



Faecalicatena faecalis sp. nov., a moderately alkaliphilic bacterial strain isolated from swine faeces

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Abstract An obligately anaerobic, Gram-stain-positive, non-motile, non-spore-forming and rod-shaped strain AGMB00832^T was isolated from swine faeces. Phylogenetic analysis based on the 16S rRNA gene, together with the housekeeping genes, *gyrB* and *rpoD*, revealed that strain AGMB00832^T belonged to the genus *Faecalicatena* and was most closely related to *Faecalicatena orotica* KCTC 15331^T. In biochemical analysis, strain AGMB00832^T was shown to be negative for catalase, oxidase and urease.

Furthermore, the isolate was positive for β-glucosidase, β-glucuronidase, glutamic acid decarboxylase, proline arylamidase, acid phosphatase and naphthol-AS-BI-phosphohydrolase. The major cellular fatty acids (> 10%) of the isolate were C_{14:0}, C_{16:0} and C_{18:1ω11t} DMA. Based on the whole genome sequence analysis, the DNA G + C content of strain AGMB00832^T was 44.2 mol%, and the genome size and numbers of rRNA and tRNA genes were 5,175,159 bp, 11 and 53, respectively. The average nucleotide identity and digital DNA–DNA hybridization values between strain AGMB00832^T and related strains were ≤ 77.4 and 22.5%, respectively.

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Furthermore, the genome analysis revealed the presence of genes for alkaline shock protein 23 and cation/proton antiporters, which may facilitate growth of strain AGMB00832^T in alkaline culture condition. On the basis of polyphasic taxonomic approach, strain AGMB00832^T represents a novel species within the genus *Faecalicatena*, for which the name *Faecalicatena faecalis* sp. nov. is proposed. The type strain is AGMB00832^T (= KCTC 15946^T = NBRC 114613^T).

Keywords *Faecalicatena faecalis* sp. nov. · Gut microbiota · Swine faeces · Taxonomy

Abbreviations

KCTC	Korean Collection for Type Cultures
NBRC	NITE Biological Resource Center
TSAB	Tryptic soy agar with 5% sheep blood
RCM	Reinforced clostridial medium
GGDC	Genome-to-genome distance calculation
MLSA	Multi-locus sequence analysis
ANI	Average nucleotide identity
CDS	Coding DNA sequence

Introduction

Trillions of microorganisms reside in the mammalian gastrointestinal tract, termed the gut microbiota. In the past decade, the gut microbiota have been shown to play a fundamental role in maintaining gut homeostasis, thereby improving resistance to infection and stimulating immune responses (Macpherson and Harris 2004; O'Hara and Shanahan 2006). Also in pigs, the population and diversity of the gut microbiota are responsible for their health including nutritional, physiological and immunological functions (Fouhse et al. 2016). In several studies, the swine gut microbiota were strongly correlated with swine health and production during different growth stages (lactation, nursery, growing and finishing) (Ramayo-Caldas et al. 2016; McCormack et al. 2017; Yang et al. 2018). However, an imbalanced gut microbiome called gut dysbiosis does often lead to reduction of gut barrier function, and give rise to pathogenic infection with potential high morbidity and mortality rates (Carding et al. 2015). Recently, to prevent these problems, lactic acid bacteria (LAB) are being used as probiotics in the swine industry. LAB strains used in swine diets

include *Lactobacillus* spp., *Bifidobacterium* spp., *Lactococcus* spp., *Lactosphaera* spp., *Leuconostoc* spp., *Melissococcus* spp., *Oenococcus* spp., *Pediococcus* spp., *Streptococcus* spp. and *Enterococcus* spp. (Yang et al. 2015). In addition, the LAB could improve their average dairy gain, nutrient digestibility and intestinal immunity and reduce incidence of diarrhea (Chang et al. 2000; Suo et al. 2012; Chen et al. 2006). Hence, the discovery of potential gut microbes other than LAB as new probiotics may enhance pig's health and production and is thus important for the swine industry.

