CURRENT MICROBIOLOGY, Vol. 4 (1980), pp. 207–212

Current Microbiology

An International Journal

Yersinia intermedia: A New Species of Enterobacteriaceae Composed of Rhamnose-Positive, Melibiose-Positive, Raffinose-Positive Strains (Formerly Called *Yersinia enterocolitica* or *Yersinia enterocolitica*–Like)

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Abstract. *Yersinia intermedia* sp. nov. is defined biochemically and genetically. *Y. intermedia* strains belong to a single DNA relatedness group that is separable from *Y. enterocolitica, Y. frederiksenii, Y. kristensenii,* and *Y. pseudotuberculosis. Y. intermedia* is positive in reactions for melibiose, raffinose, α-methyl-D-glucoside, rhamnose, and usually Simmons' citrate. It is metabolically more active at 22–28°C than at 35–37°C. These positive reactions serve to distinguish *Y. intermedia* from *Y. enterocolitica* and *Y. kristensenii.* Positive melibiose, raffinose, and α-methyl-D-glucoside reactions differentiate *Y. intermedia* from the other new rhamnose-positive species, *Y. frederiksenii. Y. intermedia* is separated from *Y. pseudotuberculosis* by its positive reactions for sucrose, indole, cellobiose, *i*-inositol, D-sorbitol, α-methyl-D-glucoside, and ornithine decarboxylase. *Yersinia* biotype X2, an additional rhamnose-positive, sucrose-negative group, as yet not identified to a species, and XI, a sucrose- and ornithine decarboxylase–negative *Yersinia* biotype, do not belong to *Y. intermedia.* Strain 3953 (=CIP 80-28 = ATCC 29909 = Bottone 48 = Chester 48) is proposed as the type strain for *Y. intermedia.*

Botzler, Wetzler, and Cowan [11] reported the isolation of strains resembling *Yersinia enterocolitica* and *Y. pseudotuberculosis* from frogs and snails. These strains gave positive reactions for rhamnose and melibiose, and most were raffinose positive but ornithine decarboxylase negative.

Lassen isolated a rhamnose-positive strain from drinking water [22]. He reported the strain to be raffinose and melibiose negative, but it was subsequently shown to be positive for these reactions (H. Bercovier, unpublished observation) [14]. In 1974, Bottone et al. isolated 12 strains that were positive in reactions for rhamnose, raffinose, melibiose, Simmons' citrate, and ornithine decarboxylase. These strains and five subsequent isolates were all from humans in Mt. Sinai Hospital, New York, but were not associated with disease typical of that caused by *Y. enterocolitica* [9,10]. Alonso et al. and Bercovier et al. studied Bottone's strains as well as 36 additional rhamnose-, raffinose-, melibiose-, and Simmons' citrate–positive strains from Canada, USA, France, Belgium, Holland, Finland, and Czechoslovakia [2,4]. Brenner et al. [14] showed that these strains were also α-methyl-D-glucoside-positive. DNA studies showed that Lassen's strain 955 and four of Bottone and Chester's strains appeared to be a species separate from *Y. enterocolitica* and that this group might be different from three rhamnose-positive, raffinose-, melibiose-, α-methyl-D-glucoside-negative strains [14]. In this report, we confirm and extend these initial observations. The melibiose-, rhamnose-, raffinose-, and α-methyl-D-glucoside-positive strains are shown to be a new species, *Yersinia intermedia. Y. intermedia* is defined biochemically and genetically

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0343-8651/80/0004-0207 $01.20

Table 1. Biochemical characteristics of 321 *Yersinia intermedia* strains.[a]

Test	Reaction	%+	%(+)	Type strain 3953
Urease	+	99		+
Simmons' citrate (28°C)	V	65	13	+
Mucate	V	12	41	(+)
Christensen's citrate	V	70		+
NO_3 reduction to NO_2/Type	+/B or A	100/53B		+/A
Tetrathionate reductase	+	93		+
Lipase (Tween 80)	V	68	11	+
Deoxyribonuclease	−	2	3	−
Polypectate	(+)		100	(+)
Acid production from:				
L-Sorbose	+	98		+
L-Rhamnose	+	95	4	+
Lactose	−	2	21	−
D-Melibiose	+	99		+
D-Raffinose	+	95	4	+
i-Inositol	+ or (+)	81	19	+
α-Methyl-D-glucoside	+	93		+
Starch	(+)		100	(+)

