Multilocus sequence analysis of *Vibrio tapetis*, the causative agent of Brown Ring Disease. Description of *Vibrio tapetis* subsp. *britanniensis* subsp. nov.

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Abstract

Vibrio tapetis is the causative agent of an epizootic infection described in adult clams called Brown Ring Disease (BRD). The isolation of the pathogen from different hosts showed the existence of variability both at serological and genetic level, being described to the date three major groups related to the host origin of the isolates. In this work we performed for the first time a phylogenetic study for this clam pathogen. When including the closest related *Vibrio* species, all strains of *V. tapetis* appeared as a robust monophyletic cluster in the trees generated from all genes studied as well as from their concatenated sequences. On the other hand, *V. tapetis* strains appeared clearly separated in two main clusters, sharing a similarity percentage for the concatenated sequences from 95 to 95.2 % and values of DDH between 65.05 to 79.8 %. Both clusters are themselves variable, being isolates within the cluster one grouped according their host origin. The two clusters are easily distinguishable for their capacity to produce acid from mannitol. Therefore, the results obtained supported the existence of two subspecies within this clam pathogen for which the names *V. tapetis* subsp. *tapetis* and *V. tapetis* subsp. *britanniensis* subsp. nov. are proposed.

Keywords: Brown ring disease (BRD), *Vibrio tapetis*, MLSA, DDH, *V. tapetis* subsp *britanniensis* subsp. nov.

INTRODUCTION

Vibrio tapetis is the causative agent of an epizootic infection described in adult clams called Brown Ring Disease (BRD) constituting a major limiting factor for the cultivation of Manila clams (*Venerupis philippinarum*) in Europe. The pathogen was first isolated in Landeda (France) in 1990 and denominated as VP1 [22], being further described as the new species *Vibrio tapetis* in 1996 [6].

This pathogen was considered for years as a highly homogeneous taxon on the basis of its phenotypical features, but the isolation of new strains from fish revealed some variability [4, 16, 18, 21, 26]. Serological and genetic studies confirmed the diversity among the isolates. Three major serological groups have been described associated with the host origin of the isolates [9, 27]. At genetic level, differences were first detected in the plasmid content and ribotypes of the different strains [8, 28]. More recently, based on ERIC-PCR (enterobacterial repetitive intergenic consensus), REP-PCR (repetitive extragenic palindromic) and RAPD (Randomly amplified polymorphic DNA analysis), three major genogroups, coincident with the serological groups, were established [27].

In the last decade, identification of genealogically closely related bacteria has been done on the basis of Multilocus Sequence Analysis (MLSA). This technique consists essentially in the concatenation of the sequence of several fragments of housekeeping genes (more than five to overcome potential effect of recombination) and the relationships between taxa are established by phylogenetic inference [17]. MLSA has been described as an accurate tool for delineation species in genus *Vibrio*, even in the most cryptic clusters exhibiting similar resolution power to other complex methods as DNA-DNA hybridization (DDH) [5, 7, 11, 23]. Furthermore, this method is often used when species boundaries are not well defined, being useful to improve species descriptions [13].

Up to date, no studies at phylogenetic level have been performed for the species *V. tapetis*. There are some works involving sequencing of 16S rRNA and housekeeping genes with identification purposes [16, 18, 26]. Recently, a preliminary MLSA analysis based on 5 housekeeping genes using representative strains of the three genogroups described for the species [3] demonstrated that the variability previously observed could be even greater than expected. Taking into account these auspicious results, the usefulness of MLSA approach to clarify the phylogeny of this clam pathogen was investigated in comparison with DNA-DNA hybridization (DDH). The present work, which constitutes the first complete phylogenetic study for *V. tapetis* including isolates

with different host and geographical origin, supported the description of the new subspecies *V. tapetis* subsp. *britanniensis* subsp. nov.

MATERIAL AND METHODS

Strains and culture conditions

Thirty strains of *V. tapetis* with different host and geographic origins were used in this study, including the type strain CECT 4600^T and the two representative strains (GR0202RD and HH6087) of the other major genetic groups described for this pathogen [27] (Tables 1 and S1). In addition, twelve type strains of different species representative of the major clades described for the genus *Vibrio* were included (Table S2).

All strains were routinely cultured on Marine Agar (MA) (Pronadisa, Madrid, Spain) and incubated for 72 h at 15ºC for *V. tapetis* and for 24 h at 25ºC in the case of the other vibrios. Stock cultures were stored at –80ºC in MB supplemented with 15% glycerol.

DNA extraction, PCR amplification and sequencing of housekeeping genes

Chromosomal DNA was extracted using InstaGene Matrix (BioRad, Madrid, Spain) as previously described by Romalde *et al.* [29]. The following genes were studied: 16S rRNA, *atp*A (α subunit of ATPase), *fst*Z (cell division protein), *gap*A (glyceraldehyde-3-phosphodehydrogenase), *pyr*H (uridyl monophosphate kinase), *rec*A (recombinase A), *rpo*A (α subunit of RNA polymerase) and *rpo*D (RNA polymerase sigma factor), *top*A (topoisomerase I). For PCR amplifications, genomic DNA was diluted to a final concentration of 1000 ng/µl.

All PCR amplifications were performed with the commercial kit Ready-To-Go^{TM} PCR beads (Amersham Pharmacia Biotech, Buckinghamshire, UK), which included all the reagents needed for the PCR reactions (dNTPs 200 µM each; 2.5 units of puReTaq DNA polymerase) except the specific primer pairs and DNA. Primers used for amplification and sequencing of these genes and PCR conditions are listed in Table S3.

Amplified products were examined by agarose gel electrophoresis after ethidium bromide staining. Amplicons were purified using QIAquick PCR purification kit and QIAquick gel extraction kit (QUIAGEN GmbH, Hilden, Germany) and sequenced in both directions by the dideoxy method using GenomeLab DTCS-Quick Start Kit (Beckman Coulter, Fulerton, CA, USA) in a Beckman Coulter CEQ 8000 sequencer

(Beckman Coulter). In the case of 16S rRNA, *atp*A, *rec*A and *top*A genes, internal primers were used to improve the quality of the sequences. In the rest of the genes, sequencing primers were the same than these used in the amplification reaction but diluted to 5 pmol (Table S3).

Electropherograms were assembled using the Seqman program from the Lasergene software package (DNAStar Ltd., London, UK). Sequences were manually corrected and Blastn and EzTaxon searches were performed against public databases for a preliminary identification. [2, 10]. Percentage of similarity of concatenated gene sequences was calculated using Lasergene Megalign program (DNAStar).

DNA sequences of protein-coding genes were aligned and translated into amino acid sequences using the MEGA5 software [34]. The concatenation of the sequences of the eight housekeeping genes was done by joining the in-frame sequences in a head-to-tail manner according to their alphabetical order.

Phylogenetic data analysis

Phylogenetic reconstructions were performed for the concatenated sequences of all the protein-coding genes and independently for each gene, using distance-based methods as well as character-based methods. Neighbour Joining (NJ) and Maximum parsimony (MP) were performed with MEGA5 software using the Kimura-2-parameters and the heuristic search option respectively, and a bootstrap of 1000 replicates in both cases. For the maximum likelihood (ML) reconstruction, optimal models of evolution were estimated from nucleotide data using jModelTest version 0.1.1 [14, 24], considering 11 substitution types. The best model was selected using Akaike Information Criterion (AIC).

Putative recombination events were detected using RDP4 Beta 4.16 [20]. This software uses two phylogenetic methods, RDP and bootscan, to identify recombination sequences and breakpoints. The program looks for the recombination when different parts of the genome result in discordant topologies using four nucleotide substitution methods, MaxChi, Chimera, Geneconv and SiScan. Statistical significance was set at $P \leq 0{,}01$ level.

NJ and MP reconstructions from amino acid data were done employing the ProtTest version 2.4 [1, 14] with the slow optimization strategy. Phylogenies using the appropriate model were constructed using PhyML 3.0 [14] with 1000 bootstrap replicates and visualized with FigTree v 1.3.1 [25].