The two phyla of *Firmicutes* and *Bacteroidetes* are dominant inhabitants of the gastrointestinal tract (Manson et al. 2008). The family *Lachnospiraceae*, belonging to the order *Clostridiales* in the phylum *Firmicutes*, belongs to the core gut microbiota colonising the intestinal lumen. The genus *Faecalicatena* of family *Lachnospiraceae* was firstly reclassified by Sakamoto et al. (2017). At the time of writing, the genus *Faecalicatena* contains three species with validly published names (<https://lpsn.dsmz.de/genus/faecalicatena>); the type species *Faecalicatena contorta*, *Faecalicatena fissicatena* and *Faecalicatena orotica* were isolated from mud, human faeces and alimentary tract of a goat, respectively, and all of them were shown to grow under alkaline conditions (Holdeman et al. 1971; Taylor 1972; Wachsmann and Barker 1954). In this study, we isolated strain AGMB00832^T from swine faeces and proposed on the basis of a polyphasic taxonomic approach that the isolate should be classified as representing a novel species of the genus *Faecalicatena*, and is a moderately alkaliphilic bacterial strain.

Materials and methods

Isolation of the bacterial strain and culture conditions

Strain AGMB00832^T was isolated from a faecal sample of swine, which did not receive any antibiotics, and was raised in the National Institute of Animal Science in Republic of Korea. For the isolation and culture of bacteria, the stool sample was weighed and serially diluted up to 10⁻⁶ in sterilised phosphate-buffered saline (PBS), followed by spreading it onto tryptic soy agar supplemented with 5% sheep blood

(TSAB). The cultivation was performed in the anaerobic chamber (Coy Laboratory Products, Michigan, USA) in an atmosphere of 86% N₂, 7% CO₂ and 7% H₂ at 37 °C. After incubation for 3 days, single colonies were transferred on new TSAB plates. The circular, white, smooth and convex colony of strain AGMB00832^T was isolated and subjected to taxonomic analysis based on phenotypic, physiological and phylogenetic studies. The isolate was preserved at – 80 °C in 10% (w/v) skim milk solution and deposited in KCTC and NBRC culture collections.

16S rRNA gene sequencing and phylogenetic analysis

For phylogenetic analysis, the 16S rRNA gene of strain AGMB00832^T was amplified by polymerase chain reaction from cell suspensions using universal 16S rRNA bacterial primers: 27 F (5'-AGAGTTT-GATCMTGGCTCAG-3') and 1492R (5'-TACGGY-TACCTTGTTACGACTT-3'). Then, the amplified 16S rRNA gene was sequenced with universal primers: 785 F (5'-GGATTAGATACCCTGGTA-3') and 907R (5'-CCGTCAATTCMTTTRAGTTT-3') (Macrogen, Inc.). The sequenced 16S rRNA was analysed by blast searches in EzBioCloud database (<http://www.ezbiocloud.net>) (Yoon et al. 2017) and GenBank/EMBL/DBJ databases (<http://www.ncbi.nlm.nih.gov/blast>). Using the BioEdit program (Hall 1999) and CLUSTAL W (Thompson et al. 1997), the 16S rRNA of strain AGMB00832^T was aligned with the sequences obtained from the blast search to construct phylogenetic trees. The phylogenetic trees were created by using the Molecular Evolutionary Genetics Analysis 7 (MEGA 7.0) software (Kumar et al. 2016) with different algorithms based on the neighbor-joining (NJ) (Saitou and Nei 1987) and maximum-likelihood (ML) (Fitch 1971) methods, with the bootstrap analysis performed based on 1000 replications. To calculate evolutionary distances for these trees, Kimura's two-parameter model was employed.

To further determine the phylogenetic position of strain AGMB00832^T, a multi-locus sequence analysis (MLSA) (Glaeser and Kämpfer 2015) was performed. For MLSA, the three housekeeping gene (16S rRNA, *gyrB* and *rpoD*) sequences of strain AGMB00832^T and the related species were extracted from draft or complete genome sequences in NCBI database. Their accession numbers are listed in Supplementary

Table 1. The 16S rRNA, *gyrB* and *rpoD* gene sequences were concatenated using MEGA X (Kumar et al. 2018) in the following order: 16S rRNA-*gyrB*-*rpoD*. Using concatenated sequences (4333 bp), the phylogenetic tree was constructed using the same methods as for the 16S rRNA gene.