[a] All incubations, except where indicated, were done at 28°C. +, 90.0% or more positive within 72 h; (+), 90.0% or more positive between 4 and 7 days; V, 10.1–89.9% positive; −, less than 10% positive after 72 h. The following tests gave positive reactions for all strains tested: catalase, motility (28°C), indole, methyl red (28°C and 37°C), Voges-Proskauer (28°C), fermentation in O-F test, ornithine decarboxylase, β-galactosidase (ONPG; 37°C), and acid production from D-glucose, glycerol, L-arabinose, ribose, D-xylose, galactose, D-fructose, D-mannose, D-cellibiose, maltose, sucrose, D-trehalose, D-mannitol, D-sorbitol, esculin, salicin, amygdalin, *N*-acetyl-glucosamine, arbutin, and dextrin. The following tests gave negative reactions for all strains tested: oxidase, motility (37°C), Voges-Proskauer (37°C), Simmons' citrate (37°C), malonate, KCN, gas from D-glucose, H_2S (Kliegler's), phenylalanine deaminase, tryptophan deaminase, lysine decarboxylase, arginine dihydrolase, β-xylosidase (PNPX; 37°C), gelatin (film), and acid production from erythritol, D-arabinose, L-xylose, adonitol, dulcitol, D-melizitose, α-methyl-xyloside, α-methyl-D-mannoside, inulin, amylose, and glycogen.

and differentiated from *Y. enterocolitica* [6], and from the newly described species *Yersinia frederiksenii* [29] and *Yersinia kristensenii* [8].

Materials and Methods

Organisms. The description of the strains used for DNA hybridization has been published [7,16,28]. Three hundred and twenty-one strains from the collection of the National Yersinia Center (Institut Pasteur, Paris) were studied biochemically.

Biochemical reactions. Biochemical tests and conditions are found and referenced in a previous paper [6].

Genetic studies. The methods used for the preparation of DNA, DNA labeling, DNA reassociation, and separation of single- and double-stranded DNA on hydroxyapatite have been described [12,13,15]. DNA base composition (mol% G+C) was determined both by optical thermal denaturation [23,26] and by CsCl buoyant density gradient ultracentrifugation [24]. The CsCl determinations were kindly done by Manley Mandel.

Results and Discussion

Yersinia intermedia strains fit the definition of Enterobacteriaceae. Their physiological and growth characteristics are similar to those of *Y. enterocolitica sensu stricto* [2,4,6,9]; however, their metabolic activity is more temperature dependent than that of *Y. enterocolitica* [2,9]. Further, *Y. intermedia* is more inhibited by selective media, such as salmonella-shigella agar, than *Y. enterocolitica* [9,10]. The biochemical reactions of the 321 National Yersinia Center strains are given in Table 1.

Bottone et al. [10], and Alonso et al. [2] showed that *Y. intermedia* is more active metabolically when incubated at 22–28°C than at 35–37°C. For instance, all *Y. intermedia* are cellobiose positive when incubated at 28°C; 80% are positive at 30°C, and only 50% are positive at 37°C. Among the tests diagnostic for *Y. intermedia*, citrate utilization is almost always negative at 37°C, and both rhamnose and raffinose fermentation may be delayed, weakly positive, or even negative. These reactions are of particular importance in the clinical laboratory where incubation is almost always done at 35–37°C.

Strains that are delayed rhamnose or raffinose positive or Simmons' citrate negative at 37°C are perfectly good members of *Y. intermedia*. Five strains that are rhamnose negative even at 22°C (5630, 6191, 6194, 6237, and 6250) and one strain (6249) that is melibose negative, but rhamnose, α-methyl-D-glucoside, raffinose, and citrate positive, were also shown to be *Y. intermedia* on the basis of DNA relatedness [16].

Different biotypes of *Y. intermedia* are shown in Table 2. At least 98% of *Y. intermedia* strains are positive in tests for at least two out of the three substrates, melibiose, rhamnose, and α-methyl-D-glucoside, and are therefore distinguishable from *Y. frederiksenii* [6, Table 3; 29]. As shown previously [6], an occasional *Y. enterocolitica* strain is either raffinose positive, α-methyl-D-glucoside positive, melibiose positive, or Simmons' citrate positive. These strains as well as Simmons' citrate- and raffinose-positive *Y. frederiksenii* [29] are not members of *Y. intermedia*.

Other *Yersinia* species have a type B nitrate reductase, *Y. intermedia* strains have either type B (53%) or type A (47%) nitrate reductase (Table 1). Strains of either type have the same level of DNA relatedness and are evenly distributed among the different biotypes.