DNA-DNA hybridization (DDH)

DDH experiments were done with the hydroxyapatite method using microtitre plates [37] with a hybridization temperature of 60ºC. The experiments were performed by triplicate using five strains, three of which were the representative strains of the three groups defined for the species by Rodríguez *et al.* [27] (CECT 4600^T, GR0202RD and HH6087), while the other two strains (102 and 127) clustered with HH6087 strain in the phylogenetic trees.

RESULTS

For each gene as well as for the concatenated sequences of the eight housekeeping genes, three phylogenetic trees were obtained based on NJ, MP and ML methods with 1000 bootstrap pseudoreplicates. In the case of ML, the optimal substitution models proposed varied from the least complex Jukes Cantor (JC) model in the case of *rpo*A, to the most parameter rich model, general time reversible (GTR) for the majority of genes (Table 2). All the models except JC (*rpo*A) and F81 (16S rRNA gene) varied in the number of transversion rates deemed necessary to model evolution. In all cases, the three methods rendered trees with equivalent topology.

Visual inspection of 16S rRNA gene tree built using the NJ algorithm with the 30 strains of *V. tapetis* and the other *Vibrio* species revealed that *V. tapetis* constitutes a robust monophyletic group (bootstrap value of 100%), although showing intraspecific diversity (Figs. 1 and S1). All *V. tapetis* strains shared 99.6 to 100% of mutual similarity percentage in the sequence of this gene and less than 97.8% with other *Vibrio* species according to EzTaxon database.

This monophyletic nature was also supported by the tree derived from the concatenated alignment (Figs. 2a and S2a), where the branch containing all the *V. tapetis* isolates displayed again a bootstrap of 100%. This tree revealed the existence of two groups, one of them (cluster I) containing the majority of the strains and the other (cluster II) composed by three isolates from halibut (*Hippoglossus hippoglossus*) and Manila clam seed with common geographic origin, the British Isles (UK and Ireland)(Figs. 2b and S2b). These two clusters displayed sequence similarities of approximately 95 % in the concatenated sequences, while strains within each cluster showed more than 98.2 (cluster 1) and 99.1% (cluster 2) gene sequence similarity (Table 3). The majority of the substitutions were located on the third position of each codon. Sequence similarities obtained for *V. tapetis* and other *Vibrio* species were in all cases lower than those

obtained between the two clusters of *V. tapetis*. Thus, the percentages obtained between *V. tapetis* and the rest of the vibrios were lower than 90.1% for *atp*A, 85.9 % for *fstZ*, 92.2 % for *gap*A, 88.7 % for *pyr*H, 86.6 % for *rec*A, 94.5 % for *rpo*A, 79.2 % for *rpo*D and 81.5 % for *top*A and 97.3 % for concatenated sequences.

A thorough analysis of the tree constructed with the concatenated sequence revealed the high variability existent in this species. In cluster I, a major well-supported branch (99% of bootstap) became evident in a first glimpse, containing all the Manila clam isolates, regardless their geographic origin or year of isolation, together with the French isolates from cockle (*Cerastoderma edule*) and European venus clam (*Venerupis aurea*). Close to that group, appeared the corkwing wrasse (*Symphodus melops*) isolate. The carpet shell clam (*V. decussata*) isolates as well as wedge sole (*Dicologlossa cuneata*) isolates formed separate groups.

The existence of the two main clusters within *V. tapetis* was also observed in all the trees based on individual protein-coding genes (Fig. S3) and the topology of each one was essentially the same, showing only minor differences in the locatation of certain isolates. Thus, in the case of *fst*Z tree the wedge sole isolates clustered with Manila clam isolates, and in *gap*A and *rpo*A trees no differences were observed among the isolates belonging to the cluster 2. Only in the case of shi drum (*Umbrina cirrosa*) isolates was not possible to establish a pattern in the phylogenetic reconstructions, appearing in an *incertae sedis* position. These incongruences in the topology are probably due to the recombinational events found for some strains (data not shown).

For the protein-encoding genes, the amino acid sequences were also examined, applying NJ and ML analyses using the Poisson correction, showing all of them the same topology. Figure 3 shows the NJ tree constructed using the concatenation of amino-acid sequences. Due to the more conservative character of aminoacidic sequences, groups of isolates appeared more defined. The existence of the two clusters is reinforced as well as the differentiation of groups of isolates related with their host origin in cluster I.

The DDH reassociation values within each cluster were always above the 70% threshold value (Table 4): 86.03-91.6% between the two representative strains of cluster 1 and 83.1-88-5% for strains belonging to cluster 2. Among the clusters these values ranged from 65.5 to 79.8 %.

DISCUSSION

MLSA represents nowadays the gold standard in microbial molecular systematic. This procedure constitutes a rapid and robust classification method for study phylogenetic relationships of very diverse taxons of prokaryotes by combining the information contained in the sequences of several specific genes [13].

Although 16S rRNA gene is useful for species delimitation, it lacks resolving power for species that diverged recently due to the slow evolutionary rate of its conserved parts. Moreover, the existence of several copies of the rrn operon in some bacteria, and more specifically in *Vibrio,* can potentially complicate the phylogenetic analysis due to the intraoperon variability [12, 35].

It has been documented that the 16S rRNA gene produces numerical values, i.e. similarity percentages that can be used as circumscription limits for taxa, especially at both genus and species level. The thirty strains of *V. tapetis* shows more than 99.6 % of mutual similarity percentage in the 16S rRNA gene sequence and less than 97.8% with other *Vibrio* species. Stackebrandt and Ebers [31] proposed a cutoff of 98.5% of similarity of 16S rRNA as the threshold value for species definition, consequently, all analyzed strains belong to *V. tapetis*.

The single housekeeping gene phylogenies showed some variation within each cluster due to the different evolutionary pressures, but even when more conserved genes, *fst*Z and *rpo*A, were used, the existence of the two clusters is clear. It has been described the usefulness of the inclusion of markers with different functional pressures, reported on different periods of evolutionary time, to give an idea of both recent and ancient evolutionary events [19].

Analysis of concatenated gene sequences enhances the quality of the phylogenetic reconstruction and optimizes the taxonomic resolution by adding more informative data and minimizing the weight of recombination events and, therefore, defines relationships more robustly among taxa for classification purposes [15, 19]. In the case of this study, the tree generated from the concatenated sequence shows two robust clusters, one containing the isolates from the British Isles and other one containing the isolates from all other geographic origins. This work demonstrated for the first time the association of the geographic origin and the variability of *V. tapetis*, although in the cluster one the isolates are arranged in branches according to their host origin as was previously described by Rodriguez et al. [27].

Although threshold value of 70% DDH was established for delineation of species [38], it has also been demonstrated that these similarity values can be within an accuracy of about 10%, so values in close vicinity should be regarded as critical [30, 36]. Taking into account that DDH reassociation values were higher than 83.1 % among the members of each cluster and ranged from 60.05 and 79.8 % between strains of clusters, and having in mind the monophylectic nature of *V. tapetis* in MLSA analysis, it seems clear that the two clusters belong to the same species. According to Staly and Krieg [33], a species may be divided into two or more subspecies based on minor but consistent phenotypic variations within the species or on genetically determined clusters of strains within the species. MLSA shows a clear separation of *V. tapetis* in two clusters being these groups supported by DDH values. Moreover, they are easily distinguishable by their capacity of mannitol and arabinose fermentation and utilization of citrate (Table S4). To our knowledge, there is not official recommendation of threshold values of DDH or similarity sequence for the definition of subspecies. The *ad hoc* committee on reconciliation of approaches to bacterial systematics has proposed that subspecies designations can be used for genetically close organisms that can be differentiated by some phenotypic characteristics.

Taken together all this considerations, we propose the existence of the subspecies *V. tapetis* subsp. *britanniensis* subsp. nov.

