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Enterovibrio norvegicus gen. nov., sp. nov., isolated from the gut of turbot (*Scophthalmus maximus*) larvae: a new member of the family *Vibrionaceae*

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Twenty-two isolates originating from the gut of healthy cultured turbot larvae in Norway were investigated using a polyphasic approach. Amplified fragment length polymorphism fingerprinting analysis showed that the isolates have typical patterns and form two main groups. Phylogenetic analysis revealed that the isolates belong to the *γ*-*Proteobacteria*, with *Vibrio hollisae* as their closest neighbour. DNA–DNA hybridization, chemotaxonomic and phenotypic analyses further proved that these isolates represent a tight novel taxon that differs from currently described species in the family *Vibrionaceae*. It is proposed that these novel isolates be accommodated in a new genus, *Enterovibrio* gen. nov., with *Enterovibrio norvegicus* sp. nov. as the type species. Isolates were motile by a polar flagellum, positive for oxidase, catalase, arginine dihydrolase and *β*-galactosidase, but negative for the Voges–Proskauer reaction. They produced indole, did not reduce nitrate and were resistant to the vibriostatic agent O/129. The DNA G+C content of *E. norvegicus* was 47·1–47·9 mol%. The type strain is *E. norvegicus* LMG 19839^T (= CAIM 430^T).

Keywords: *Vibrionaceae*, *Enterovibrio norvegicus* gen. nov., sp. nov., gut micro-organism, turbot (*S. maximus*)

INTRODUCTION

Turbot (*Scophthalmus maximus*) is a commercially important species that has been intensively fished and reared in different continents. Recently, there have been several reports showing that the intestinal microflora of sea-water fish is dominated by members of the family *Vibrionaceae* and that the gut microflora plays an important role in the health of early life stages of fish (Hansen & Olafsen, 1999; Ring & Birkbeck, 1999). Mortalities in early larval stages of intensively cultured marine fish are often very high and related to bacterial infections in which opportunistic bacteria play an important role (Ishimura *et al.*, 1996; Diggles *et al.*, 2000). On the other hand, it has also been proved that certain *Vibrio* strains isolated from the gut of *S. maximus* larvae, when added to the culture water, improve larval survival and growth (Huys *et al.*, 2001). Culturable microflora from the gut of fish larvae have been the subject of many reports, but these micro-organisms have generally been identified only at the family and/or genus level (Blanch *et al.*, 1997; Ring & Gatesoupe, 1998). It is likely that phenotype-based fingerprinting techniques applied in many previous studies have hampered the correct taxonomic identification of several taxa (Cerdà-Cuéllar *et al.*, 1997; Hansen & Olafsen, 1999; Onarheim *et al.*, 1994; Ring & Birkbeck, 1999). The usefulness of genomic fingerprinting techniques such as amplified fragment length polymorphism (AFLP), pulsed-field gel electro-

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Abbreviation: AFLP, amplified fragment length polymorphism.

The EMBL accession numbers for the 16S rDNA sequences of strains LMG 19839^T, LMG 19840 and LMG 19842 are respectively AJ316208, AJ316207 and AJ437193.

A list of less-common phenotypic reactions of members of the *Vibrionaceae* is available as supplementary data in IJSEM Online (http://ijs.sgmjournals.org/).

phoresis and repetitive elements palindrome PCR for studies on bacterial evolution, phylogeny and taxonomy have recently been recognized (Rademaker *et al.*, 2000; Van Belkum *et al.*, 2001). Several researchers have also suggested that AFLP could be an alternative to whole-genome sequencing and DNA–DNA hybridization experiments (Coenye *et al.*, 1999; Huys *et al.*, 1996; Janssen, 2001).

In the present study, phenotypic and genomic features of 22 isolates from the gut of turbot larvae are described. It is also shown that, phenotypically, the isolates resemble the genus *Vibrio*, but at the genomic level they clearly represent a novel genus, for which the name *Enterovibrio* gen. nov. is proposed; *Enterovibrio norvegicus* sp. nov. is the type species.