One hundred eighty-six (58%) of the 321 *Y. intermedia* strains belong to a known serogroup [30].

Table 2. Biotypes of *Yersinia intermedia*.

	Biotype[a]							
	1	2	3	4	5	6	7	8
D-Melibiose	+	+	+	+	+	+	+	−
L-Rhamnose	+	+	+	−	−	+	+	+
α-Methyl-D-glucoside	+	+	−	+	−	+	−	+
D-Raffinose	+	+	+	+	+	−	−	+
Simmons' citrate	+	−	+	+	+ or −	−	−	+
Strains studied by DNA hybridization	See Table 1 of reference 16	6151	5797	5630 6191 6194 6237 6250	NT	6262	6251	6249
% of the 321 studied strains	69	20	4	3	2	<1	1	<1

[a] NT, not tested, + or −, variable reaction with most strains (80% or more) being positive; see Table 1 for definition of +, V, and −.

Serogroup O4 (14% of the strains) and O17 (8%) predominate; the other typable strains are found in 25 different serogroups. It is not surprising that most *Y. intermedia* strains are untypable, since Wauters' serotyping scheme [30] was based mainly on typical *Y. enterocolitica* strains. Only serogroup O17 was defined by the melibiose-, rhamnose-, α-methyl-D-glucoside-, raffinose-, Simmons' citrate–positive strain 955. It is therefore not surprising to find serogroup O17 well represented among *Y. intermedia* strains. H antigens [30] and structural antigens such as β-lactamases [25] from *Y. intermedia* also differ from those of *Y. enterocolitica* and other *Yersinia* species [6,8,25].

Y. intermedia has been isolated in 15 different countries (Norway, Denmark, Sweden, Iceland, Germany, Netherlands, Rumania, Czechoslovakia, Italy, France, Spain, Canada, USA, Japan, and Australia). There is little doubt that the failure to isolate *Y. intermedia* from other parts of the world is due to a lack of effort on the part of bacteriologists, rather than to a limited geographical distribution.

Freshwater or sewage isolates represent 74% of the 321 studied strains, and 8% of the strains were isolated from fish, oysters, shrimp, or snails. Thus, 82% of the strains originate from water or marine animals. Four percent of the strains are from wild rodents, and 2% are from milk, cream, or meat. Human strains represent only 13% of the total. Among them, 11 strains were isolated from stools, 14 from blood, and 16 from extraintestinal sources [10,11]. A closer examination of the epidemiological data reveals that *Y. intermedia* is rarely isolated from stools during gastrointestinal disease [2], and cold enrichment techniques are usually needed for isolation. The 14 blood isolates [17] were obtained from children in the same hospital admitted for various reasons, and whose symptomatology could not be related to these isolates. Twelve of the 16 strains isolated from extraintestinal sources were also from one hospital [10].

Y. intermedia has rarely been isolated from humans, and hardly at all from humans with gastrointestinal illnesses. These data suggest that *Y. intermedia* behaves more like an agent of nosocomial infection than as an etiological agent of diarrhea. In the environment, workers exploring aquatic ecosystems [19,20,21,22,27,31] frequently find *Y. intermedia*, but workers exploring terrestrial ecosystems

Table 3. Intra- and interspecies relatedness of *Yersinia intermedia*.

	Labeled DNA from *Y. intermedia* strain:[a]																	
	3953 (Bottone 48)									A1251								
	RBR 60°C			%D			RBR 75°C			RBR 60°C			%D			RBR 75°C		
Source of unlabeled DNA	No.	Range	Avg	No.	Range	Avg	No.	Range	Avg	No.	Range	Avg	No.	Range	Avg	No.	Range	Avg
Y. intermedia	36	77–100	95	14	0.0–4.5	1.5	19	77–100	91	12	75–94	79	12	0.0–5.0	3.5	12	66–95	73
Y. enterocolitica	17	52–76	61	7	12.0–13.5	13.0	13	21–36	29	6	53–60	56	4	11.5–14.0	12.5	2	26–31	29
Y. kristensenii	11	55–71	62	3	12.0–12.5	12.5	5	22–36	30	10	47–59	54	2	11.0–14.0	12.5	1		29
Y. frederiksenii	9	45–65	58	3	12.5–13.0	12.5	9	15–31	23	6	54–61	59	6	11.5–14.5	13.0	1		32

[a] RBR, relative binding ratio; %D, percent divergence in related DNA sequences; No., number of strains tested. Homologous reactions are arbitrarily deemed to have 100% RBR and 0.0% D. Homologous reactions are not included in number, range, or average.

