

1 **Reclassification of *Catabacter hongkongensis* as *Christensenella hongkongensis***

2 **comb.nov. based on whole genome analysis**

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10 **Keywords:** whole genome phylogeny, reclassification, *Christensenella*, *Catabacter*

11 **Abstract**

12

13 The genera *Catabacter* (family *Catabacteraceae*) and *Christensenella* (family
14 *Christensenellaceae*) are close relatives within the phylum Firmicutes. Members of these
15 genera are strictly anaerobic, non-spore forming, short straight rods with diverse phenotypes.
16 Phylogenetic analysis of 16S rRNA genes suggest that *Catabacter* splits *Christensenella* into
17 a polyphyletic clade. In an effort to ensure that family/genus names represent monophyletic
18 clades, we performed a whole-genome based analysis of the genomes available for the
19 cultured representatives of these genera: four species of *Christensenella* and two strains of
20 *Catabacter hongkongensis*. A concatenated alignment of 135 shared protein sequences
21 indicates that *C. hongkongensis* is indeed nested within the *Christensenella* clade. Based on
22 their evolutionary relationship, we propose the transfer of *Catabacter hongkongensis* to the
23 new genus as *Christensenella hongkongensis* comb.nov.

24 Introduction

25 *Catabacter hongkongensis* was first isolated in 2007 from the blood cultures of four
26 patients in Hong Kong and Canada. Based on phylogenetic positioning of 16S rRNA
27 sequences and phenotypic characteristics, it was proposed as a new genus and new family,
28 *Catabacteriaceae* [1]. The genus *Catabacter* comprises just one species, with the type strain
29 *Catabacter hongkongensis* HKU16^T. Based on 16S rRNA gene sequencing surveys, *C.*
30 *hongkongensis* has been detected in the blood of patients with diseases such as intestinal
31 obstruction, gastrointestinal malignancy, acute cholecystitis and hypertension, in Europe,
32 North America and Asia [1-5].

33 In 2012, Morotomi and colleagues isolated a novel bacterium from the stool of a
34 healthy male adult, and based on 16S rRNA gene sequence analysis and physiological data,
35 named it *Christensenella minuta* DSM 22607^T within the novel family *Christensenellaceae*
36 [6]. In addition to *Christensenella minuta* DSM 22607^T, three other species have been
37 proposed based on additional isolates from human feces: *Christensenella massiliensis*
38 Marseille-P2438 [7], *Christensenella timonensis* Marseille-P2437 [8], and *Christensenella*
39 *intestinihominis* AF73-05CM02^{PP} [9]. *Christensenella intestinihominis* AF73-05CM02^{PP} is
40 proposed in a pending patent.

41 16S rRNA gene sequence identity (%ID) has been used to delineate genus (95 %ID)
42 and species (98.7 %ID) cutoffs [10, 11]. The 16S rRNA gene sequence of *C. hongkongensis*
43 HKU16^T has 96-97 %ID with the 16S rRNA genes of the four species of *Christensenella*,
44 which places them in the range of sharing a genus using that criterion. In addition to sequence
45 similarity, the 16S rRNA gene-based phylogenetic relationships of these taxa indicate they
46 form a monophyletic clade [12].

47 Whole genome-based analysis with concatenated protein sequences has recently
48 replaced 16S rRNA-based phylogenetics as a basis for determining the evolutionary history

49 of members of the Bacteria and Archaea [13]. Based on whole genome comparisons,
50 *Catabacter* and *Christensenella* were annotated as belonging to the family
51 *Christensenellaceae* in the order *Christensenellales* in the Genome Taxonomy Database
52 (GTDB; R05-RS95 17th July 2020) [14]. Twenty-one genomes within the family
53 *Christensenellaceae* are included in GTDB R05-RS95 as of 01 August 2020. These include
54 metagenome-assembled genomes and genomes derived from isolates. A formal
55 reclassification of *Catabacter* as *Christensenella* would clarify the nomenclature of this
56 taxon.

