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Characterization of *Yersinia enterocolitica sensu stricto*

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Abstract. The species *Yersinia enterocolitica* is defined *sensu stricto* on the bases of biochemical and other phenotypic characteristics. Biochemically, *Y. enterocolitica* contains five major biotypes: 1 through 4 of Niléhn and of Wauters, and the trehalose-negative, metabolically inactive, so-called hare strains in biotype 5 of Niléhn and of Wauters, and biochemically atypical strains, including urease-negative, Simmons' citrate–positive, and lactose- and raffinose-positive strains. *Y. enterocolitica sensu stricto* was distinguishable from the newly described species *Yersinia kristensenii* by sucrose and Voges-Proskauer reactions (negative in *Y. kristensenii*). These species were previously separated by DNA relatedness. *Y. enterocolitica* was also separable biochemically and by DNA relatedness from the two newly proposed rhamnose-positive species, *Yersinia intermedia* and *Yersinia frederiksenii*. Strain 161(=CIP 80-27=ATCC 9610) is proposed as the neotype for *Y. enterocolitica*.

The organism now named *Yersinia enterocolitica* was first reported in 1934 (McIver and Picke; cited in reference [6]). The first recognized description was that by Schleifstein and Coleman in 1939, of five human isolates [28]. As a human pathogen, *Y. enterocolitica* is most frequently associated with acute diarrhea, terminal ileitis, mesenteric lymphadenitis, and pseudoappendicitis. *Y. enterocolitica* is found in the environment and in a wide range of animal hosts, including the cat, chinchilla, mink, dog, galago, cow, beaver, monkey, deer, goose, raccoon, robin, oyster, pig, rabbit, fox, horse, ocelot, sheep, snail, frog, and many species of small rodents [1,7,20,23,26,29,37] (H. H. Mollaret, unpublished data). *Y. enterocolitica* has been isolated in every country in which it has been looked for.

In addition to having a ubiquitous distribution and a wide host range, *Y. enterocolitica* strains are biochemically heterogeneous. Because of this, various biotyping schemes were developed [18,27,32], but the biochemical parameters for *Y. enterocolitica* were controversial [18,24].

In this report, we present results of a detailed phenotypic study in order to define *Y. enterocolitica sensu stricto* and to separate it from the newly described species *Y. intermedia* [8], *Y. frederiksenii* [30], and *Y. kristensenii* [4], which were formerly called *Yersinia enterocolitica*–like organisms [18].

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Materials and Methods

Organisms. Seven thousand strains of *Yersinia enterocolitica sensu stricto* from the culture collection of the National Yersinia Center (Institut Pasteur, Paris) were studied biochemically. Strains studied both biochemically and by DNA relatedness are listed in reference [10].

Phenotypic tests. Biochemical tests were done at 22°C, 28°C, and 35–37°C. Reactions at 22°C and 35–37°C were done according to Edwards and Ewing [14] or Ewing and Davis [15]. Biochemical tests at 28°C were done as described by Bercovier et al. [2,3]. Methods used for serotyping and phage typing are cited in the text.

Results and Discussion

Yersinia enterocolitica is a Gram-negative, oxidase-negative, catalase-positive facultatively anaerobic, fermentative rod that grows on common laboratory media (e.g., nutrient agar, nutrient broth) and reduces nitrates to nitrites (except for Wauters' biotype 5). It is rarely pigmented and is asporogenous and

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Table 1. Biochemical characteristics of *Yersinia enterocolitica sensu stricto.*[a]

Test	Reaction	%+	%(+)	Neotype strain 161
Motility (28°C)	+ or (+)	88	10	+
Urease	+	99		+
Indole	V*	27	10	+
Methyl red (28°C)	+ or (+)	60	35	+
Voges-Proskauer (28°C)	+**	90	8	+
Simmons' citrate (28°C)	−	<1		−
Christensen's citrate	V	65		+
NO_3 reduction to NO_2/Type	+**/B	97/B		+/B
Tetrathionate reductase	V*	35		+
Ornithine decarboxylase	+**	97		+
β-Galactosidase (ONPG) (37°C)	+**	96		+
Lipase (Tween 80)	V*	21	9	+
Deoxyribonuclease	V*	40	28	−
Polypectate	(+)		100	(+)
Acid production from:				
D-Arabinose	−	<1		−
L-Arabinose	+	99		+
D-Xylose	V*	26	15	+
Galactose	+	99		+
L-Sorbose	+**	90	4	+
D-Cellobiose	+	99		+
Maltose	+	99		+
Lactose		8	15	−
D-Melibiose	−	<1		−
Sucrose	+**	98		+
D-Trehalose	+**	97		+
D-Raffinose	−	<1		−
i-Inositol	+ or (+)**	70	21	+
D-Sorbitol	+**	97		+
Esculin	V	31	25	+
Salicin	V	15	16	+
Amygdalin	V	15	70	+
Arbutin	V	60	16	+
Dextrin	−	5	25	−
Starch	(+)	22	78	(+)