METHODS

Twenty-two isolates [LMG 19839^T (= CAIM 430^T), LMG 19840 (= CAIM 427), LMG 19841 (= CAIM 436), LMG 19842 (= CAIM 451), LMG 20957 (= CAIM 428), R-3719, R-3668, R-3678, R-3708, R-3717, R-3727, R-3729, R-3731, R-3749, R-3759, R-3764, R-3929, R-3773, R-3792, R-3814, R-3819, R-3847], isolated from the gut of healthy turbot larvae at the Aquaculture Research Station of Austevoll (Norway) during the summer of 1997 as described previously (Huys *et al.*, 2001), were analysed. All strains included in this study were deposited in the BCCM/LMG Bacteria Collection at Ghent University and in the CAIM collection of the Centre of Research on Nutrition and Development (CIAD) in Mazatlán, Mexico. Strains were grown on marine agar 2216E (MA; Difco) at 28 °C for 24 h unless otherwise stated. Colony morphology was examined on cultures grown on thiosulfate-citrate-bile salts-sucrose agar (TCBS; Difco) and tryptone soy agar (TSA; Oxoid) supplemented with 2% (w/v) NaCl using a stereoscopic microscope. Cell morphology was examined on wet mounts using a phase-contrast microscope.

Bacterial DNA was extracted following the technique of Pitcher *et al.* (1989). Fluorescent AFLP patterns and 16S rDNA sequences were generated on an ABI Prism 377 DNA sequencer (Applied Biosystems) and analysed as described previously (Thompson *et al.*, 2001). The consensus sequences were transferred into BIONUMERICS 2.0 software (Applied Maths) and phylogenetic trees were constructed based on the neighbour-joining (Saitou & Nei, 1987) and maximum-parsimony methods. The 16S rDNA sequences of the type strains of *Vibrio ichthyoenteri* and *Vibrio penaeicida* were determined in the course of the present study. The 16S rDNA sequences of the other type strains included in this study were retrieved from the EMBL database. DNA–DNA hybridization was performed under stringent conditions using the microplate technique with photobiotin-labelled DNA at a temperature of 38 °C for 3 h, as described previously (Willems *et al.*, 2001). The DNA G+C content was determined by HPLC (Tamaoka & Komagata, 1984).

Phenotypic characterization of the isolates was performed using API 20E, API ZYM (bioMérieux) and Biolog GN metabolic fingerprinting following the instructions of the manufacturers, with slight modifications (Thompson *et al.*, 2002). Classical phenotypic tests were performed as described previously (Baumann *et al.*, 1984; Delafield *et al.*, 1965; Farmer & Hickman-Brenner, 1992; Thompson *et al.*, 2002; Vandamme *et al.*, 1998). Antibiograms were carried out using disc diffusion methodology (Acar & Goldstein, 1996) with commercial discs (Oxoid). The inhibition zone of each antibiotic was measured on strains grown on brain-heart infusion broth (BHI; Difco) supplemented with 1·5% (w/v) bacteriological agar no. 1 (Oxoid) and with 1·5% (w/v) NaCl for 24 h at 28 °C. Fatty acid methyl ester analysis was carried out as described by Huys *et al.* (2001). Isolates were grown on trypticase soy broth (Becton Dickinson) supplemented with 1·5% (w/v) Bacto agar (Becton Dickinson) and 1·5% (w/v) NaCl and on MA at 28 °C for 24 h. Approximately 50 mg cells was harvested and the fatty acids were isolated and analysed using the Microbial Identification System software package, version 3.9 (Microbial ID).