Emended description of *Vibrio tapetis*

Colonies are circular, regular in shape, translucent, and unpigmented. Swarming has not been detected in any of the media tested. Cells are gram negative motile coccobacilli. It grows on marine agar (Difco) and in media supplemented with 1 to 3% (wt/vol) NaCl but not in media with salinity higher than 5% NaC1. Facultatively anaerobic and chemoorganotrophic. Glucose metabolism is fermentative. Tests for catalase, oxidase, and nitrate reduction to nitrite are positive. Susceptible to vibriostatic agent 0/129 (150 μg). Growth occurs between 4 and 22°C but not at higher temperatures being the optimal growth temperature 15 to 20°C. Voges-Proskauer, HS production, arginine dehydrolase, and lysine and ornithine decarboxylase negative but indole production and P-galactosidase positive. The strains degrade casein, gelatin, starch, and Tween 80 but are not able to hydrolyze urea and alginate. Acid is produced from D-fructose, D-glucose, D-galactose, D-mannose, N-acetylglucosamine, and maltose, but not from L-arabinose, D-mehbiose, L-rhamnose, D-sorbitol, myo-inositol, or lactose.

The characteristics modified from the original description of Borrego et al. [6] are the capacity of some strains to produce acid from mannitol and sucrose, being now variable for these characters. In addition, in the original description is stated that *V. tapetis* had been only isolated from Manila and fine clams (*V. philippinarum* and *V. decussata*), causing the brown ring disease, but now has been also isolated from other mollusks and fish species.

***V. tapetis* subsp. *tapetis* subsp. nov.**

Vibrio tapetis subsp. *tapetis* characteristics are those stated in the emended description of *V. tapetis* with the exception of the capacity of acid production from mannitol, which is negative.

The type strain is B1090^T (= CECT 4600^T).

***V. tapetis* subsp. *britanniensis* subsp. nov.**

V. tapetis subsp. *britanniensis* subsp. nov. (bri.tan.nien'sis. L.. masc. adj. britanniensis, [pertaining to Britannia, latin name for the British Isles, where the isolates were obtained]).

Characteristics of this subspecies are the same as for the species with the exception of the capacity to produce acid from mannitol, which is positive.

The type strain HH6087^T (=CECT 8161^T = CAIM XXXX^T) was isolated by Reid et al. in 2001 [26] from *Hippoglossus hippoglossus* at the Marine Harvest Cultivation Unit at Inverailort (Scotland).

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Table 1.-Number of strains of *Vibrio tapetis* used in this study grouped according to their host and geographic origin.

Number of strains	Host	Country	Years
7	*Venerupis philippinarum*	France	1988, 1990, 1991
8	*V. philippinarum*	Spain	1994, 2005, 2007
2	*V. philippinarum* seed	Ireland	2005
2	*V. decussata*	Spain	1994
1	*Venerupis aurea*	France	1990
1	*Cerastoderma edule*	France	1990
1	*Hippoglossus hippoglossus*	England	2001
3	*Umbrina cirrosa*	Spain	2007
4	*Dicologlossa cuneata*	Spain	2005
1	*Symphodus melops*	Norway	1999

Table 2.- Sequence information. MP, Parsimony-informative sites (percentage in parentheses); ML model, optimal evolutionary model applied in maximum-likelihood estimated using the Akaike information criterion with the program ModelTest; F81,Felsenstein 1981 model; SYM, symmetrical model; G, rate variation among sites taken into account; GTR, general time-reversible model; HKY, Hasegawa, Kishino and Yano model; I, invariable sites included; JC, Jukes-Cantor model ;ND, no determined.

	Length (nt)	MP (%)	ML model
16S rDNA	1509	ND	F81
*atp*A	1203	28 (2.23)	SYM + G
*fst*Z	612	37 (6.04)	GTR
*gap*A	714	7 (0.98)	HKY + I
*pyr*H	516	34 (6.58)	GTR
*rec*A	804	69 (11.23)	JC
*rpo*A	840	0	GTR + G
*rpo*D	768	48 (6.25)	HKY + I
*top*A	666	79 (11.86)	GTR + G
MLSA	6123	316 (5.16)	GTR + I + G

Table3.- Sequence distances as percentage of similarity of differences in total nucleotide positions between the two subclades generated for the species and among them.

	Between clusters	Cluster 1	Cluster 2
16S rRNA	99.6-100	99.8-100	100
*atp*A	97.3-98.1	98.5-100	99.8-99.9
*fst*Z	93.0-93.8	98.2-100	99.5-99.7
*gap*A	98.9-99.0	99.7-100	100
*pyr*H	93.2-93.8	99.4-100	99.6
*rec*A	91.3-92	99-100	99.5-99.8
*rpo*A	99.2-99.3	99.9-100	100
*rpo*D	93.9-95.4	98.4-100	99.1-99.9
*top*A	88.0-88.6	99.1-100	99.5-99.8
MLSA	95.0-95.2	99.2-100	99.7-99.8

Table 4.-DNA-DNA hybridization among the 5 representative strains of *V. tapetis*.

	CECT 4600^T *	GR0202RD *	HH6087 *
CECT 4600^T	100	91.6 ± 4.3	74.8 ± 5.3
GR0202RD	86.03 ± 3.2	100	74.9 ± 4.8
HH6087	69.5 ± 8.0	74.1 ± 5.1	100
102	79.8 ± 1.5	65.5 ± 10.3	83.1 ± 2.6
127	77.8 ± 2.1	76.1 ± 1.8	88.5 ± 3.4

Figure Legends

Figure 1.- Phylogenetic reconstruction based on the nucleotide sequences of 16S rRNA gene of *V. tapetis* and related *Vibrio* species by NJ method. Bar, expected nucleotide substitutions per site. Only bootstrap values above 70% are shown (1000 resamplings) at each branch point.

Figure 2.- Phylogenetic reconstruction based on the concatenation of nucleotide sequences of the *atp*A, *fst*Z, *gap*A, *pyr*H, *rec*A, *rpo*A, *rpo*D and *top*A genes by NJ method, for *V. tapetis* and other *Vibrio* species (A) and only for the 30 strains of *V. tapetis* (B). Bar, expected nucleotide substitutions per site. Only bootstrap values above 70% are shown (1000 resamplings) at each branch point.

Figure 3.- Phylogenetic reconstruction based the concatenation of the amino-acid sequence of AtpA, FstZ, GapA, PyrH, RecA, RpoA, RpoD and TopA. Analysis was done using the NJ method. Bar, expected nucleotide substitutions per site. Only bootstrap values above 70% are shown (1000 resamplings) at each branch point.

Figure 1

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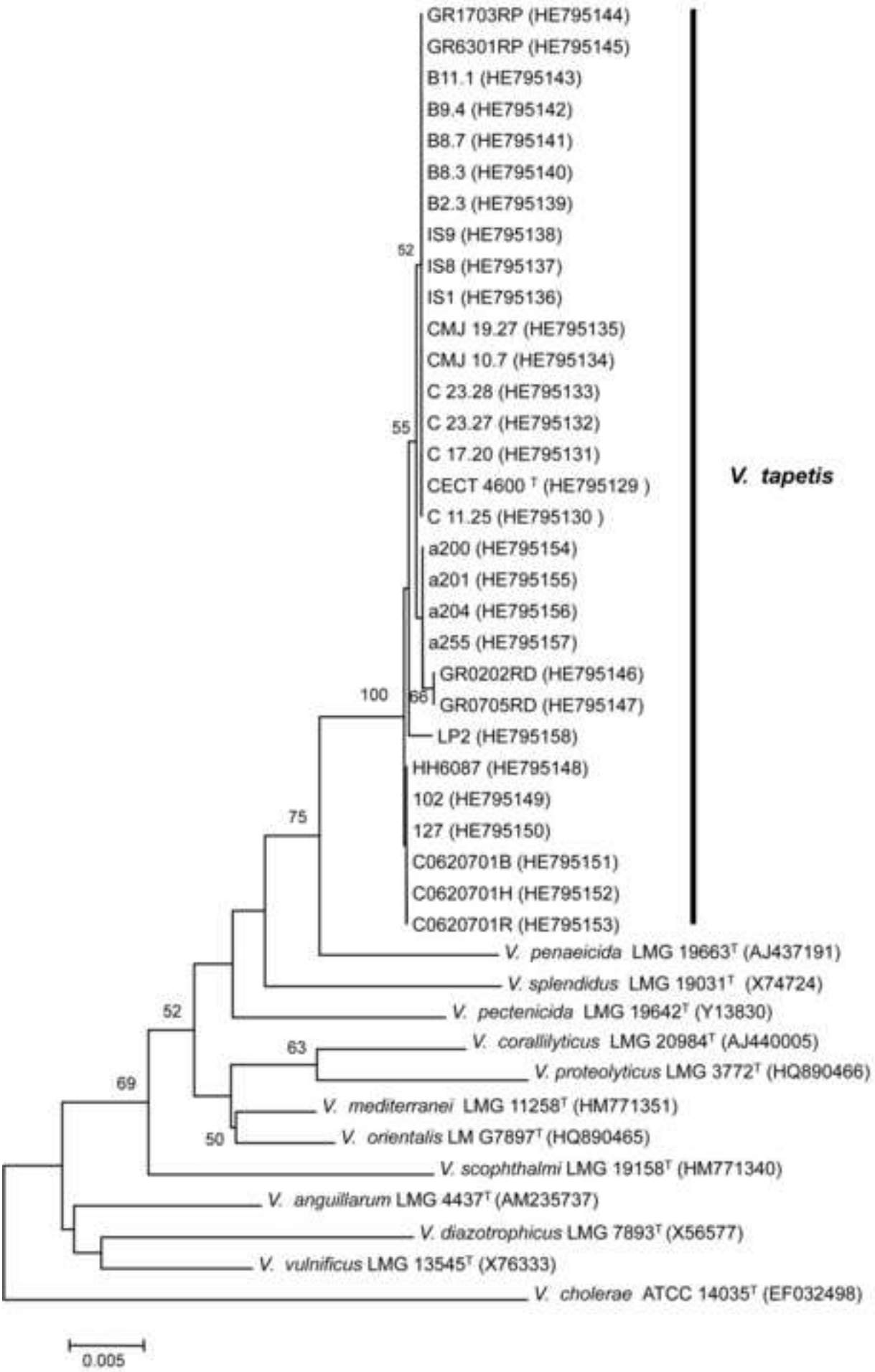