[a] All incubations, except where indicated, were done at 28°C. +, 90% or more positive within 72 h; (+), 90% or more positive between 4 and 7 days; V, 10.1–89.9% positive; −, less than 10% positive after 72 h; *, reaction varies in different biotypes; **, most negative strains are in biotype 5. The following tests gave positive reactions for all strains tested: catalase, methyl red (37°C), fermentation in O-F test, and acid production from D-glucose, glycerol, ribose, D-fructose, D-mannose, D-mannitol, and *N*-acetyl-glucosamine. The following tests gave negative reactions for all strains tested: oxidase, motility (37°C), Voges-Proskauer (37°C), Simmons' citrate (37°C), malonate, mucate, 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, L-xylose, adonitol, L-rhamnose, dulcitol, D-melizitose, α-methyl-xyloside, α-methyl-D-mannoside, α-methyl-D-glucoside, inulin, amylose, and glycogen.

noncapsulated when grown in vitro. It contains relatively few peritrichous flagella [27]. On the basis of these characteristics, it is a member of the family Enterobacteriaceae. The morphological, cultural, and biochemical characteristics of *Y. enterocolitica* have been recently reviewed [2,6,24,25,27,32].

Table 2. Biotypes of *Yersinia enterocolitica.*[a]

Test	Biotype 1	2	3	4	5
Lipase	+	−	−	−	−
DNase	−	−[b]	−[b]	+	+
Indole	+	+	−	−	−
D-Xylose	+	+	+	−	−[b]
Sucrose	+	+	+	+	V
D-Trehalose	+	+	+	+	−
NO_3 reduction to NO_2	+	+	+	+	−

[a] See Table 1 for a definition of +, −, V, and for incubation temperature.
[b] Some strains give a delayed positive reaction (after 72 h).

Like other *Yersinia* species, *Y. enterocolitica* produces colonies of 0.5–1 mm in diameter after 24 h incubation on nutrient agar at temperatures ranging from 22°C to 37°C. On bile salts selective media used to detect pathogens in human stools, *Y. enterocolitica* grows much better at 28°C than at 37°C [27,33]. This temperature dependence is also reflected in many of its physiological characteristics. *Y. enterocolitica* strains are usually prototrophic when incubated at 28°C, but require growth factors when incubated at 37°C [11]. They are almost always nonmotile at 37°C. They are motile at 30°C and almost all strains are motile at 25°C. The growth range of *Y. enterocolitica* strains is from 4°C to 41°C, and the optimal temperature for the expression of many phenotypic characters is 29°C [2].

Temperature-dependent biochemical tests include the Voges-Proskauer test and those for β-galactosidase, fermentation of some sugars, and sometimes ornithine decarboxylase. These tests are usually positive for cultures incubated at 28°C; they are often negative for cultures grown at 37°C.

In addition to previously mentioned reactions, *Y. enterocolitica* is characterized by rapid urease activity on urea-indole medium [2], a positive ornithine decarboxylase test, and a negative phenylalanine deaminase test. The biochemical characteristics of *Y. enterocolitica*, based on the study of 7,000 strains received at the National Yersinia Center (Institut Pasteur, Paris), are given in Table 1.

Reactions for amygdalin, salicin, dextrin, esculin, and sometimes inositol were weak, delayed, or irregular when studied in the API 50E or in sugar peptone water. For this reason, these tests should not be considered as definitive for biochemical characterization of *Y. enterocolitica.*

Several different schemes have been proposed for biotyping *Y. enterocolitica* strains [2,19,27,32]. We have slightly modified Wauters' biotyping scheme,

Table 3. Differentiation of *Yersinia enterocolitica* and other *Yersinia* species.[a]