Phenotypic and biochemical analyses

For morphological observation of strain AGMB00832^T, cells were cultivated on reinforced clostridial medium (RCM) agar plate for 3 days at 37 °C in anaerobic chamber, and then they were observed by a phase-contrast microscope (Eclipse 80i, Nikon, Tokyo, Japan), a scanning electron microscope (SEM; CX-200TA, Coxem, Daejeon, Korea) and a transmission electron microscope (TEM; CM-120, Philips, Amsterdam, Netherland). For SEM analysis, the cells were fixed with 4% paraformaldehyde and dehydrated with gradient ethanol solutions, followed by isoamyl acetate and hexamethyldisilazane. The dehydrated sample was dried and coated with gold in a sputter coater (SPT-20, Coxem, Daejeon, Korea) and observed using the SEM. For TEM analysis, the fixed cells were applied to carbon-coated grids that had been glow-discharged for 3 min in air. 1% uranyl acetate was then used for the negative staining of the grid, which were examined using the TEM. Gram-staining was performed as described by Buck (1982). Oxygen requirements for bacterial growth was checked by growing the bacterial cells in aerobic, microaerophilic (CO₂ incubator with 5% O₂) and anaerobic condition (anaerobic chamber) for 3 days at 37 °C. The optimal temperature for growth (10–55 °C at intervals of 5 °C units but with 37 °C instead of 35 °C) was examined on RCM plate. The optimal pH values for growth was assessed in RCM broth adjusted to pH 4–10 using 1 M solutions of NaOH or HCl (at intervals of 1 pH unit). The growth in the presence of NaCl was examined in RCM broth, supplemented with 0–6% NaCl (at intervals of 1%, w/v). The bile resistance was examined in the presence of 0.5–2% (at intervals of 0.5%, w/v) Bacto-Oxgall (Difco, New Jersey, USA), which is equivalent to 5–20% (w/v) bile. The catalase and oxidase activity tests were performed by using a commercial reagent (bioMérieux, Marcy-l'Étoile, France) following the manufacturer's instructions. The biochemical analysis of strain AGMB00832^T were determined by using the API 20A, API ZYM and

Rapid ID 32A strips according to the manufacturer's instructions (bioMérieux, Marcy-l'Étoile, France).

Chemotaxonomic and genomic characteristics

For the analysis of chemotaxonomic characteristics, the cellular fatty acid composition of strain AGMB00832^T and reference strains were examined. After harvesting the cells grown for 72 h, whole cellular fatty acids were obtained by saponification, methylation and extraction according to the protocol of the MIDI/Hewlett Packard Microbial Identification System (Sasser 1990). The cellular fatty acids were analysed by gas chromatography (6890 N with 7683 autosampler, Agilent Technologies, California, USA) and classified by using the Sherlock Microbial Identification System with the Anaerobe database version 6.1. To check the presence of isoprenoid quinones, the crude quinones were extracted from 100 mg of lyophilised cells using chloroform/methanol (2:1, v/v). The extracted quinones were purified by thin layer chromatography (TLC; 20 mm × 20 mm, silica gel 60 F254 plate, Merck) and acetone extraction (Komagata and Suzuki 1988). The purified quinones were then analysed by reversed-phase high-performance liquid chromatography (HPLC) with a mixture of methanol and isopropyl ether (3:1, v/v) as the mobile phase.

For genomic analysis, the genomic DNA of strain AGMB00832^T was extracted with phenol: chloroform: isoamylalcohol method described by Wilson et al. (1990). The whole genome sequencing of the extracted genomic DNA was performed by using Illumina MiSeq (Illumina) technology, and then De novo assembly for AGMB00832^T genome was conducted using SPAdes ver. 3.13.0. Genome annotation was performed using the NCBI Prokaryotic Genome Annotation Pipeline (PGAP) (Tatusova et al. 2016). To analyse the sequence similarity between strain AGMB00832^T and the closely related references, the pairwise average nucleotide identity (ANI) values was determined using ChunLab's Orthologous Average Nucleotide Identity Tool (Lee et al. 2016). Additionally, in silico DNA–DNA hybridization was predicted using the Genome-to-Genome Distance Calculator (GGDC) version 2.1 (<https://ggdc.dsmz.de/ggdc.php#>) (Meier-Kolthoff et al. 2013).