RESULTS AND DISCUSSION

Fingerprinting analysis of the whole genome from the novel isolates representing *Enterovibrio* gen. nov. clearly showed that they possess typical AFLP patterns consisting of 78 ± 9 bands (Fig. 1). Intraspecific genomic diversity exists among the 22 isolates, and at least two main groups of genomes exist, corresponding to AFLP clusters A68 and A69 found in a previous study (Thompson *et al.*, 2001). Some isolates (R-3749, R-3847 and R-3773; R-3717 and R-3929; R-3731 and R-3668; LMG 19841 and R-3708; R-3719 and LMG 19839^T) clustered at the reproducibility level (i.e. $\geqslant 88\%$ pattern similarity) and were thus indistinguishable by AFLP. Visual examination and numerical analysis of the AFLP patterns of the *Enterovibrio* isolates revealed that they form a cluster that is completely separate from currently known species in the family *Vibrionaceae* (Thompson *et al.*, 2001), supporting our conclusion that *Enterovibrio* species possess a unique genome.

Fig. 2 shows a neighbour-joining tree with the estimated positions of most representatives of the *Vibrionaceae* and bootstrap values after 500 simulations, based on almost complete 16S rDNA sequences. Six main branches could be distinguished within this family by both neighbour-joining and maximum-parsimony methods. The first branch harboured the *Enterovibrio* isolates. *Vibrio hollisae* formed a second branch sharing only 94% 16S rDNA similarity with *Enterovibrio* gen. nov., its closest neighbour. The 16S rDNA sequences of these two taxa clearly indicate that they represent two new genera within the family *Vibrionaceae*. It has been previously concluded that 95–96% 16S rDNA similarity is the level for circumscribing different genera within the family *Vibrionaceae* (Kita-Tsukamoto *et al.*, 1993). It has been suggested that *V. hollisae* should be elevated to genus rank because of its great divergence from other *Vibrio* species (Dorsch *et al.*, 1992; Kita-Tsukamoto *et al.*, 1993). The third branch harboured the *Photobacterium* species, which had 16S rDNA sequence similarity values of 93·9–97·8%. The fourth branch consisted of the psychrophilic species *Vibrio fischeri*, *Vibrio wodanis*, *Vibrio salmonicida* and *Vibrio logei*, which had similarities of 95·2–98·3%. The fifth branch harboured all other *Vibrio* species (except *V. hollisae*), *Listonella pelagia* and *Listonella anguillarum*,

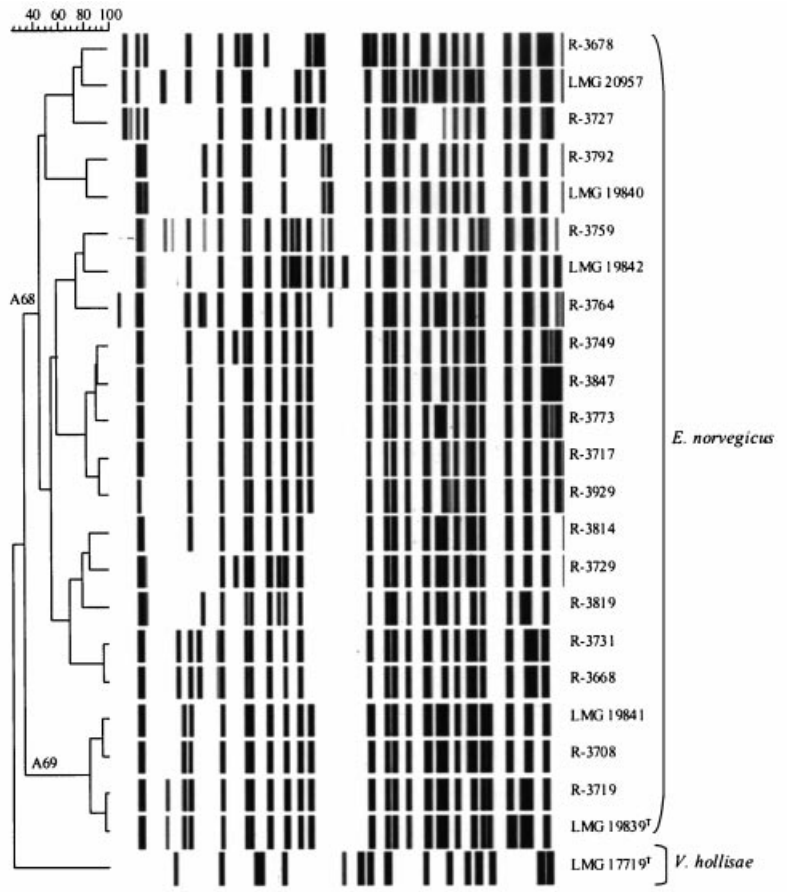

Fig. 1. Dendrogram of the AFLP patterns of 22 isolates of *Enterovibrio norvegicus* gen. nov., sp. nov. *Vibrio hollisae* LMG 17719^T, the closest phylogenetic neighbour of *E. norvegicus*, was included as an outlier. A band-based (Dice) cluster analysis (Ward) was used.