Table 4. DNA relatedness of *Yersinia intermedia* strains to other *Yersinia* strains.

Source of labeled DNA	RBR 60°C[a]			%D			RBR 75°C		
	No.	Range	Avg	No.	Range	Avg	No.	Range	Avg
Y. enterocolitica 498-70	11	53-67	59	3	11.5-12.0	12.0	7	22-36	28
Y. enterocolitica 1	12	46-65	57	5	11.0-11.5	11.0	2	24-34	29
Y. kristensenii 5920	13	49-57	51	13	10.0-12.0	11.0	14	19-24	21
Y. kristensenii 1474	13	56-68	62	12	9.5-14.0	12.0	13	23-35	33
Y. kristensenii 6048	6	61-68	64	3	10.5-11.5	11.0	6	26-35	31
Y. frederiksenii 6175	3	58-64	61	2	10.5-11.5	11.0	3	23-30	27
Y. frederiksenii 2581-77	2	48-50	49	1		13.0	1		16
Y. frederiksenii 867	15	53-65	59				3	19-26	23

[a] See Table 3 for explanation of RBR, %D, and No.

rarely isolate it [1,3,5]. Therefore, *Y. intermedia* seems to be a normal component of an aquatic ecosystem.

The presence of *Y. intermedia* in food [18] might be due to the processing of that food (e.g., the washing of meat carcasses by nonchlorinated water containing *Y. intermedia* and then enrichment for *Yersinia* by cold storage of the food). For the present, *Y. intermedia* should be considered a possible opportunistic pathogen for humans.

G+C content in DNA was determined to be 48.5 ± 0.5 mol% in eight strains of *Y. intermedia* (strains A0235, A1246, A1267, 74-1093, 3953, 6151, 6300, 6521).

Relatedness results of *Y. intermedia* strains to one another and to other *Yersinia* species were obtained using labeled DNA from *Y. intermedia* strain 3953 [16]. We now extend these observations with results from a second labeled *Y. intermedia* strain, A1251 (Table 3). Both the previous and present results are summarized in Table 3.

Thirty-six strains of *Y. intermedia* gave an average of 95% relatedness to *Y. intermedia* strain 3953 in 60°C reactions. Where determined, percent divergence (%D) averaged 1.5 and relatedness in 75°C reactions averaged 91%. The range of relatedness and %D of *Y. intermedia* A1251 to 12 *Y. intermedia* strains was similar to that obtained with *Y. intermedia* strain 3953. Average relatedness with strain A1251, however, was only 79% at 60°C and 73% at 75°C. The lower relatedness values obtained with strain A1251 has two possible explanations. Strain A1251 may, in fact, be somewhat less related than strain 3953 to most strains of *Y. intermedia.* Alternatively, strain A1251 may have a larger genome size than strain 3953. These possibilities can be tested by determining relatedness in reciprocal reactions between strain 3953 and strain A1251. If the level of relatedness between these strains is similar, regardless of which strain is labeled, then A1251 is less related to other strains of *Y. intermedia.* If, however, nonreciprocal relatedness values are obtained between strain 3953 and A1251, then these organisms have different genome sizes. Labeled DNA from strain 3953 was 85% related to unlabeled DNA from strain A1251 [16], whereas labeled DNA from A1251 was only 75% related to unlabeled DNA from strain 3953. Thus, 75% of the A1251 genome is equal to 85% of the 3953 genome, or the A1251 genome is approximately 11% larger than the 3953 genome. This fact accounts for the lower average relatedness of strain A1251 to *Y. intermedia* strains. Two *Yersinia* biotype X2 strains (6005 and 5850) were about 55% related to *Y. intermedia* strain 3953 in 60°C reactions and 30% related to 3953 in 75°C reactions [16]. Relatedness between *Y. intermedia* and two *Yersinia* biotype X1 strains was 60% [16].

DNA relatedness of *Y. intermedia* to other *Yersinia* species is also shown in Table 3. *Y. intermedia* strain 3953 is about 60% related to strains of *Y. enterocolitica, Y. frederiksenii,* and *Y. kristensenii.* Relatedness of *Y. intermedia* strain A1251 to these species is between 54% and 59%. Reciprocal reactions with labeled strains of *Yersinia* species and unlabeled *Y. intermedia* strains are shown in Table 4. Relatedness values are from 50% to slightly more than 60%. %D in these reactions is 11 to 13, and interspecies relatedness falls to between 20% and 30% in 75°C reactions.