Results and discussion

Phylogenetic analysis

Comparative analysis using the 16S rRNA gene sequences showed that strain AGMB00832^T had 96.7–97.2% similarity with the most closely related strains, *F. orotica* KCTC 15331^T (97.2%, 16S rRNA similarity), *F. fissicatena* KCTC 15010^T (97.1%) and *F. contorta* KCTC 5831^T (96.7%). The phylogenetic tree reconstructed revealed that strain AGMB00832^T formed a stable cluster with the tree most closely related *Faecalicatena* strains (Fig. 1). Additionally, multi-locus sequence analysis (MLSA) based on concatenated three housekeeping genes (16S, *gyrB* and *rpoD*) indicated that the evolutionary distance values between strain AGMB00832^T and the most closely related *Faecalicatena* species were 0.128, 0.160 and 0.171, respectively, which are above the cut off of 0.7 for species definition (Fig. S1). These phylogenetic data suggested that strain AGMB00832^T represents a novel species of the genus *Faecalicatena*. Hence, *F. orotica* KCTC 15331^T, *F. fissicatena* KCTC 15010^T and *F. contorta* KCTC 5831^T were selected as reference species for further comparative tests.

Phenotypic and biochemical characteristics

Strain AGMB00832^T was Gram-positive, non-motile, non-spore-forming and rod-shaped (Fig. S2) that only grew under anaerobic conditions. Growth of strain AGMB00832^T occurred in the temperature range of 25–40 °C (optimum, 37 °C). Interestingly, the isolate could grow in mildly alkaline condition (pH 6–10; optimum, pH 8), but did not grow in acidic environment (pH 4–5) (Fig. S3). In addition, the isolate was able to grow up to 2% (w/v) NaCl (optimum, 0%) and 20% (w/v) bile (optimum, 0%). Strain AGMB00832^T was negative for catalase and oxidase activity. Based on the API ZYM, Rapid ID 32A and API 20A results, strain AGMB00832^T was positive for enzyme activities of β-glucosidase, β-glucuronidase, glutamic acid decarboxylase, proline arylamidase, acid phosphatase and naphthol-AS-BI-phosphohydrolase. The isolate was negative for urease activity. The acid production was occurred from D-glucose, D-saccharose, D-maltose, salicin, D-xylose, L-arabinose, D-mannose, D-melezitose, D-sorbitol, D-rhamnose and D-trehalose.