Figure 2

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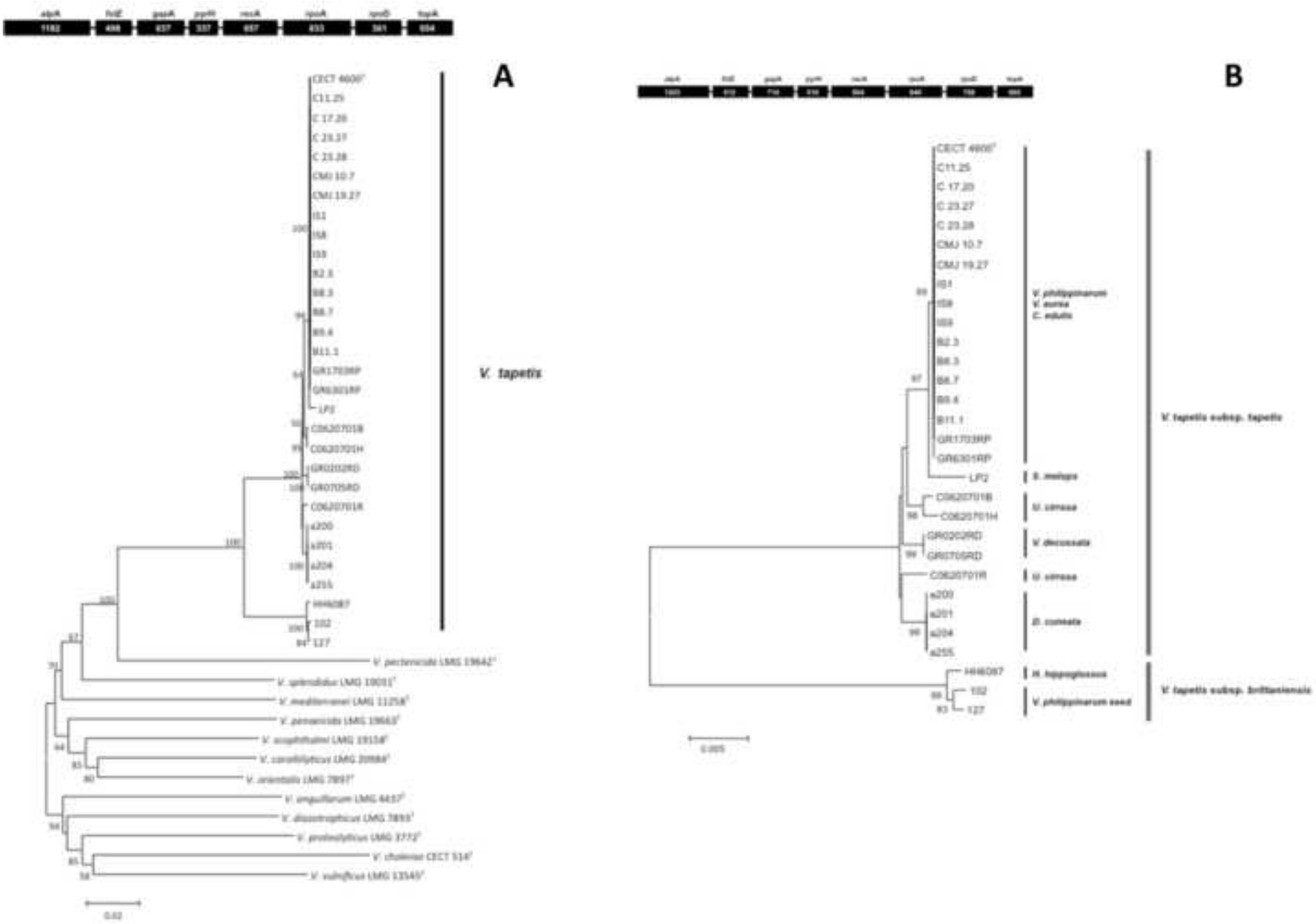

Figure 3

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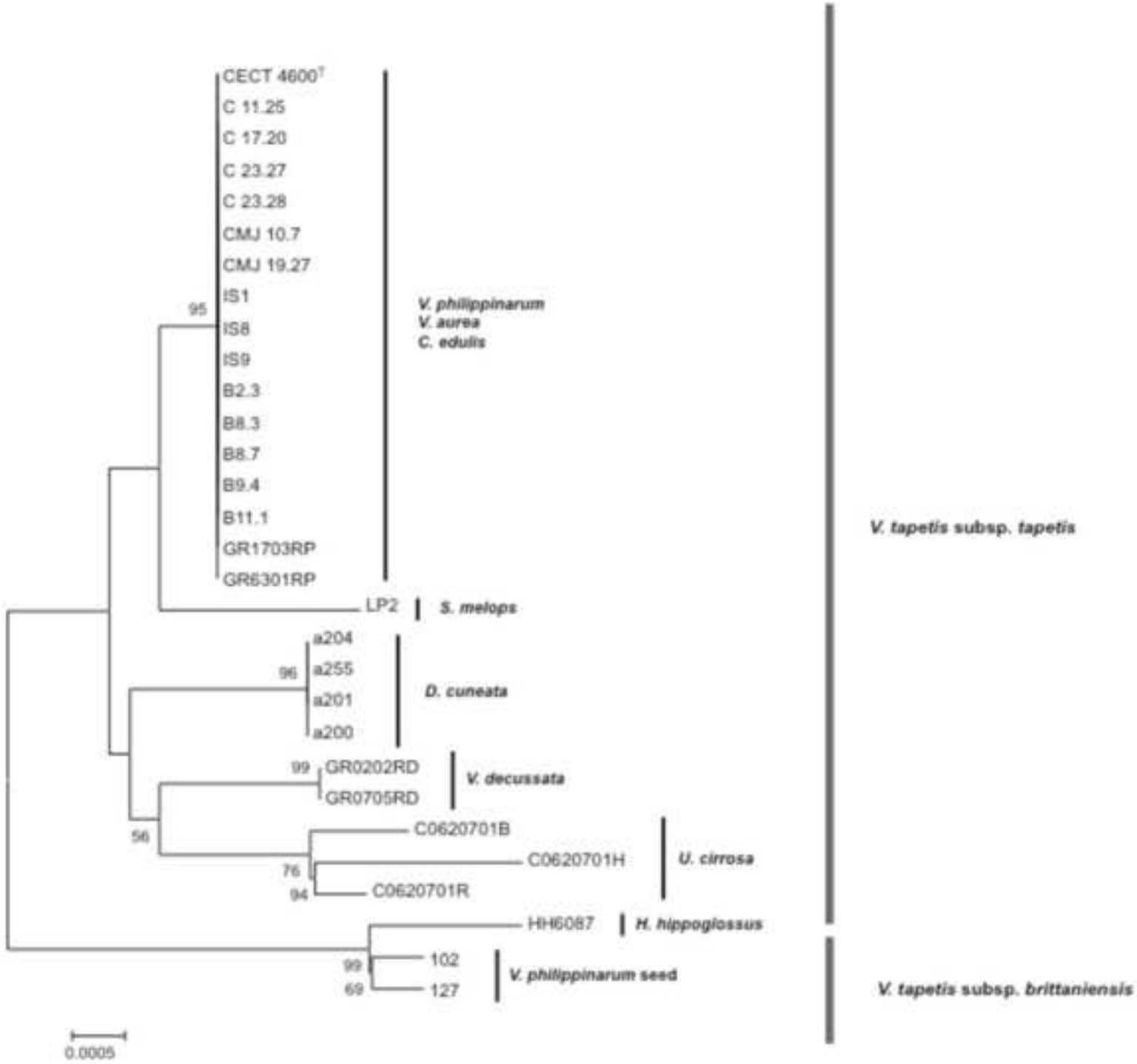