Test	*Y. enterocolitica* biotype 1-4	*Y. enterocolitica* biotype 5	S *Y. kristensenii*	Rh+ *Y. frederiksenii*	Mel+ *Y. intermedia*	X1	X2	*Y. pseudotuberculosis*
$NO_3 \rightarrow NO_2$	+	−	+	+	+	+	+	+
Voges-Proskauer	+	+	−	+	+	−	+	−
D-Cellobiose	+	+	+	+	+	+	−	−
Sucrose	+	V	−	+	+	−	−	−
D-Trehalose	+	−	+	+	+	+	+	+
L-Rhamnose	−	−	−	+	+	−	+	+
D-Melibiose	−	−	−	−	+	−	−	+
α-Methyl-D-glucoside	−	−	−	−	+	−	−	−
Ornithine decarboxylase	+	V	+	+	+	−	+	−
Indole	V	−	V	+	+	−	−	−
L-Sorbose	+	V	+	+	+	−	−	−
D-Sorbitol	+	−	+	+	+	−	+	−
D-Raffinose	−	−	−	−	+	−	−	V (11%+)
Citrate (Simmons')	−	−	−	V	+	−	+	−
Maltose	+	+	+	+	+	+	−	+
β-Xylosidase (PNPX)	−	−	−	V	−	−	−	+

[a] See Table 1 for definition of +, −, and V, and for incubation temperature.

and the definitions of five biotypes are given in Table 2. Biotype 5 strains have only been isolated from hares in Europe [25]. They do not reduce nitrates to nitrites and are always trehalose negative. Strains of other biotypes are trehalose positive and reduce nitrates to nitrites with a type B nitrate reductase [2].

Typical *Y. enterocolitica* are easily differentiated from other *Yersinia* species and from X1 and X2 strains on the basis of the reactions shown in Table 3. Rarely occurring strains of *Y. enterocolitica* give atypical reactions in various biochemical tests (see below). Therefore, the diagnostic identification of *Y. enterocolitica* and its differentiation from other *Yersinia* species should be based on the overall biochemical profile of the strain.

A variety of thermostable O somatic antigens permit *Y. enterocolitica* to be subdivided into serogroups. Winblad [38] established an antigenic scheme with 9 O-antigen groups. This scheme was enlarged by Wauters et al. [35,36], who characterized 34 O-antigen and 20 flagellar (H)-antigen groups. Most *Y. enterocolitica sensu stricto* strains share at least one H antigen, whereas other *Yersinia* species [34,36] have H antigens that differ from those of *Y. enterocolitica*. Eighty-two percent of the more than 7,000 strains received at the National Yersinia Center are typable. The frequency of the different serogroups mainly reflects the epidemiology of this organism, which is discussed below.

Y. enterocolitica has been isolated from a wide variety of sources in all countries where studies have been conducted [23]. It has been recognized as pathogenic for chinchillas [22], hares [25], and humans [17,21,28,29].

The number of human isolates of *Y. enterocolitica* began to increase dramatically as clinical bacteriologists became aware of its pathogenic potential and as better isolated methods were developed. The documented incidence of human *Y. enterocolitica* infection has increased [6,23], and in countries such as Belgium and Germany, where detection is good, it ranks between *Salmonella* and *Shigella* as a cause of diarrhea [5,31].

Strains belonging to serogroups O3, O9, and O5,27 are responsible for most gastrointestinal infections, but extraintestinal infections are caused by strains belonging to the other serogroups, usually from biotype 1. However, biotype 1, serogroup O8 strains have been isolated from patients in the United States with acute mesenteric infections [16].

Phage typing is also used to subdivide *Y. enterocolitica* [26]. It is a useful epidemiological tool. For instance, serogroup O3 strains isolated in Europe (phage type VIII), Canada (phage type IX_b), or South Africa (phage type IX_a) have different phage types. Correlations between serogroup, biotype, phage type, and pathogenicity for different susceptible hosts are summarized in Table 4.

The G+C content in the DNA of 5 *Y. enterocolitica sensu stricto* strains (strains 1, 106, 497-70, 1144, and 4052) was 48.5 ± 1.5 mol% [10].