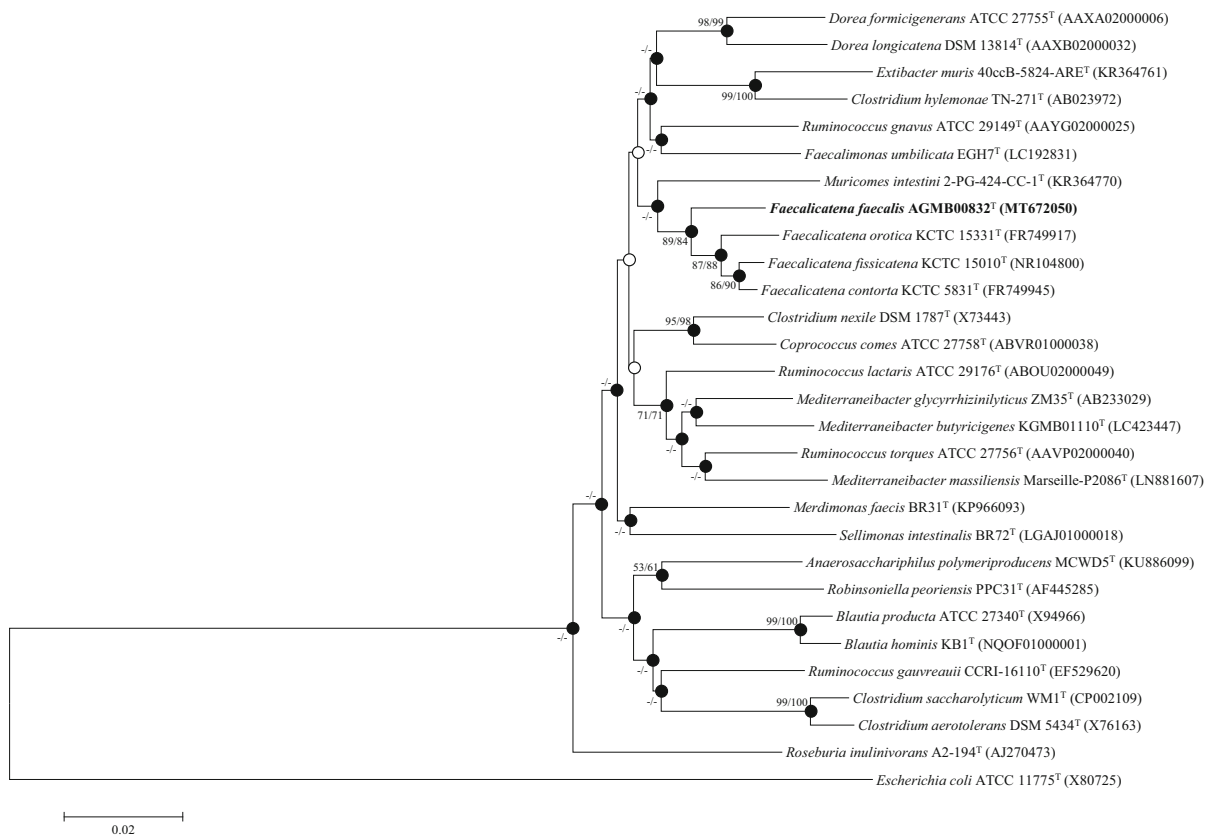


Fig. 1 Phylogenetic tree showing the position of strain AGMB00832^T among the genus *Faecalicatena* based on 16S rRNA sequences of strain AGMB00832^T and closely related taxa. Numbers at nodes refer to bootstrap values (based on 1000

replicates, only values >50% are shown at branch points). Filled circles indicate that the corresponding nodes (groupings) were recovered by both the NJ and ML methods. The bar represents 2% of sequence divergence

Additional distinct phenotypic characteristics of strain AGMB00832^T were described in Table 1.

Chemotaxonomic and genomic characteristics

The major cellular fatty acids (> 10%) of AGMB00832^T were C_{14:0} (10.7%), C_{16:0} (34.4%) and C_{18:1ω11t} DMA (12.7%). C_{18:1ω11t} DMA was a major fatty acid in strain AGMB00832^T but not in the related strains *F. orotica* KCTC 15331^T (9.0%), *F. fissicatena* KCTC 15010^T (8.6%) and *F. contorta* KCTC 5831^T (not detected) (Table 2). The respiratory quinones of strain AGMB00832^T were not detected as previously reported for the references. Moreover, peptidoglycan of the cell walls of the isolates contained meso-diaminopimelic acid (meso-DAP) as the diagnostic diamino acid, consistent with the reference strains (Fig. S4).

The draft genome of AGMB00832^T was determined; genome coverage was 797.0X and 56 contigs were obtained. Based on the genomic analysis of strain AGMB00832^T, the length of the genome is 5,175,159 bp and it contained 4650 total coding genes, 11 rRNA genes (one 5S, four 16S and six 23S) and 53 tRNA genes. The genomic G + C content of strain AGMB00832^T was 44.2 mol% (Supplementary Table 2). 3878 genes were functionally assigned to categories based on clusters of orthologous group (COG) assignments, revealing that the largest functional category of strain AGMB00832^T accounts for function unknown (22.7%), followed by carbohydrate transport and metabolism (11.1%) and transcription (10.2%) (Supplementary Table 3). The ANI values between strain AGMB00832^T and closely related species, *F. orotica* KCTC 15331^T (GenBank assembly accession No. GCA_003149245.1), *F. fissicatena*

Table 1 Differential characteristics between strain AGMB00832^T and related taxa of the genus *Faecalicatena*

Characteristics	1	2	3	4
Isolated from	Swine faeces	Alimentary tract of goat ^a	Human faeces ^b	Mud ^c
DNA G + C content (%)	44.2	44.7	45.6	46.0
Spore formation	–	+	–	–
Esculin hydrolysis	+	+	–	–
Acid produced from (API 20A)				
D-mannitol	–	+	w	–
D-lactose	–	+	–	–
D-mannose	+	–	+	+
D-melezitose	+	+	+	–
D-raffinose	–	+	–	–
D-sorbitol	+	+	–	–
Enzymatic activities of (API ZYM and Rapid ID 32A)				
α -galactosidase	–	w	w	–
β -galactosidase	w	–	–	–
α -glucosidase	–	–	–	+
β -glucosidase	+	+	–	–
β -glucuronidase	+	w	–	w
Proline arylamidase	+	+	+	–
Leucine arylamidase	–	–	–	w
Acid phosphatase	+	+	–	w
Naphthol-AS-BI-phosphohydrolase	+	–	–	–

Strains: 1, AGMB00832^T; 2, *F. orotica* KCTC 15331^T; 3, *F. fissicatena* KCTC 15010^T; 4, *F. contorta* KCTC 5831^T. +, positive; –, negative; W, weakly positive

^aData from Wachsman and Barker (1954)

^bData from Taylor (1972)

^cData from Holdeman et al. (1971)

KCTC 15010^T (GCA_001028025.1) and *F. contorta* KCTC 5831^T (GCA_902375555.1) were 77.4, 75.7 and 75.2%, respectively. Moreover, the DDH relatedness values between strain AGMB00832^T and the reference strains were 22.5, 21.7 and 21.0% (using formula 2), respectively (Table 3).