Multilocus sequence analysis of *Vibrio tapetis*, the causative agent of Brown Ring Disesase. Description of *Vibrio tapetis* subsp. *britanniensis* subsp. nov.

Sabela Balboa and Jesús L. Romalde*

Supplementary Material

Table S1.- Strains of *V. tapetis* employed in this study with their host and geographical origin. Sequence accession numbers are indicated. Sequences represented by accession numbers in italics were retrieved from public databases

Strain	**Host**	**Country and date**	**16S rDNA**	***atp*A**	***fst*Z**	***gap*A**	***pyr*H**	***rec*A**	***rpo*A**	***rpo*D**	***top*A**
CECT 4600^T	*V. philippinarum*	France, 1990	HE795129	HE795159	HE795317	HE795369	HE795189	HE795219	HE795340	HE795279	HE795249
C 11.25	*V. philippinarum*	Spain, 2005	HE795130	HE795160	HE795309	HE795370	HE795190	HE795220	HE795341	HE795280	HE795250
C 17.20	*R. philippinarum*	Spain, 2005	HE795131	HE795161	HE795318	HE795371	HE795191	HE795221	HE795342	HE795281	HE795251
C23.27	*V. philippinarum*	Spain, 2007	HE795132	HE795162	HE795319	HE795372	HE795192	HE795222	HE795343	HE795282	HE795252
C23.28	*V. philippinarum*	Spain, 2007	HE795133	HE795163	HE795320	HE795373	HE795193	HE795223	HE795344	HE795283	HE795253
CMJ 10.7	*V. philippinarum*	Spain, 2005	HE795134	HE795164	HE795321	HE795374	HE795194	HE795224	HE795345	HE795284	HE795254
CMJ 19.27	*V. philippinarum*	Spain, 2007	HE795135	HE795165	HE795310	HE795375	HE795195	HE795225	HE795346	HE795285	HE795255
IS 1	*V. philippinarum*	France, 1988	HE795136	HE795166	HE795311	HE795376	HE795196	HE795226	HE795347	HE795286	HE795256
IS 8	*V. aurea*	France, 1990	HE795137	HE795167	HE795322	HE795377	HE795197	HE795227	HE795348	HE795287	HE795257
IS 9	*C. edulis*	France, 1990	HE795138	HE795168	HE795312	HE795378	HE795198	HE795228	HE795349	HE795288	HE795258
B 2.3	*V. philippinarum*	France, 1991	HE795139	HE795169	HE795323	HE795379	HE795199	HE795229	HE795350	HE795289	HE795259
B 8.3	*V. philippinarum*	France, 1991	HE795140	HE795170	HE795338	HE795380	HE795200	HE795230	HE795351	HE795290	HE795260
B 8.7	*V. philippinarum*	France, 1991	HE795141	HE795171	HE795324	HE795381	HE795201	HE795231	HE795352	HE795291	HE795261
B 9.4	*V. philippinarum*	France, 1991	HE795142	HE795172	HE795313	HE795382	HE795202	HE795232	HE795353	HE795292	HE795262
B 11.1	*V. philippinarum*	France, 1991	HE795143	HE795173	HE795325	HE795383	HE795203	HE795233	HE795354	HE795293	HE795263
GR1703RP	*V. philippinarum*	Spain, 1994	HE795144	HE795174	HE795326	HE795384	HE795204	HE795234	HE795355	HE795294	HE795264
GR6301RP	*V. philippinarum*	Spain, 1994	HE795145	HE795175	HE795327	HE795385	HE795205	HE795235	HE795356	HE795295	HE795265
GR0202RD	*V. decussatus*	Spain, 1994	HE795146	HE795176	HE795328	HE795386	HE795206	HE795236	HE795357	HE795296	HE795266
GR0705RD	*V. decussatus*	Spain, 1994	HE795147	HE795177	HE795329	HE795387	HE795207	HE795237	HE795339	HE795297	HE795267
HH6087	*H. hippoglossus*	UK. 2001	HE795148	HE795178	HE795330	HE795388	HE795208	HE795238	HE795358	HE795298	HE795268
102	*R. philippinarum* seed	Ireland,2005	HE795149	HE795179	HE795314	HE795389	HE795209	HE795239	HE795359	HE795299	HE795269
127	*R. philippinarum* seed	Ireland, 2005	HE795150	HE795180	HE795315	HE795390	HE795210	HE795240	HE795360	HE795300	HE795270
C0620701B	*Umbrina cirrosa*	Spain, 2007	HE795151	HE795181	HE795331	HE795391	HE795211	HE795241	HE795361	HE795301	HE795271
C0620701H	*U.cirrosa*	Spain, 2007	HE795152	HE795182	HE795332	HE795392	HE795212	HE795242	HE795362	HE795302	HE795272
C0620701R	*U.cirrosa*	Spain, 2007	HE795153	HE795183	HE795316	HE795393	HE795213	HE795243	HE795363	HE795303	HE795273
a200	*D. cuneata*	Spain, 2005	HE795154	HE795184	HE795333	HE795394	HE795214	HE795244	HE795364	HE795304	HE795274
a201	*D.cuneata*	Spain, 2005	HE795155	HE795185	HE795334	HE795395	HE795215	HE795245	HE795365	HE795305	HE795275
a204	*D.cuneata*	Spain, 2005	HE795156	HE795186	HE795335	HE795396	HE795216	HE795246	HE795366	HE795306	HE795276
a255	*D.cuneata*	Spain, 2005	HE795157	HE795187	HE795336	HE795397	HE795217	HE795247	HE795367	HE795307	HE795277
LP2	*S. melops*	Norway, 1999	HE795158	HE795188	HE795337	HE795398	HE795218	HE795248	HE795368	HE795308	HE795278

Table S2.- Strains of *Vibrio* spp. employed in this study. Sequence accesión numbers are indicated. Sequences represented by accession numbers in italics were retrieved from public databases