DNA relatedness clusters among *Y. intermedia* strains and between *Y. intermedia* and *Y. enterocolitica, Y. frederiksenii,* and *Y. kristensenii* are shown in Fig. 1. *Y. intermedia* relatedness is shown in two clusters. This is to point out differences in relatedness values due to the differences in genome size in labeled strains 3953 and A1251. If a third strain of intermediate genome size were used, the values would fall between these two clusters. The relatedness clusters of *Y. intermedia* with other *Yersinia* species are clearly separable from the intraspecies *Y. intermedia* clusters by their lower relatedness, higher %D, and

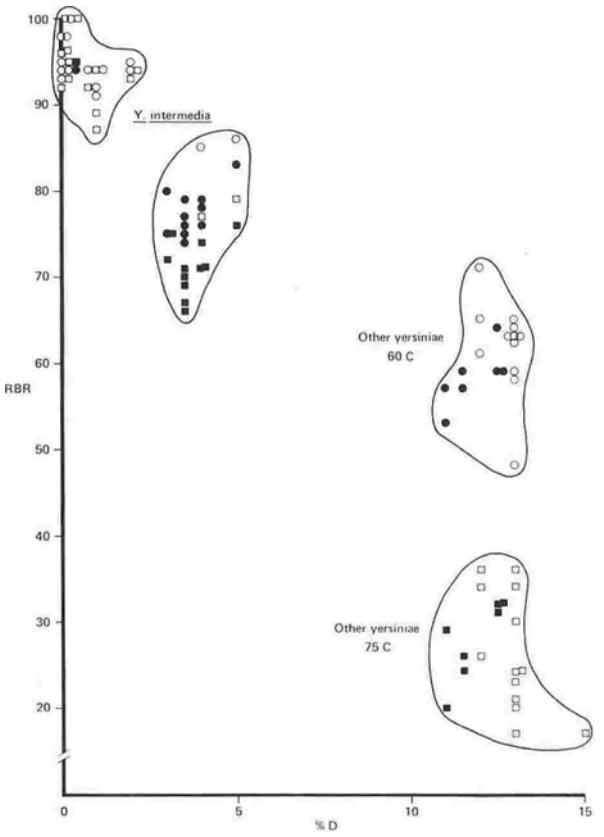

Fig. 1. Relatedness clusters of *Yersinia intermedia* strains and other *Yersinia* species to *Y. intermedia* strains 3953 and A1251. Labeled DNA from *Y. intermedia* strain 3953 or strain A1251 was reacted with unlabeled DNA from *Y. intermedia*, *Y. enterocolitica*, *Y. frederiksenii*, and *Y. kristensenii* strains at 60°C and 75°C. Thermal stability profiles were done at 60°C to determine percent divergence (%D). Relative binding ratios (RBR; % relatedness) were plotted against %D. Circles represent relatedness values obtained in 60°C reactions and squares represent relatedness values obtained in 75°C reactions. Open circles and squares represent reactions with labeled DNA from *Y. intermedia* strain 3953. Closed circles and squares represent reactions with labeled DNA from *Y. intermedia* strain A1251.

substantial decrease in relatedness in 75°C reactions.

Yersinia intermedia is 45–55% related to *Y. pseudotuberculosis* with some 12% divergence [7,16]. This observation is particularly important because *Y. pseudotuberculosis* is rhamnose positive and melibiose positive. One could argue that *Y. intermedia* is a biotype of *Y. pseudotuberculosis*, just as the metabolically inactive biotype 5 strains belong to *Y. enterocolitica*. The DNA relatedness data show conclusively that this is not the case. *Y. intermedia* has not been tested directly with *Y. pestis*. Since *Y. pestis* and *Y. pseudotuberculosis* have been shown to be 90% related [7], one can assume with certainty that *Y. intermedia* is about 50% related to *Y. pestis*. *Y. intermedia* was 38% related to *Y. ruckeri* and between 5% and 26% related to species of Enterobacteriaceae outside of *Yersinia* [16].

The name *Yersinia intermedia* was suggested by E. J. Bottone and B. Chester (personal communication) because the biochemical reactions of this organism seemed midway between *Y. enterocolitica* and *Y. pseudotuberculosis*. It is pronounced "in-ter-mee'-dee-uh". The type strain of *Y. intermedia* is 3953 (=CIP80-28 = ATCC 29909 = Bottone 48 = Chester 48). Strain 3953 was isolated by Bottone from human urine [16]. It agglutinates in serogroup O17. Its biochemical characteristics are given in Table 1.

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