57 Here, we used comparative genomics as a basis for proposing that the genus name
58 *Catabacter* and the family name Catabacteraceae be removed from the nomenclature.
59 Genome sequences of six cultured isolates belonging to the families *Catabacteriaceae* and
60 *Christensenellaceae* and four species from sister clades in GTDB were selected for
61 phylogenomic analysis. The average nucleotide identity (ANI) of the six genomes in the
62 family of *Catabacteriaceae* and *Christensenellaceae* were compared. Based on the resulting
63 phylogeny, we recommend that *Catabacter hongkongensis* be renamed *Christensenella*
64 *hongkongensis* comb.nov.

65

66 **Methods**

67 **Phylogeny based on whole genomes**

68 We based this analysis on whole genome sequences of six cultured isolates:
69 *Catabacter hongkongensis* strains HKU16^T and ABBA15k, *Christensenella minuta* DSM
70 22607^T, *Christensenella massiliensis* Marseille-P2438, *Christensenella timonensis* Marseille-
71 P2437, *Christensenella intestinhominis* AF73-05CM02^{PP}. The general information about
72 genomes in this study is listed in Table 1. In addition, we selected for the outgroup the
73 species *Clostridium novyi* NT (GenBank accession number: GCA_000014125.1),

74 *Clostridium butyricum* DSM 10702^T (GenBank accession number: GCA_000409755.1),
75 *Clostridium thermobutyricum* DSM4928^T (GenBank accession number: GCA_002050515.1)
76 and *Eubacterium limosum* ATCC 8486^T (GenBank accession number: GCA_000807675.2).

77 Whole genome sequences were obtained from NCBI.

78 We used Anvi'o v5.2.0 for constructing the whole-genome phylogenomic tree [15].
79 Briefly, contig databases were created from the genome FASTA files. Prodigal v2.6.3 with
80 default settings [16] was used to identify open reading frames in contigs. Hidden Markov
81 model (HMM) profiles were used to extract the set of single-copy marker genes defined by
82 Campbell et al. [17]. The best HMM hit was selected if a gene was found with multiple
83 copies in a genome. We limited the set of single-copy core genes shared to those present in
84 all analyzed genomes and aligned the concatenated protein sequences using muscle [18].
85 FastTree 2 [19] was used for constructing approximately-maximum-likelihood phylogenomic
86 tree with the Jones-Taylor-Thornton model [20]. SH-like local support values [21] are
87 shown on the nodes. The phylogenetic tree was visualized by using the online tool iTOL [22].

88

89 **Average nucleotide identity and phenotype predictions**

90 We used FastANI with default settings [23] to generate a pairwise ANI comparison of
91 the six *Christensenella* and *Catabacter* genomes. A heatmap of ANI values was generated
92 and visualized in R [24] with the package ggplot2 [25]. Traitair [26] trait analyzer was used
93 for phenotypic trait prediction based on genome sequences. ABRicate
94 v1.0.1 (<https://github.com/tseemann/ABRicate>) was used for the detection of genes involved
95 in antimicrobial resistance (AMR), and the annotation was derived from the default NCBI
96 database AMRFinderPlus.

97

98 **Results and Discussion**

99 The genome sizes of the six *Catabacter* and *Christensenella* species/strains range
100 from 2.5 Mbp to 3.3 Mbp and the G+C content of genomic DNA from 48.53 to 52.07 %.
101 Based on the pairwise comparison of the six genomes in the family of *Catabacteriaceae* and
102 *Christensenellaceae*, we observed that the ANI of the two *Catabacter hongkongensis* strains
103 (HKU16^T and ABBA15k) was >98.97 % (Fig. 1), confirming that the two strains belong to
104 the same species. Moreover, the ANI values for the six genomes were between 77.56-
105 83.48 %, which corresponds to the accepted ANI cut-off 94-96 % used to designate the same
106 species [27-29] and <83 % for inter-species ANI values [23]. *Christensenella*
107 *intestinihominis* AF73-05CM02^{PP} and *C. minuta* DSM 22607^T showed the highest ANI
108 similarity values (83.48%) between different species.