	16S rDNA	***atp*A**	***fst*Z**	***gap*A**	***pyr*H**	***rec*A**	***rpo*A**	***rpo*D**	***top*A**
V. anguillarum LMG4437^{T}	*AM235737*	*EF601227*	*DQ907334*	*DQ907275*	Taxvibrio [a]	*AJ842375*	*AJ842561*	HE820026 [b]	*DQ907471*
V. cholerae CECT 514^{T}	*EF032498* [c]	HE805628	HE805627	HE805629	*FM202582*	*FJ479704*	HE805630	*AM942060*	HE805631
V. coralliilyticus LMG 20984^{T}	*AJ440005*	*EF601315*	*DQ907341*	*DQ907279*	*GU266292*	*AJ842402*	*AJ842587*	*EEX34866* [d]	*EF114213*
V. diazotrophicus LMG7893^{T}	*X56577*	*EF601270*	*DQ907342*	*DQ907280*	HE805632	*AJ842411*	*AJ842598*	HE805633	*DQ907480*
V. mediterranei LMG11258^{T}	*HM771351*	*EF601242*	*DQ907356*	*DQ907290*	*GU266288*	*AJ842459*	*AJ842644*	HE805635	*DQ907495*
V. orientalis LMG7897^{T}	*HQ890465*	*EF601341*	*DQ907365*	*EU130488*	*EU118243*	*AJ842485*	*AJ842672*	HE805636	*DQ907507)*
V. penaeicida LMG 19663^{T}	*AJ437191*	*EF601263*	*DQ907370*	*DQ907303*	Taxvibrio	*AJ842496*	*AJ842683*	HE820027 [e]	*DQ907512*
V. pectenicida LMG19642^{T}	*Y13830*	*EF601264*	*DQ907368*	*DQ907301*	Taxvibrio	*AJ842491*	*AJ842678*	HE805637	*DQ907510*
V. proteolyticus LMG 3772^{T}	*HQ890466*	*EF601259*	*EF114210*	Taxvibrio	Taxvibrio	*AJ842499*	*AJ842686*	HE805638	*DQ907514*
V. scophthalmi LMG 19158^{T}	*HM771340*	*EF601261*	*DQ907376*	*DQ907309*	*HM771376*	*HM771381*	*HM771386*	HE805639	*HM771335*
V. splendidus LMG19031^{T}	*X74724*	*EF601244*	*DQ481635*	*DQ481622*	*EU118241*	*EU130529*	*AJ842725*	*AY751355* [f]	*DQ481661*
V. vulnificus LMG13545^{T}	*X76333*	*AE016795.3* [g]	*DQ907382*	*GQ382185* [h]	*GQ382226*	*AJ580890*	*GQ382243*	HE805634	*DQ907522*

[a] Taxvibrio, The Taxonomy of the Vibrios (http://www.taxvibrio.nlcc.br)
[b] Sequence of rpoD gene is deposited under the name ATCC 19264^{T}
[c] Sequence of 16S rRNA gene is deposited under the name ATCC 14035 ^{T}
[d] Sequence for *rpo*D gene is deposited under the name ATCC BAA-450
[e] Sequence for *rpo*D gene is deposited under the name AM101
[f] Sequence for *rpo*D gene is deposited under the name LMG 4042^{T}
[g] sequence for *atp*A gene is deposited under the name CMP6
[h] sequence obtained for *gap*A gene is deposited under the name ATCC 2756^{T}.

Table S3.- PCR condition and primer sequence of PCR used in this study.

Locus	Primer	Primer sequence	Length (bp)	PCR cycling	Reference
***atp*A**	1F*	CTDAATTCHACNGAAATYAGY	1322	5 min 95ºC 3 x (45s 95ºC, 2 min 55ºC, 1 min 72ºC) 30x (20 s 95ºC, 1 min 55ºC, 1 min 72ºC) 7 min 72ºC.	Thompson *et al*., 2007
	2F	GCNATGGGBGAATAYTTCCG			
	3R	CGGAARTATTCVCCCATNGC			
	4R*	TTACCARGWYTGGGTTGC			
	5R	GCHAGHGCDGTACGRATACC			
	6F	AGCGAWCTRATYAARCARCG			
***fst*Z**	75F	GCTGTTGAACACATGGTACG	750	5 min 94 ºC, 30 x (1 min 94 ºC, 1min 50.5 ºC, 1 min 72 ºC), 7 min 72 ºC	Sawabe *et al*. 2007
	800R	GCACCAGCAAGATCGATATC			
***gap*A**	150F	AACTCACGGTCGTTTCAAC	750	5 min 94ºC 30x (1 min 94ºC, 1 min 55ºC, 1 min 72ºC) 10 min 72ºC.	Sawabe *et al*. 2007
	899R	CGTTGTCGTACCAAGATAC			
***pyr*H**	4F	ATGASNACBAAYCCWAAACC	599	5 min 95ºC 3 x (1 min 95ºC, 2 min 15 s 50ºC, 1 min 15 s 72ºC) 30x (35 s 95ºC, 1 min 45 s 50ºC, 1 min 15 s 72ºC) 7 min 72ºC.	Thompson *et al.* 2005
	2R	GTRAABGCNGMYARRTCCA			
***rec*A**	1F*	TGARAARCARTTYGGTAAAGG	783	5 min 95ºC 3 x (45s 95ºC, 2 min 55ºC, 1 min 72ºC) 30x (20 s 95ºC, 1 min 55ºC, 1 min 72ºC) 7 min 72ºC.	Thompson *et al*. 2004
	2R*	RTCRCCNTTRTAGCTRTACC			
	3F	FTYGGBGTGATGTTYGGTAACC			
	4R	GGGTTACCRAACATCACVCC			
***rpo*A**	1F*	ATGCAGGGTTCTGTDACAG	931	5 min 95ºC 30x (1 min 95ºC, 2 min 15 s 55ºC, 1 min 15s 72ºC) 7 min 72ºC.	Thompson *et al.* 2005
	3R*	GHGGCCARTTTTCHARRCGC			
	5F	GCAGCDCGTGTWGARCARCG			
	6R	RCGYTGYTCWACACGHGCTGC			
***rpo*D**	70F	ACGACTGACCCGGTACGCATGTAYATGMGNGARATGGGNACNGT	780	5 min 95ºC, 30x (1 min 94ºC, 45s 59ºC, 2 min 72ºC) 10 min 72ºC	Pascual *et al.* [2010
	70R	ATAGAAATAACCAGACGTAAGTTNGCYTCNACCATYTCYTTYTT			
topA	400F	GAGATCATCGGTGGTGATG	800	5 min 95ºC, 30x (1 min 95ºC, 45s 50ºC, 1 min 72ºC) 10 min 72ºC.	Sawabe *et al.*, 2007
	1200R	GAAGGACGAATCGCTTCGTG			

(*)Primers used to amplify the gene. The rest of the primers are internal and were used only for sequencing

Figure S1.- Phylogenetic reconstruction based on the nucleotide sequence of 16S rRNA gene of *V. tapetis* and other *Vibrio* species using the ML method. Bar, estimated nucleotide substitutions per site. Numbers in the branches indicates length branch.