which had similarities of 92·9–99·2 %. *Enterovibrio* was distantly related to *Vibrio cholerae*, the type species of the family *Vibrionaceae*, sharing only 91·6 % 16S rDNA similarity. Some members of the fourth branch have been referred to as the *Vibrio* core group (Dorsch *et al*., 1992). It is noticeable that this branch is quite diverse. The genus *Listonella*, which was proposed based on the 5S rDNA sequence (Macdonell & Colwell, 1985), cannot be distinguished from the other vibrios. The 16S rDNA sequences of *V. ichthyoenteri* LMG 19664^T and *V. penaeicida* LMG 19663^T, determined in this study, belonged to the fifth branch and were respectively closely related to *Vibrio scophthalmi* (99·2 %) and *Vibrio nigripulchritudo* (97·2 %). *Salinivibrio costicola* formed the sixth branch, having 92·6 % similarity to the *Enterovibrio* isolates. The 16S rDNA similarities of *Enterovibrio* isolates towards representative species of related genera, *Shewanella benthica* (X82131), *Moritella marina* (X74711) and *Pseudoalteromonas haloplanktis* (X67024) were respectively 90·7, 89·5 and 89·1 %. Based on 16S rDNA similarity values among the *Enterovibrio* isolates and other members of the family *Vibrionaceae*, it can be concluded that the *Enterovibrio* isolates represent a new taxon in this family.

DNA–DNA hybridization experiments revealed that the *Enterovibrio* isolates form a single tightly related group that exhibits at least 87 % DNA similarity (Table 1). *Enterovibrio* showed only 22 % DNA similarity with its closest phylogenetic neighbour, *V. hollisae*. These results confirmed our findings from AFLP and 16S rDNA sequence analyses and proved that the *Enterovibrio* isolates should be regarded as a novel taxon. The *Enterovibrio* isolates possessed DNA G+C contents of 47·1–47·9 mol %.

The *Enterovibrio* isolates shared the main phenotypic features of the genus *Vibrio*. However, some characteristics useful in differentiating *Enterovibrio* from other genera of the family *Vibrionaceae* were found and are listed in Table 2 (a list of less-common phenotypic reactions of members of the *Vibrionaceae* is available as supplementary data in IJSEM Online; http://ijs.sgmjournals.org/). The novel species is easily differentiated from *Photobacterium* and *Salinivibrio* species since it produces indole but not acetoin. It can also be distinguished from *Salinivibrio* strains by its β-galactosidase activity and the absence of gelatinase activity. Most vibrios reduce nitrate (except *Vibrio cyclitrophicus*, *Vibrio gazogenes*, *Vibrio metschnikovii* and *V. salmonicida*) and utilize pyruvate (except *Vibrio halioticoli* and *Vibrio tapetis*), whereas the *Enterovibrio* isolates do not. Moreover, *Enterovibrio* is not susceptible to the vibriostatic agent O/129, unlike most vibrios (except *Vibrio lentus* and *Vibrio aerogenes*). The G+C contents of the DNA of the *Enterovibrio* isolates partially overlap the G+C contents of vibrios.