Investigators agree that *Y. enterocolitica* is biochemically an extremely diverse species. Several groups have attempted to define its biochemical

Table 4. Correlation between serogroup, biotype, phage type, ecology and pathogenicity of *Yersinia enterocolitica.*

O Antigen	Biotype	Phage type	Source	Diseases caused and carriers	Predominant geographic distribution
5,27 6 8 Various	1, 2, or 3	X_r or X_O	Human	Healthy carriers Gastrointestinal disease Extraintestinal infection Septicemia	Australia, Europe, Japan, United States
			Environment and food	—	
9	2	X_3	Human	Gastrointestinal disease Secondary nonsuppurative arthritis	Europe
			Pig	Healthy carriers	
1, 2a, 3	3	II	Chinchilla	Mesenteric lymphadenitis Septicemia	Europe United States
3	4	VIII	Human	Gastrointestinal disease	Europe, Japan
			Pig	Healthy carriers	
		IX_a	Human	Gastrointestinal disease	South Africa
			Pig	Healthy carriers	
		IX_b	Human	Gastrointestinal disease	Canada
			Pig	Healthy carriers	
2a, 2b, 3	5	XI	Hare	Mesenteric lymphadenitis Septicemia	Europe

boundaries, but none of the proposed definitions were totally acceptable [18,19,24,27,32]. There has been general agreement that biotypes 1 through 4 of Wauters and Nilehn belong to *Y. enterocolitica sensu stricto.* The problem has been to determine whether biotype 5, atypical strains, and so-called *Y. enterocolitica*-like organisms belong to *Y. enterocolitica sensu stricto*, or to one or more separate species.

Brenner et al. [9] showed that strains conforming to a genetic definition of *Y. enterocolitica* (minimum of 70% relatedness in 60°C reactions, percent divergence [%D] below 5, and 60% or more relatedness in 75°C reactions) varied in reactions for indole, esculin, xylose, salicin, lactose, Christensen's citrate, cetrimide, *i*-inositol, Jordan's tartrate, DNase, and β-galactosidase. They also reported that one or two strains atypical in reactions for urease (negative), raffinose (positive), or ornithine decarboxylase (negative) belonged to *Y. enterocolitica.*

In a subsequent study, a much larger number of biotype 1 through 4 strains were systematically tested, and they were all highly related [10]. Included among these strains were urease-negative strains (3969, 4553, 7308, 7309, 7310, 7333), raffinose-positive, lactose-positive strains (184-77, 185-77, 842, 2725-75, 3968-76, 3974-76, 6168), Simmons' citrate-positive strains (6155, 6166), and melibiose-positive strains (2649-77, 2650-77). Thus, strains exhibiting these atypical biochemical reactions belong to *Y. enterocolitica.* Metabolic plasmids that specify both raffinose and lactose have been isolated from *Y. enterocolitica* [12,13]. Strains of *Escherichia coli* that are atypically Simmons' citrate positive are suspected of containing a plasmid-mediated gene (I. K. Wachsmuth and B. R. Davis, personal communication). The gene for citrate utilization also may be plasmid mediated in *Y. enterocolitica.*

Most biotype 5 strains of *Y. enterocolitica* were isolated from hares in Europe [25]. They differ from other biotypes in their negative reaction for trehalose and nitrate reductase and are often negative in reactions for sucrose, ornithine decarboxylase, sorbose, *i*-inositol, and β-galactosidase. DNA relatedness reactions conclusively showed that biotype 5 strains, regardless of variability in sucrose and other reactions (Table 2), are members of *Y. enterocolitica* [10]. Furthermore, intragroup relatedness within biotype 1 through 4 strains and within biotype 5 strains is somewhat higher than intergroup relatedness between biotype 1 through 4 and biotype 5 strains [10]. Sucrose-negative and sucrose-positive biotype 5 strains are essentially identical genetically [10]. Therefore, all of these trehalose-negative, metabolically inactive, biotype 5 strains constitute a single group within *Y. enterocolitica.* This is not too surprising, since they were isolated from the same animal host in the same general area.

The S^- group of *Y. enterocolitica*-like organisms has been named *Yersinia kristensenii* [4]. This group differs from biotypes 1 through 4 of *Y. enterocolitica* only by its negative sucrose and Voges-Proskauer reactions (Table 3). The S^- strains are easily differentiated from biotype 5 strains by their positive reactions for trehalose, ornithine decarboxylase, and reduction of nitrates to nitrites (Table 3).