By performing genome mining of AGMB00832^T, the alkaliphilic characteristic of the strain growing at pH range 6–10 was investigated. First, we found the two genes encoding the alkaline stress protein 23 (WP_216242579.1 and WP_216240781.1). It was reported that the proteins play a key role in alkaline tolerance (Kuroda et al. 1995). In addition, two copies of cation/proton antiporter gene (WP_216239024.1 and WP_216243597.1), which is essential for maintenance of pH homeostasis (Krulwich et al. 1985), were detected in the genome of strain AGMB00832^T.

These data suggested the relation of the alkaliphilic property of strain AGMB00832^T with its genome.

Taxonomic conclusions

The phylogenetic analysis based on 16S rRNA gene sequence and MLSA suggests that strain AGMB00832^T belongs to the genus *Faecalicatena*. However, 16S rRNA similarity, MLSA evolutionary distance, ANI, dDDH values, fatty acid composition as well as some physiological characteristics from API 20A, API ZYM, and Rapid ID 32A test showed that strain AGMB00832^T is distinguishable from the closely related species, *F. orotica* KCTC 15331^T, *F. fissicatena* KCTC 15010^T and *F. contorta* KCTC 5831^T. On the basis of the phylogenetic, physiological and chemotaxonomic analyses, we suggest that strain

Table 2 Cellular fatty acid profiles of strain AGMB00832^T and related taxa of the genus *Faecalicatena*

Fatty acids	1	2	3	4
C _{12:0}	3.2	3.5	3.9	–
C _{14:0}	10.7	10.8	26.6	–
C _{16:0}	34.4	38.3	25.5	47.3
C _{18:0}	2.1	1.4	–	6.3
C _{16:0} ALDE	1.4	1.8	–	–
C _{11:0} DMA	2.3	2.7	2.0	–
C _{14:0} DMA	5.7	6.3	7.7	–
C _{16:0} DMA	7.5	9.0	4.5	5.2
C _{18:0} DMA	1.7	–	–	–
C _{16:1} ω9c	3.8	3.5	3.6	–
C _{18:1} ω11c	–	–	–	9.1
C _{16:1} ω9c DMA	4.2	6.4	8.7	27.9
C _{18:1} ω11t DMA	12.7	9.0	8.6	–
Summed feature 1	1.5	1.8	2.2	–
Summed feature 4	–	1.4	2.7	–
Summed feature 7	–	–	–	4.2
Summed feature 8	1.9	1.4	–	–
Summed feature 10	6.8	2.8	4.0	–

Strains 1, AGMB00832^T; 2, *F. orotica* KCTC 15331^T; 3, *F. fissicatena* KCTC 15010^T; *F. contorta* KCTC 5831^T. All data are determined from this study. Data are reported as the percentage of total fatty acid represented representing more than 1%. –, not detected. Major components (> 10%) are highlighted in bold

* Summed feature 1 contains C_{13:1}ω1c and/or C_{14:0} ALDE. Summed feature 4 contains an unknown fatty acid of equivalent chain length (ECL) 14.762, C_{15:2} and/or C_{15:1}ω8c. Summed feature 7 contains an unknown fatty acid of ECL 16.760 and/or C_{17:1}ω8c. Summed feature 8 contains an unknown fatty acid of ECL 16.801 and/or C_{17:1}ω9c. Summed feature 10 contains one or more of an unknown fatty acid of ECL 17.834 and/or C_{18:3}ω11c/9t/6t. ALDE, aldehyde; DMA, dimethyl acetal

AGMB00832^T represents a novel species of genus *Faecalicatena*, for which the name *Faecalicatena faecalis* sp. nov. is proposed.

Description of *Faecalicatena faecalis* sp. nov.