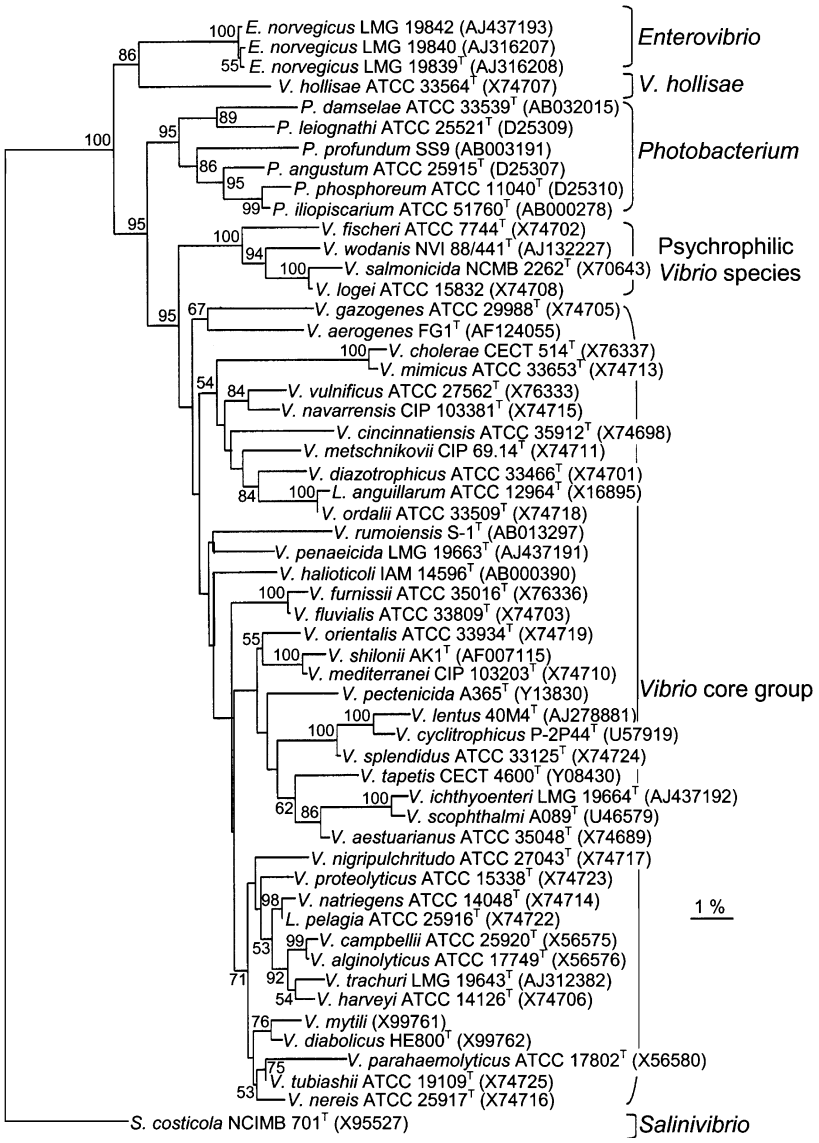

Fig. 2. Phylogenetic tree with the estimated positions of most representatives of the family *Vibrionaceae* using the neighbour-joining method based on almost complete 16S rDNA sequences. Bootstrap percentages after 500 simulations are shown. Bar, 1% estimated sequence divergence.

Table 1. DNA similarity among *E. norvegicus* isolates and *V. hollisae* LMG 17719^T and their G+C content

Strain	G+C content (mol%)	DNA similarity (%) with:					
		1	2	3	4	5	6
E. norvegicus gen. nov., sp. nov.							
1. LMG 19840	47·9	100					
2. LMG 20957	47·1	94	100				
3. LMG 19839^T	47·5	87	103	100			
4. LMG 19841	47·4	92	104	99	100		
5. LMG 19842	47·6	91	99	91	92	100	
V. hollisae							
6. LMG 17719^T	48·5	20	21	22	22	21	100

Table 2. Useful features for differentiating genera in the family *Vibrionaceae*

Data were obtained from Alsina & Blanch (1994), Benediktsdóttir *et al.* (2000), Borrego *et al.* (1996), Hedlund & Staley (2001), Ishimaru *et al.* (1995), Ishimaru *et al.* (1996), Lambert *et al.* (1998), Macián *et al.* (2001), Onarheim *et al.* (1994), Pujalte *et al.* (1993), Raguénès *et al.* (1997), Sawabe *et al.* (1998), Urdaci *et al.* (1991) and Yumoto *et al.* (1999). A list of less-common phenotypic reactions of members of the *Vibrionaceae* is available as supplementary material in IJSEM Online (http://ijs.sgmjournals.org/).