109 We identified 135 protein-encoding single-copy core genes present in the genomes of
110 *Christensenella*, *Catabacter* and the outgroup taxa. We used these 135 genes in a
111 concatenated alignment resulting in a total of 51,813 aligned amino acid sites. In the
112 resulting phylogenetic tree (Fig. 2), the *Catabacter* and *Christensenella* species and strains
113 formed a monophyletic clade with high bootstrap support, indicating a shared common
114 ancestor. The species *C. timonensis* Marseille-P2437 is basal and forms a sister clade to the
115 rest of the taxa in the phylogeny. The two strains of *Catabacter hongkongensis* (HKU16^T and
116 ABBA15k) are, as expected based on their high ANI, on the same branch of the phylogeny.
117 The *Catabacter* branch is a sister taxon to the remaining *Christensenella* species (*C. minuta*
118 DSM 22607^T, *C. massiliensis* Marseille-P2438, *C. intestinihominis* AF73-05CM02^{PP}).

119 The position of *Catabacter* (and its family *Catabacteriaceae*) nested within the
120 *Christensenella* clade splits the *Christensenellaceae* family and genus, such that neither are
121 monophyletic. For the family and genus names to represent monophyletic groups the
122 renaming of *Catabacter hongkongensis* to *Christensenella hongkongensis* would be required.

123 As a consequence, the genus name *Catabacter* and Catabacteriaceae should be removed from
124 the nomenclature.

125 The cultured strains of the species of *Catabacter* (*C. hongkongensis* HKU16^T and
126 ABBA15k) and *Christensenella* (*C. minuta* DSM 22607^T, *C. massiliensis* Marseille-P2438,
127 *C. timonensis* Marseille-P2437, *C. intestinhominis* AF73-05CM02^{PP}) have been shown to be
128 strictly anaerobic and non-spore forming rods with varied motility, Gram stain reaction and
129 the catalase reaction [1, 6-9]. The different phenotypic characteristics of the species
130 compared in this study is summarized in Table 1. *Catabacter hongkongensis* HKU16^T and
131 ABBA15k strains are reported to be Gram-positive, while the four species of *Christensenella*
132 are reported either Gram-positive or Gram-negative. Morotomi and colleagues reported that
133 *C. minuta* DSM 22607^T is Gram-negative [6], while another group reports *C. minuta* stains
134 consistently as Gram-positive [30], which is consistent with our observations [12]. The
135 Gram-variable reaction might be due to the age of the culture for staining [31]. However,
136 based on the phenotype predictions of the included genomes by using Traitair trait analyzer,
137 all of the strains in those two genera are predicted to produce a cell wall that would be
138 consistent with a Gram-positive reaction.

139 *C. hongkongensis* strains (HKU16^T, HKU17, CA1, CA2) and most clinical derived
140 isolates are reported to be motile and resistant to cefotaxime [1, 2, 5, 32] except for
141 *C. hongkongensis* ABBA15k, which was isolated in 2016 from the blood of a patient with a
142 fever in Sweden [33]. Strain ABBA15k showed 100% 16S rRNA gene identity with
143 *Catabacter hongkongensis* HKU16^T. However, the genome of *C. hongkongensis* ABBA15k
144 is smaller than *C. hongkongensis* HKU16^T, and the genes coding for chemotaxin (*cheA*) and
145 flagellar assembly (*flhA* and *MotA*) were not present in the genome of *C. hongkongensis*
146 ABBA15k [33]. The tetracycline resistance gene *tet* was detected in the genome of

147 *C. hongkongensis* HKU16^T, but no resistance genes were detected in the genome of
148 *C. hongkongensis* ABBA15k [33].