Faecalicatena faecalis sp. nov. (*fae.ca'lis*. N.L. masc. adj. *faecalis*, derived from *faeces*)

Cells are rod-shaped, obligate anaerobic, Gram-positive, non-motile, mesophilic, non-spore-forming, catalase-, urease- and oxidase-negative. Colonies grown on RCM agar under anaerobic conditions are circular, white, smooth and convex. Growth is observed at 25–40 °C (optimum, 37 °C), pH 6.0–10.0 (optimum, pH 8), 0–2% (w/v) NaCl (optimum 0%) and 0–20% (w/v) bile (optimum 0%). In API 20A strips, acid production is occurred from following carbohydrates: D-glucose, D-saccharose, D-maltose, salicin, D-xylose, L-arabinose, D-mannose, D-melezitose, D-sorbitol, D-rhamnose and D-trehalose. Cells are negative for indole formation. Esculin is hydrolysed. In API ZYM strips, cells are positive for acid phosphatase, naphthol-AS-BI-phosphohydrolase, β-glucuronidase and β-glucosidase, but negative for alkaline phosphatase, esterase (C4), esterase lipase (C8), lipase (C14), leucine arylamidase, valine arylamidase, cystine arylamidase, trypsin, α-chymotrypsin, α-galactosidase, α-glucosidase, N-acetyl-β-glucosaminidase, α-mannosidase and α-fucosidase. In Rapid ID 32A strips, the type strain is positive for glutamic acid decarboxylase and proline arylamidase. Weakly positive for β-galactosidase, but negative for arginine dihydrolase, α-galactosidase, β-galactosidase 6-phosphate, α-glucosidase, α-arabinosidase, N-acetyl-β-glucosaminidase, α-fucosidase, arginine

Table 3 Digital DNA–DNA hybridization (dDDH) values obtained by genome comparison of strain AGMB00832^T and reference strains using Genome-to-Genome Distance Calculator (GGDC) server (formula 2)

Query strain	Subject strain	dDDH (%)	Confidence Interval (%)
<i>Faecalicatena faecalis</i> strain AGMB00832 ^T	<i>Faecalicatena orotica</i> strain KCTC 15331 ^T	21.0	19.8–24.5
<i>Faecalicatena faecalis</i> strain AGMB00832 ^T	<i>Faecalicatena fissicatena</i> strain KCTC 15010 ^T	21.7	19.4–24.1
<i>Faecalicatena faecalis</i> strain AGMB00832 ^T	<i>Faecalicatena contorta</i> strain KCTC 5831 ^T	22.5	20.2–24.9

arylamidase, leucyl glycine arylamidase, phenylalanine arylamidase, leucine arylamidase, pyroglutamic acid arylamidase, tyrosine arylamidase, alanine arylamidase, glycine arylamidase, histidine arylamidase, glutamyl glutamic acid arylamidase and serine arylamidase. The cells were negative for reduction of nitrates. The predominant fatty acids (> 10%) are C_{14:0}, C_{16:0} and C_{18:1} ω11t DMA. Peptidoglycan of the cell walls contains meso-DAP.

The type strain, AGMB00832^T (= KCTC 15946^T = NBRC 114613^T) was isolated from swine faeces.

The genomic G + C content of the type strain is 44.2 mol%.

The GenBank/EMBL/DDBJ accession number for the 16S rRNA gene sequence of strain AGMB00832^T is MT672050, and the GenBank/EMBL/DDBJ accession number for the whole genome sequence of strain AGMB00832^T is JABACJ000000000.2.

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Authors' contributions Byeong Seob Oh performed all the experiments and data analysis, and wrote the manuscript. Ji-Sun Kim, Seung Woo Ryu, Seung Yeob Yu, Jung-Sook Lee, Seung-Hwan Park, Se Won Kang, Jiyoung Lee, Mi-Kyung Lee, Won Yong Jung, Hyunjung Jung, Tai-Young Hur, Hyeun Bum Kim, Jae-Kyung Kim, Ju-Hoon Lee, Jae-Ho Jeong and Ju Huck Lee guided the experimental design and data interpretation. Jae-Ho Jeong and Ju Huck Lee edited the manuscript and supervised this study. All authors approved the manuscript.

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Declarations

Conflict of interest The authors declare that there are no conflicts of interest.

Ethics approval The experimental protocols for this study were reviewed and approved by the Institutional Animal Care and Use Committee of the National Institute of Animal Science (NIAS-2019-1731).

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