Characteristic	*Enterovibrio*	*Photobacterium*	*Salinivibrio*	*Vibrio*
ONPG	+	+*	−	+*
Gelatinase activity	−	−†	+	+*
Acetoin production	−	+*	+	−†
Indole production	+	−	−	+*
Arginine dihydrolase	+	+	+	−*
Nitrate reduction	−	+*	−	+†
Susceptibility to O/129 (150 μg)	−	+	+	+†
Utilization of:				
Citrate	−	−	−	+*
Pyruvate	−	+†	+	+†
Propionate	−	−	+	+*
L-Proline	−	−†	+	+†
D-Alanine	−		+	+†
Aconitate	−		−	+†
DNA G+C content (mol%)	47·1–47·9	40·0–44·0	49·0–50·5	38·8–50·6‡

* Over 65% of species show this feature (exceptions are listed in the supplementary material).

† Over 85% of species show this feature.

‡ Over 65% of species have G+C contents that are not within the range 47–48 mol%.

The *Enterovibrio* isolates possess typical fatty acid patterns and phenotypic features that differentiate them from other arginine dihydrolase- and indole-positive species of the family *Vibrionaceae* (Table 3).

The genomic and phenotypic features of the *Enterovibrio* isolates presented in this study clearly prove that these isolates represent a novel taxon within the family *Vibrionaceae*. Therefore, it is proposed to include these isolates into a new genus, *Enterovibrio* gen. nov., with *Enterovibrio norvegicus* sp. nov. as the type species.

Description of *Enterovibrio* gen. nov.

Enterovibrio (En.te.ro.vib′ri.o. Gr. n. *enteron* intestine; L. n. *vibrio* that which vibrates; N.L. n. *Enterovibrio* enteric vibrio).

Gram-negative, motile, oxidase- and catalase-positive. DNA G+C content of 47·1–47·9%. The most abundant fatty acids are 16:1ω7*c* and/or 15:0 iso 2-OH, 16:0 and 18:1ω7*c*. Chemoheterotrophic, mesophilic and moderately halophilic. *Enterovibrio* strains utilize dextrin, *N*-acetyl D-glucosamine and α-D-glucose as sole carbon sources. Arginine dihydrolase, indole and β-galactosidase are positive. Voges–Proskauer and lysine and ornithine decarboxylases are negative. Nitrate is not reduced. Resistant to the vibriostatic agent O/129 (10 and 150 μg). Member of the γ-*Proteobacteria*. Type species is *Enterovibrio norvegicus*.

Description of *Enterovibrio norvegicus* sp. nov.

Enterovibrio norvegicus (nor.ve′gi.cus. M.L. adj. *norvegicus* of Norway, where the organism was isolated).

Description is as for the genus with the following additional features. Cells are 0·8 × 1·0–1·2 μm and motile by means of a polar flagellum when grown in liquid medium. They form smooth, rounded colonies with raised margins, beige in colour and about 1 mm in diameter after 2 days incubation on MA at 27–28 °C. These facultative anaerobic isolates also grow well on TSA and BHI agar supplemented with 1·5% NaCl. The isolates grow slowly on TCBS, forming green colonies after 3 days at 28 °C. No growth occurs in the absence of NaCl or with ⩾ 8·0% NaCl. No growth occurs at 4 or ⩾ 35 °C. Prolific growth occurs in media containing 2% NaCl at 20–28 °C. Has both an oxidative and a fermentative metabolism. Aerobic utilization of different carbon sources is summarized in Table 4. All strains ferment α-D-glucose. None of the strains ferment arabinose, amygdalin, melibiose, sucrose, L-rhamnose, D-sorbitol, *myo*-inositol or D-mannitol. Produces β-galactosidase, alkaline phosphatase, esterase, esterase lipase, lipase, leucine arylamidase, acid phosphatase and naphthol-AS-BI-phosphohydrolase, but not tryptophan deaminase, urease, gelatinase, DNase, valine arylamidase, cystine arylamidase, trypsin, chymotrypsin, α-galactosidase,