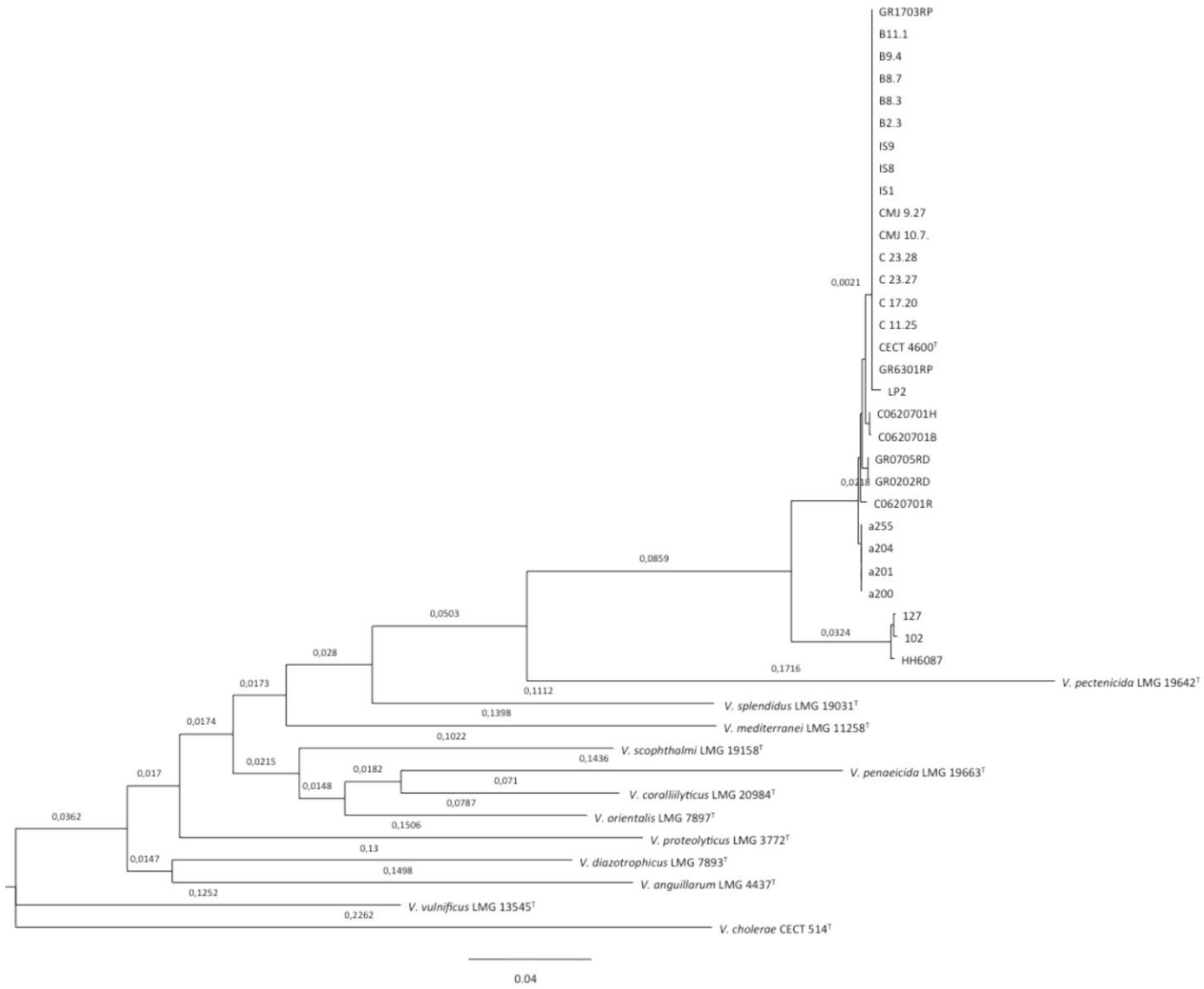


Figure S2.- Phylogenetic reconstruction based on the concatenated sequences the *atp*A, *fst*Z, *gap*A, *pyr*H, *rec*A, *rpo*A, *rpo*D and *top*A genes of *V. tapetis* and other *Vibrio* species (A), and only *V. tapetis* isolates (B), using the ML method. Bar, estimated nucleotide substitutions per site. Numbers in the branches indicates length branch.

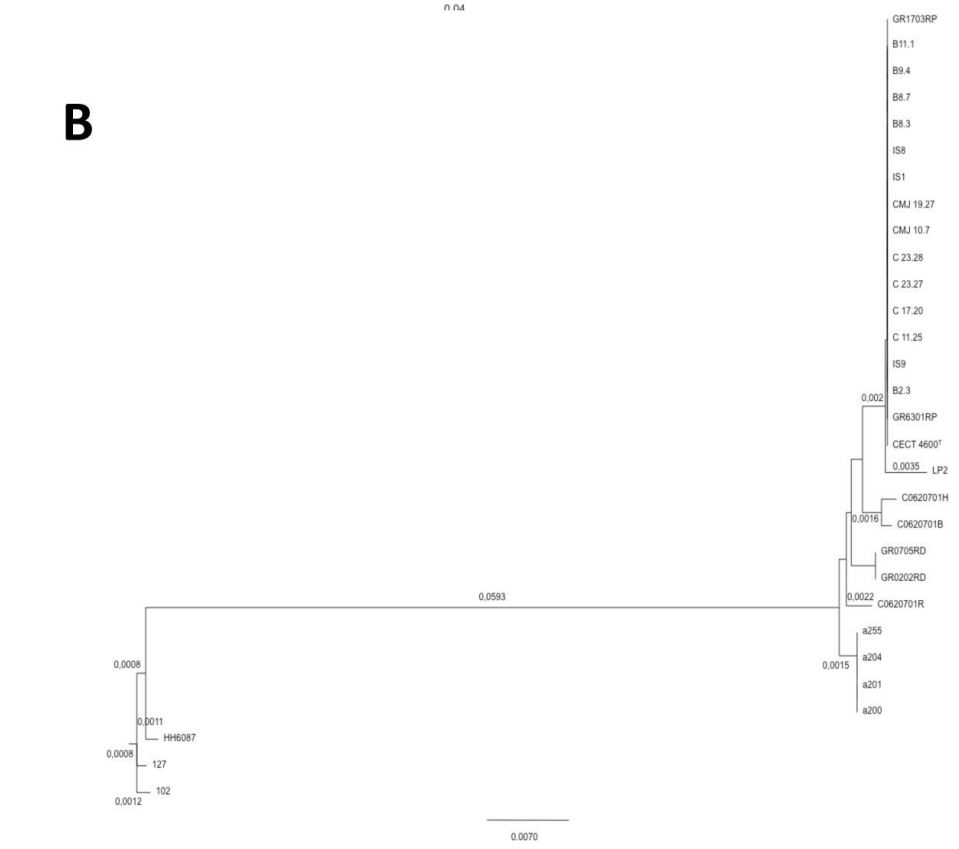
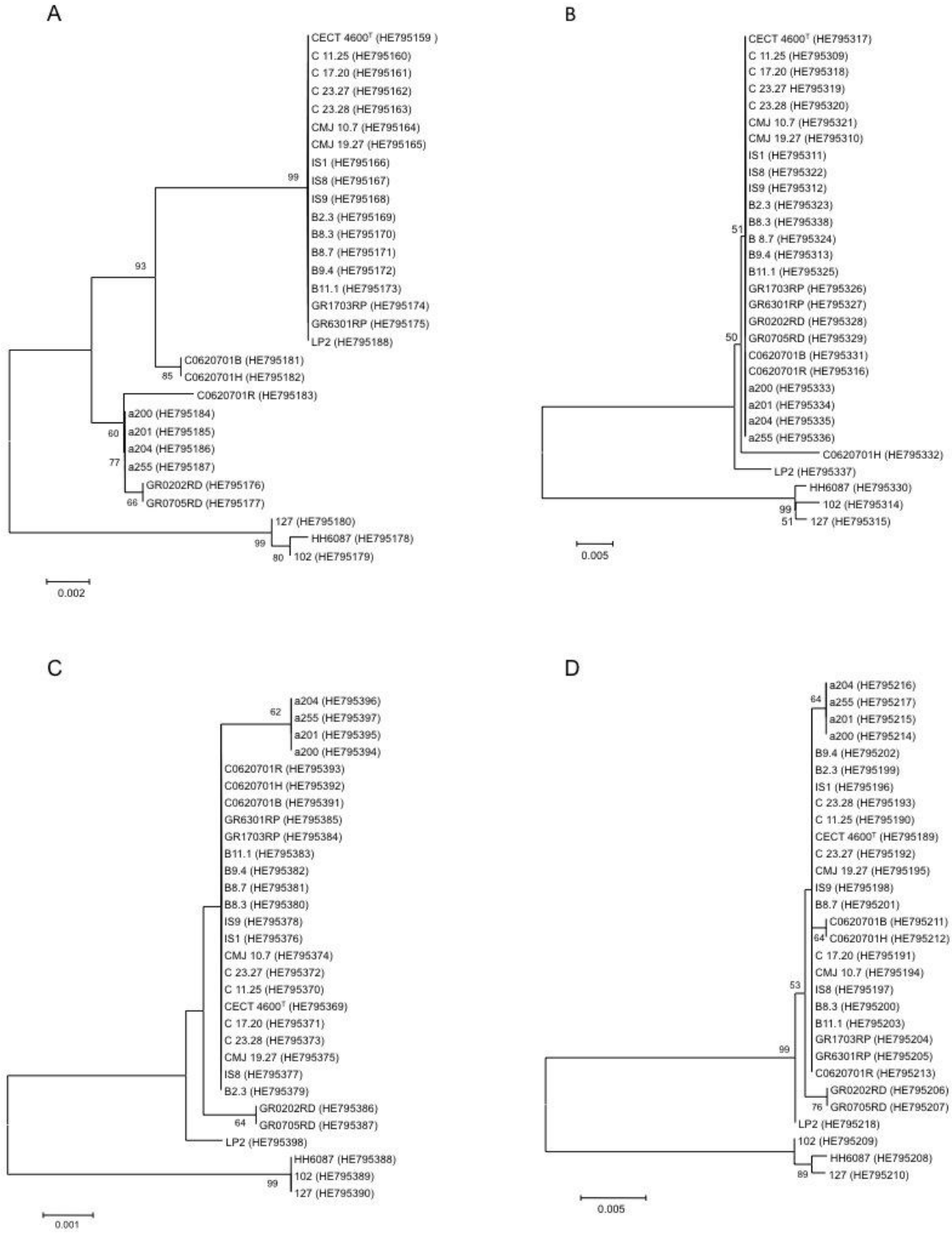
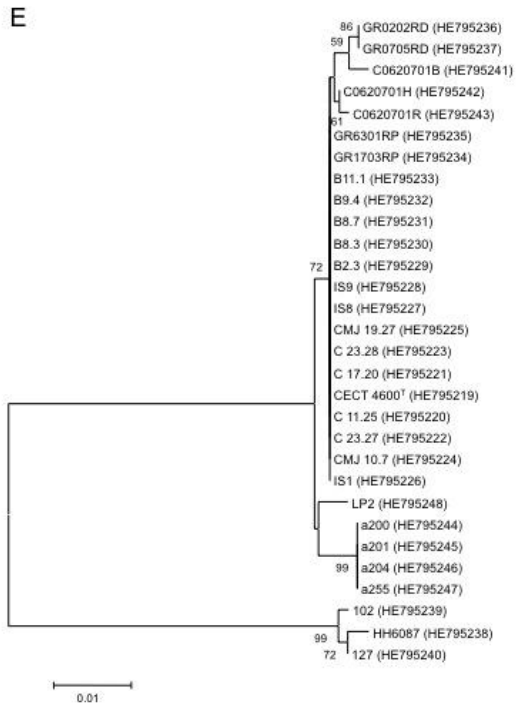