149 Screening for AMR genes of the genomes with ABRicate in this study showed that
150 the *tet* gene was also present in the genomes of *Christensenella minuta* DSM 22607^T,
151 *Christensenella massiliensis* Marseille-P2438, *Christensenella timonensis* Marseille-P2437
152 and *Catabacter hongkongensis* HKU16^T but not in *Christensenella intestinihominis* AF73-
153 05CM02^{PP} and *Catabacter hongkongensis* ABBA15k. A Streptomycin resistance gene
154 (*aadE*) was also detected in the genome of *Christensenella massiliensis* Marseille-P2438.

155 The detailed information about AMR genes is listed in Table 2. *Christensenella*
156 *intestinihominis* AF73-05CM02^{PP} and *Catabacter hongkongensis* HKU16^T were predicted to
157 be motile by Traitax. However, *Christensenella intestinihominis* AF73-05CM02^{PP} was
158 classified as non-motile in the original phenotypic characterization [9], which might be
159 attributable to the growth conditions used. It is also possible that the genome of the strain
160 may not contain all genes required for flagellar formation.

161 In conclusion, both *Catabacter* and *Christensenella* genera include species and
162 strains that are strictly anaerobic, non-spore forming, short straight rods and have diverse
163 phenotypes regarding motility, Gram-staining and antibiotic resistance. The genus
164 *Catabacter* was proposed earlier, however, only one species exists within in genus and the
165 family Catabacteriaceae, while four species have been proposed for the genus
166 *Christensenella* and the family Christensenellaceae. Based on previously reported pairwise
167 16S rRNA gene sequence identities and our genome-based phylogenomic analysis, we
168 propose that the genus *Catabacter* and the family Catabacteriaceae be removed from the
169 nomenclature and that the species *Catabacter hongkongensis* be renamed *Christensenella*
170 *hongkongensis* comb.nov.

171

172 **Description of *Christensenella hongkongensis* comb.nov**

173 The description of *Christensenella hongkongensis* is identical to that proposed for *Catabacter*

174 *hongkongensis* [1].

175 The type strain is HKU16^T (= DSM 18959^T = JCM 17853^T = CCUG 54229^T).

176

177 **Acknowledgements**

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179 **Competing interests**

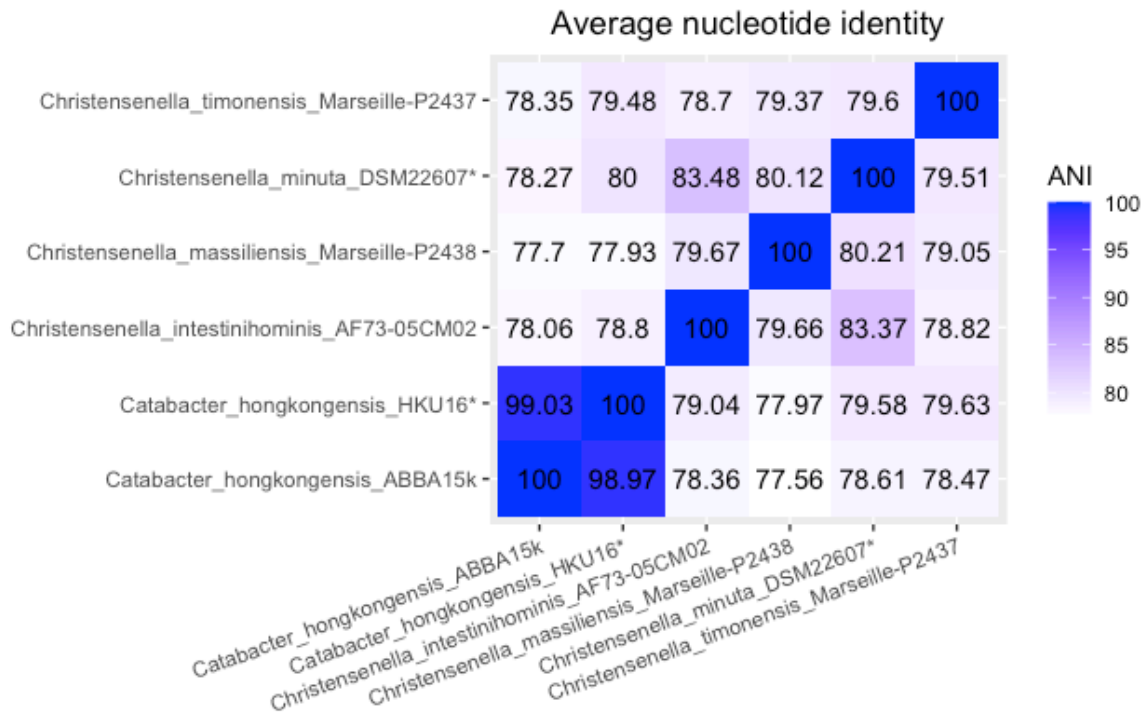
180 The authors declare that they have no competing interests.