Table 3. Useful features for differentiating arginine dihydrolase- and indole-positive species of the family *Vibrionaceae*

Taxa: 1, *E. norvegicus* gen. nov., sp. nov. ($n = 22$); 2, *V. aestuarianus* ($n = 3$); 3, *V. anguillarum* ($n = 3$); 4, *V. diazotrophicus* ($n = 3$); 5, *V. fluvialis* ($n = 2$); 6, *V. furnissii* ($n = 2$); 7, *V. mediterranei* ($n = 5$); 8, *V. metschnikovii* ($n = 3$); 9, *V. mimicus* ($n = 1$); 10, *V. nereis* ($n = 3$); 11, *V. orientalis* ($n = 2$); 12, *V. proteolyticus* ($n = 2$); 13, *V. splendidus* ($n = 1$); 14, *V. tubiashii* ($n = 3$); 15, *P. damselae* subsp. *damselae* ($n = 2$). ND, Not detected; v, variable; empty cells, no data available. Phenotypic data were obtained from this study and from Alsina & Blanch (1994). *V. diazotrophicus*, *V. mediterranei*, *V. metschnikovii*, *V. mimicus*, *V. orientalis*, *V. splendidus* and *V. tubiashii* have variable arginine dihydrolase reactions.

Feature	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Fatty acid methyl esters (%):*															
14:0	2·7±0·8	5·5±0·7	5·6±0·7	4·0±1·0	3·6±0·3	4·0±0·3	8·3±1·8	5·1±0·5	4·1	5·4±0·5	10·0±5·6	3·5±0·3	9·4	4·9±1·0	5·7±1·5
16:0	20·9±1·5	23·1±1	27·2±2·8	21·7±2·8	14·3±2·5	14·8±2·3	18·1±3·0	19·2±1·1	21	14·3±2·8	21·2±6·1	14·6±0·6	27·7	17·9±0·6	18·5±2·7
16:1ω9*c*	3·5±0·3	ND	1·2±0·4	ND	ND	ND	ND	ND	1·2	0·4	ND	0·4±0·0	ND	0·6	ND
18:1ω9*c*	2·7±0·2	ND	ND	0·1	0·2	0·3	ND	0·3±0·1	0·7	0·2	ND	0·2	5·3	0·4	ND
18:1ω7*c*	15·0±2·0	16·1±0·6	12·3±0·2	17·5±0·9	17·8±1·5	22·2±0·0	20·8±2·5	22·8±0·6	16·2	23·1±1·5	22·4±10·8	15·5±1·4	12	23·7±2·6	16·4±6·0
ONPG	+	v*	+	+	v	+	v	v	+	−	−*	−	v	+	+
Gelatinase activity	−	+	+	−	+	+	+	+	+	v	+	v	+	+	−
Acetoin production	−	−	+	−	−	−	v	v	v	−	−	v	−	−	+
Nitrate reduction	−	+	+	+	+	+	−	−	+	+	+	+	+	+	+
Susceptibility to O/129 (150 µg)	−	+	+	+	+	+	−	+	−	+		v	−	+	+
Utilization of D-mannitol	v†	+	+	+	+	+	v	v	v	v	+	v	+	+	−
Acid from sucrose	−	+	+	+	+	+	+	+	−	+	+	−	v	+	v
Growth on/at:															
8% NaCl	−	v	−	+	v	+	v	v	−	+	+	+	v	v	v
35 °C	−	+	+	+	+	+	v	+	+	+	+	+	v	v	

* Our own data.

† 95% of the *Enterovibrio* isolates do not utilize D-mannitol.