On the basis of DNA relatedness, one can argue

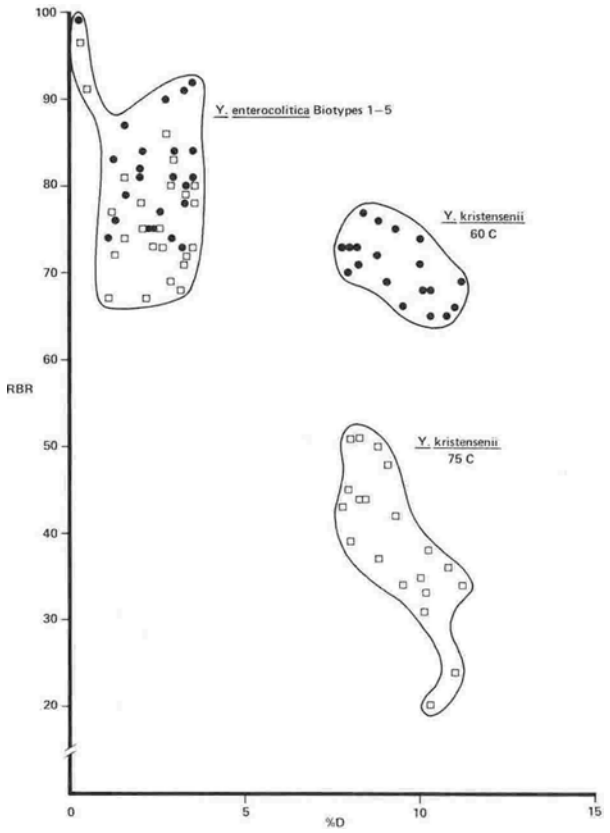

Fig. 1. Relatedness clusters of *Yersinia enterocolitica* strains and *Y. kristensenii* strains to *Y. enterocolitica* strain 498-70. Labeled DNA from *Y. enterocolitica* strain 498-70 was reacted with unlabeled DNA from *Y. enterocolitica* and *Y. kristensenii* strains at 60°C and 75°C. Thermal stability 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; squares represent relatedness values obtained in 75°C reactions. Data used in this figure are taken from Table 2 in reference [10].

that *Y. kristensenii* remains as a biotype of *Y. enterocolitica* [4,10]. *Y. enterocolitica* (all biotypes) are 75–100% related in 60°C DNA relatedness tests [10]. Relatedness between *Y. enterocolitica* and *Y. kristensenii* in 60°C reactions is usually 65–75% [10]. Thus, the highest interspecies relatedness values obtained between *Y. enterocolitica* and *Y. kristensenii* DNA overlap the lowest relatedness values obtained between strains of *Y. enterocolitica* (Fig. 1). Genetic differences between *Y. enterocolitica* and *Y. kristensenii* are much more pronounced when the thermal stability of related DNA sequences is studied (%D) and when reactions are done at 75°C, where only highly related DNA sequences can reassociate [4,10]. Such data (Fig. 1) indicate that 2–4% divergence is present in *Y. enterocolitica*–*Y. enterocolitica* reactions, compared to 7–12% divergence in *Y. enterocolitica*–*Y. kristensenii* reactions. At 75°C, relatedness between *Y. enterocolitica* remains high (65–97%), while relatedness between *Y. enterocolitica* and *Y. kristensenii* drops significantly to between 20 and 50% (Fig. 1). The genetic and phenotypic data justifying the separation of *Y. kristensenii* from *Y. enterocolitica* are discussed in more detail elsewhere [4].

Another *Y. enterocolitica*–like group, X1, is sucrose and ornithine decarboxylase negative. X1 differs from *Y. enterocolitica* biotype 5 by positive nitrate and trehalose reactions, and from *Y. kristensenii* in several reactions (Table 3). X1 and *Y. enterocolitica* are genetically related at a level compatible with different species in the same genus.

The three remaining groups of *Y. enterocolitica*–like organisms, Mel^+, Rh^+ and X2, differ from *Y. enterocolitica sensu stricto* by their ability to ferment rhamnose. The Mel^+ group has been named *Yersinia intermedia* [8] and the Rh^+ group has been named *Yersinia frederiksenii* [30]. Biochemical reactions for differentiating each of these three rhamnose-positive groups from *Y. enterocolitica* and from one another are given in Table 3. DNA relatedness data [8,10,30] support the inclusion of these three groups in the genus *Yersinia* and their exclusion from *Y. enterocolitica.*

For the reasons cited above, we propose that *Y. enterocolitica* contains only strains from biotypes 1 through 5, including the biochemically atypical strains in these biotypes. Strain 161 (=CIP 80-27 = ATCC 9610), isolated in 1932 by R. M. Picke in the United States, is proposed as the neotype strain of *Y. enterocolitica.* Strain 161 belongs to biotype 1, serogroup O8, and phage type X_2. The biochemical characteristics of strain 161 are given in Table 1.

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