181

182 **References**

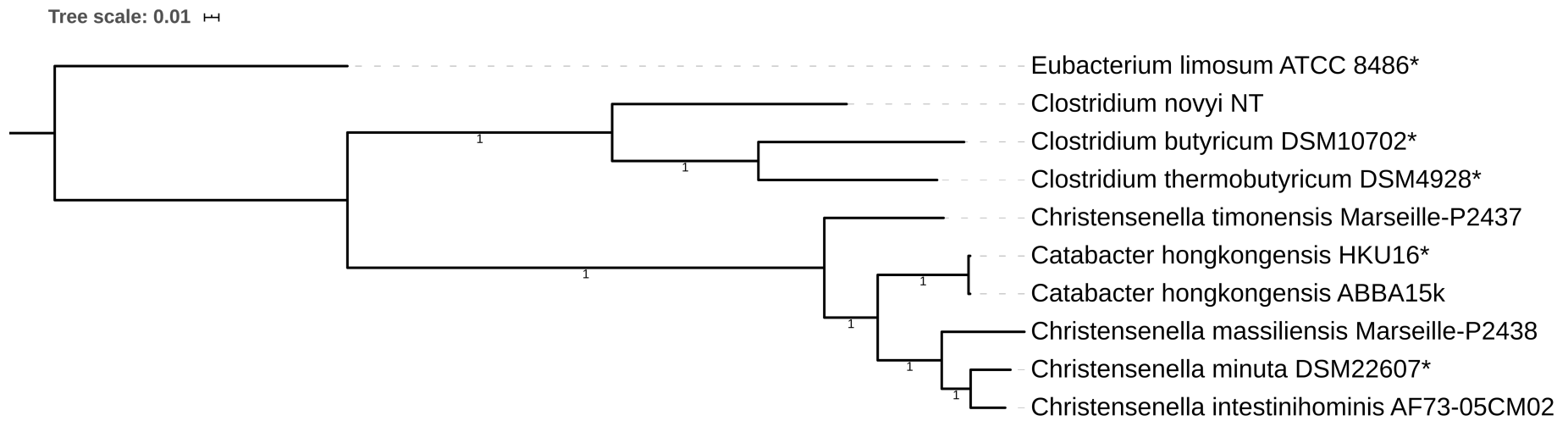
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268 Fig. 1 Heatmap of ANI values amongst the genomes of *Catabacter hongkongensis* strains
 269 and *Christensenella* species in this study. Type strains are marked with asterisk.



270

271 Fig. 2 Phylogeny reconstructed by approximately-maximum-likelihood showing the position of *Catabacter* relative to *Christensenella* based on
 272 135 concatenated core protein sequences with 51,813 aligned amino acid sites. All the nodes are strongly supported with SH-like support values
 273 of 1. Type strains are marked with asterisk. *Clostridium* and *Eubacterium* are used for the outgroup. The tree is rooted by *Eubacterium limosum*
 274 ATCC 8486. Scale bar indicates 0.01 amino acid substitutions per site.