Table 4. Variable phenotypic features of the *E. norvegicus* isolates

All isolates utilized dextrin, *N*-acetyl D-glucosamine and α-D-glucose as sole carbon sources. None of the isolates utilized α-cyclodextrin, *N*-acetyl D-galactosamine, adonitol, L-arabinose, D-arabitol, cellobiose, *i*-erythritol, L-fructose, D-galactose, α-D-lactose, lactulose, D-melibiose, methyl β-D-glucoside, D-raffinose, L-rhamnose, methyl pyruvate, mono-methyl succinate, *cis*-aconitic acid, citric acid, formic acid, D-galactonic acid, D-galacturonic acid, γ-hydroxybutyric acid, *p*-hydroxyphenylacetic acid, itaconic acid, α-ketobutyric acid, α-ketovaleric acid, malonic acid, propionic acid, quinic acid, D-saccharic acid, bromosuccinic acid, succinamic acid, glucuronamide, alaninamide, D-alanine, glycyl-L-glutamic acid, L-histidine, hydroxy L-proline, L-leucine, L-ornithine, L-phenylalanine, L-pyroglutamic acid, D-serine, γ-aminobutyric acid, urocanic acid, phenylethylamine, putrescine, 2-aminoethanol, 2,3-butanediol, glycerol or glycerol phosphate.

Substrate	*E. norvegicus* ($n = 22$)*	LMG 19839^T
D-Mannose	16	+
Maltose, acetic acid	15	+
Inosine	14	−
D-Trehalose	12	+
D-Fructose	12	+
Uridine	9	−
L-Alanine	8	−
L-Glutamic acid	6	−
β-Hydroxybutyric acid	5	−
DL-Lactic acid	4	−
Psicose	4	+
Malonic acid, succinic acid, gentiobiose	2	−
Glycogen, D-mannitol, D-sorbitol, D-galacturonic acid, L-alanyl-glycine, L-asparagine, thymidine	1	−

* Numbers of positive isolates are given.

β-glucuronidase, H_2S or acetoin. Is not luminescent and is methyl red-negative and does not degrade poly(hydroxybutyrate). Resistant to the vibriostatic agent O/129 at 10 and 150 μg, streptomycin (10 μg), trimethoprim (1·2 μg) and fusidic acid (10 μg). Intermediate susceptibility to penicillin G (10 U), novobiocin (5 μg), chloramphenicol (30 μg), polymixin B (300 U), ampicillin (10 μg), oxytetracycline (30 μg) and nalidixic acid (30 μg). The major fatty acids of isolates grown on TSA/MA are summed feature 3 (35·8±0·5/36·2±0·9%; comprising 16:1ω7*c* and/or 15:0 iso 2-OH), 16:0 (20·9±1·5/19·3±0·7%), 18:1ω7*c* (15·0±2·0/14·8±1·1%), 12:0 (4·2±0·6/3·4±0·2%), 16:1ω9*c* (3·5±0·3/3·1±0·2%), 16:0 iso (2·9±1·8/2·6±0·5%), 14:0 (2·7±0·8/1·3±0·2%), 18:1ω9*c* (2·7±0·2/3·1±0·2%), summed feature 2 (2·5±0·4/2·4±0·2%; comprising 14:0 3-OH and/or 16:1 iso I and/or an unidentified fatty acid with equivalent chain length of 10·928 and/or 12:0 ALDE), 12:0 3-OH (1·9±0·4/2·9±0·2%), 18:0 (1·8±0·5/2·4±0·2%), an unidentified fatty acid with equivalent chain length of 12·484 (TSA only: 1·1±0·2%), summed feature 7 (TSA only: 0·9±0·3%; 19:1ω6*c* and/or an unidentified fatty acid with equivalent chain-length value of 18·846), 14:0 iso (TSA only: 0·6±0·5%), 17:1ω8*c* (MA only: 2·1±0·2%), 17:0 (MA only: 1·4±0·2%) and 18:0 iso (MA only: 1·0±0·1%). Isolated from the gut of larvae of the turbot (*Scophthalmus maximus*). The DNA G+C content of the type strain is 47·7 mol%. The type strain is strain LMG 19839^T (= CAIM 430^T).

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