophiles (Grimes, 1961). Non-pigmented strains of this group could certainly be classified as *Enterobacter liquefaciens*.

Strain 38 does not fit any published description.

Fulton *et al.* (1959) observed that their 'pattern 1 strains... are the ones to be expected from clinical sources' and 'a different *Serratia*, not so far encountered in clinical materials, is also described'. We can extend their statement to our results. As we have pointed out, all the strains isolated from humans fell into phenon A. Strains of phenon B and C did not grow at 40 °C; this may account for the rare occurrence of these strains in clinical materials.

The differentiating tests listed in Table 3 were applied to three reference strains recently received from P. H. A. Sneath. We may say that working type strain D318 (NCTC 1377) corresponds to the description of phenon A. Strain D317 (NCTC 9493) corresponds to the description of phenon C. These two strains were included in the study of Bascomb *et al.* (1971) and were placed as follows: strain NCTC 1377 was in their biotype I and strain NCTC 9493 stood apart from this biotype. A third strain, D119, labelled '*Serratia marinorubra* type strain' seems to fit with the description of our phenon B.

The splitting of phenon A in two smaller phenon is less clear and these subgroups may overlap. A study in progress in our laboratory is revealing that most strains of subgroup A₁ carry R factors. The question may be asked: 'are not these subgroup A₁ strains identical?' However unpublished data on phage sensitivity, R-factor transfer, colicinogeny and biochemical tests, do not allow the reduction of the 12 strains of subgroup A₁ to less than ten epidemiological entities.

Another problem is whether or not we may include in a taxometric study some features given by plasmids. In fact we know that resistance to antibiotics may be due to plasmids in this study, but we do not know if other features are also plasmid-linked. Our opinion is that a phenetic classification must rely on the phenotype of organisms regardless of the location of genes (a situation which is not immutable). We do not yet have enough genetic knowledge.

Therefore, the existence of a subgroup A₁ 'plasmid-made' may represent the evolution of the classical *Serratia marcescens* species towards an 'iatrogenic' variety.

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