275 Table 1 Phenotypic characteristics of the strains of *Catabacter* and *Christensenella* based on literature review. Data for the strains are from
 276 references [1, 6-9, 30]. +, Positive; -, negative; ND, not determined. The G+C contents and N50, contig numbers, genome size and genome
 277 coverages were retrieved from the GTDB records of the strains.

Characteristics	<i>Christensenella minuta</i> DSM 22607 ^T	<i>Christensenella intestinhominis</i> AF73-05CM02 ^{PP}	<i>Christensenella massiliensis</i> Marseille-P2438	<i>Christensenella timonensis</i> Marseille-P2437	<i>Catabacter hongkongensis</i>	
					HKU16 ^T	ABBA15k
Gram stain	Negative/Positive	Positive	Negative	Negative	Positive	Positive
Motility	Nonmotile	Nonmotile	Nonmotile	Nonmotile	Motile	Nonmotile
Catalase activity	-	-	-	-	+	ND
Metabolite utilization	Arabinose, Glucose, Mannose, Rhamnose, Salicin, Xylose	Arabinose, Glucose, Mannose, Rhamnose, Xylose, Mannitol, Maltose, Sulphate, Pine syrup, Raffinose, Sorbitol	ND	ND	Arabinose, Glucose, Mannose, Xylose	ND
G+C content (%)	51.48%	52.07%	50.38%	51.71%	48.53%	48.79%
Contig number	45	36	1	2	134	113
Protein count	2776	2791	2437	2430	3071	2625
Completeness (Contamination)	98.39% (0.81%)	99.19% (0.81%)	98.79 % (0.81%)	97.98% (0.81%)	97.55% (2.97%)	97.9% (3.5%)
Genome size	2,940,227 bp	3,026,655 bp	2,560,186 bp	2,650,850 bp	3,203,641 bp	2,797,114 bp
GenBank Assembly Accession	GCA_001678855.1	GCA_001678845.1	GCA_900155415.1	GCA_900087015.1	GCA_000981035.1	GCA_001507385.1

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Table 2 Antimicrobial resistance genes (AMR) detected for the genomes of *Catabacter hongkongensis* strains and *Christensenella* species. Coverage refers to the proportion of the gene in the reference gene sequence.

Strain	Contig (Position Strand)	Reference Gene (Accession)	Coverage	Identity %	Gene product	Resistance
<i>Christensenella timonensis</i> Marseille-P2437	FLKP01000002.1 (1477797–1479716 +)	<i>tet(W)</i> (NG_048299.1)	1-1920/1920	99.53	tetracycline resistance ribosomal protection protein Tet(W)	TETRACYCLINE
	FLKP01000002.1 (1480702–1481922 +)	<i>tet(40)</i> (NG_048141.1)	1-1221/1221	99.67	tetracycline efflux MFS transporter Tet(40)	TETRACYCLINE
<i>Christensenella massiliensis</i> Marseille-P2438		<i>tet(W)</i> (NG_048281.1)	1-1920/1920	100	tetracycline resistance ribosomal protection protein Tet(W)	TETRACYCLINE
	LT700187.1 (1980989–1981855 +)	<i>aadE</i> (NG_047378.1)	1-867/867	99.77	aminoglycoside 6- adenylyltransferase AadE	STREPTOMYCIN
<i>Catabacter hongkongensis</i> HKU16 ^T	LAYJ01000061.1 (37275–39194 +)	<i>tet(32)</i> (NG_048125.1)	1-1920/1920	100	tetracycline resistance ribosomal protection protein Tet(32)	TETRACYCLINE
<i>Christensenella minuta</i> DSM 22607 ^T	MAIR01000011.1 (54376-56295 +)	<i>tet(W)</i> (NG_048281.1)	1-1920/1920	100	tetracycline resistance ribosomal protection protein Tet(W)	TETRACYCLINE

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