Figure S3: Phylogenetic reconstruction based on the nucleotide sequence of individual analysis of *atp*A (A), *fst*Z(B), *gap*A(C), *pyr*H(D), *rec*A(E), *rpo*A(F), *rpo*D(G) and *top*A(H) genes of *V. tapetis* using the neighbour-joining method. Bar, expected nucleotide substitutions per site. Only bootstrap values above 70% are shown (1000 resamplings) at each branch point.

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B11.1 (HE795233)
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B8.3 (HE795230)
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IS9 (HE795228)
IS8 (HE795227)
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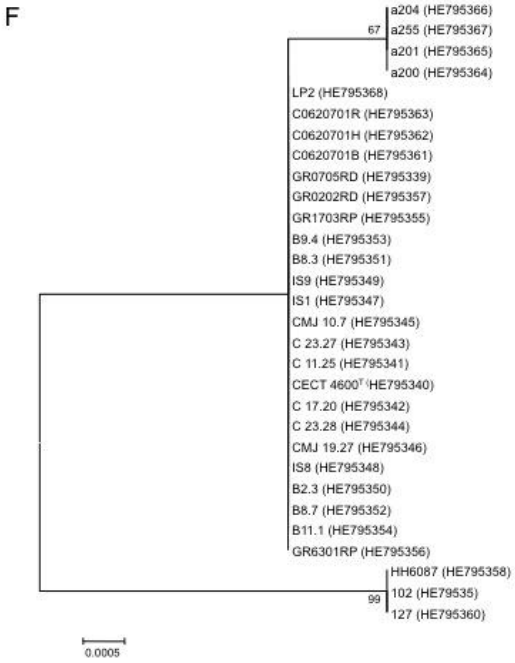
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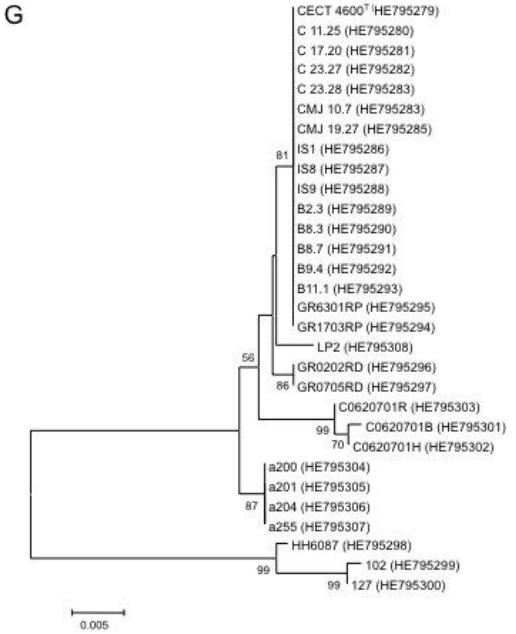
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CMJ 19.27 (HE795285)
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IS8 (HE795287)
IS9 (HE795288)
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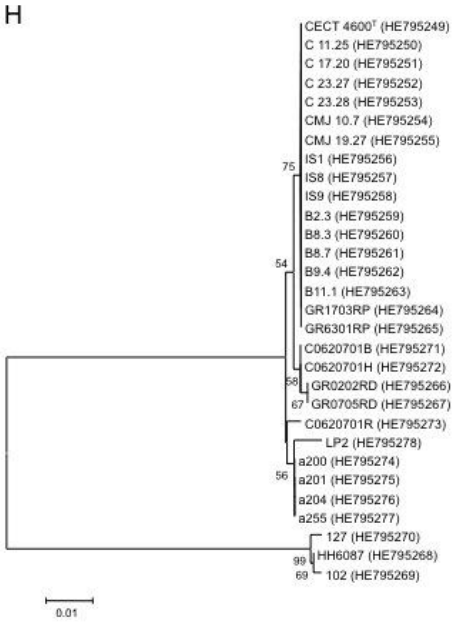
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Phenotypical characterization

Phenotypic characteristics were determined using standard methods and by commercial miniaturized kits (API 20E and API ZYM [bioMérieux] and GN2 MicroPlate [Biolog]). Readings were taken at 24, 48, and 72h. Readings after 72 h of incubation were considered as the final result. For API 20E and API ZYM, standard methodologies were used except that the SS was used to prepare the bacterial suspensions. In all cases, incubation was done at 25ºC. Routine phenotypic tests were performed following the methodologies described by Lemos et al. (1985), West et al. (1986), Romalde & Toranzo (1991) and MacFaddin (1993). All media were supplemented with 1% NaCl when required. Nutritional screening on multi-inoculated basal medium plates were performed by using previously described methods (Baumann & Baumann, 1981)

Table S4.- Differential biochemical tests between the two subespecies of *V. tapetis,* obtained from a comparative characterization of 30 isolates in a set of more than 180 phenotypical tests.

	V. tapetis* subsp. *tapetis	***V. tapetis* subsp. *britanniensis***
Fermentation of		
Arabinose	–	+
Mannitol	–	+
Utilization of		
Citrate	–	+

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>V. anguillarum LMG4437T(AM235737)
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>V. corallilyticus LMG20984T (AJ440005)

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>V. mediterranei LMG11258 (HM771351)

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>V. orientalis LMG7897T (HQ890465)

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>V. penaeicida LMG19663T (AJ437191)
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>V. proteolyticus LMG3772T (HQ890466)

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>V.splendidus LMG19031T (X74724)

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>V. vulnificus LMG13545T (X76333)

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VNIVERSITAT DE VALÈNCIA

CERTIFICATE OF DEPOSIT

Paterna, July the 12th 2012

Vibrio tapetis subsp. britanniensis
strain HH6087 was deposited in the CECT by

Jesús López Romalde

UNIVERSIDAD DE SANTIAGO DE COMPOSTELA. Facultad Biología. Dpto. Microbiología y Parasitología. Centro de Investigaciones Biológicas (CIBUS)

Spain

on 14-06-2012

and was accessioned CECT 8161

This strain has been checked for viability, purity and authenticity in the CECT facilities and it has been preserved using standard methods. It is publically available according to the CECT MTA.