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Original research

Dysosmobacter welbionis is a newly isolated human commensal bacterium preventing diet-induced obesity and metabolic disorders in mice

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ABSTRACT

Objective To investigate the abundance and the prevalence of *Dysosmobacter welbionis* J115^T, a novel butyrate-producing bacterium isolated from the human gut both in the general population and in subjects with metabolic syndrome. To study the impact of this bacterium on host metabolism using diet-induced obese and diabetic mice.

Design We analysed the presence and abundance of the bacterium in 11 984 subjects using four human cohorts (ie, Human Microbiome Project, American Gut Project, Flemish Gut Flora Project and Microbes4U). Then, we tested the effects of daily oral gavages with live *D. welbionis* J115^T on metabolism and several hallmarks of obesity, diabetes, inflammation and lipid metabolism in obese/diabetic mice.

Results This newly identified bacterium was detected in 62.7%–69.8% of the healthy population. Strikingly, in obese humans with a metabolic syndrome, the abundance of *Dysosmobacter* genus correlates negatively with body mass index, fasting glucose and glycated haemoglobin. In mice, supplementation with live *D. welbionis* J115^T, but not with the pasteurised bacteria, partially counteracted diet-induced obesity development, fat mass gain, insulin resistance and white adipose tissue hypertrophy and inflammation. In addition, live *D. welbionis* J115^T administration protected the mice from brown adipose tissue inflammation in association with increased mitochondria number and non-shivering thermogenesis. These effects occurred with minor impact on the mouse intestinal microbiota composition.

Conclusions These results suggest that *D. welbionis* J115^T directly and beneficially influences host metabolism and is a strong candidate for the development of next-generation beneficial bacteria targeting obesity and associated metabolic diseases.

Significance of this study

What is already known on this subject?

- Numerous bacteria from the human gut remain to be identified.
- The vast majority of bacteria detected by sequencing methods have never been cultured.
- Several bacteria have been shown to be positively or negatively associated with metabolic health but few of them have been tested in preclinical studies and then validated in human studies.

What are the new findings?

- *Dysosmobacter welbionis* is a newly isolated commensal bacterium found in 70% of the general population.
- *D. welbionis* is inversely correlated with body mass index (BMI), glycaemia and glycated haemoglobin in overweight and obese subject with a metabolic syndrome.
- Mice treated with live *D. welbionis* J115^T are partially protected against diet-induced obesity and fat mass gain, have improved glucose tolerance and lower insulin resistance.
- Live *D. welbionis* J115^T reduces white adipose tissue hypertrophy and inflammation together with increased number of mitochondria in brown-adipose tissue and non-shivering thermogenesis.
- Pasteurisation of *D. welbionis* J115^T abolishes its beneficial effects.

How might it impact on clinical practice in the foreseeable future?

- These findings suggest that *D. welbionis* J115^T is a next-generation beneficial bacterium that should be investigated in other clinical paradigm than obesity and diabetes. This bacterium should be tested in humans for its positive effects on host metabolism.

INTRODUCTION

Variations of the intestinal microbiota composition and functionality have an impact on host physiology by influencing metabolism, immunity, ageing and behaviour.[1 2] The intestinal microbiota is mainly studied by culture-independent methods based on faecal DNA sequencing such as 16S rRNA gene sequencing or metagenomic sequencing.

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These observational studies provide initial evidence of an association between gut microbiota composition and/or functionality and host pathophysiology.[3–5] Yet, moving from association to causation for specific taxa requires growing the bacteria of interest in pure culture. Despite large-scale efforts to cultivate previously uncultured prokaryotic members of the human intestinal microbiota,[6–10] recent estimates indicate that it comprises at least 4664 species, of which only 1332 have a cultivated representative.[7] Moreover, the effect of specific species on the development of obesity and associated metabolic disorders has been demonstrated only for a handful of species. For example, it has been shown that the colonisation of germ-free mice with a strain of *Enterobacter cloacae* aggravates obesity and insulin resistance on high-fat diet (HFD)[11] and that supplementation of conventionally raised mice with *Bilophila wadsworthia* aggravates glucose intolerance and hepatic steatosis on HFD without effect on the body weight.[12] Conversely, a beneficial impact of other bacteria has been observed: administration of *Anaerobutyricum soehngenii* (formerly designated as *Eubacterium hallii* strain L2-7) to genetically obese/diabetic mice increased energy expenditure and decreased adiposity.[13] In humans, *A. soehngenii* administration is associated with improved peripheral insulin sensitivity.[14] Colonisation of germ-free mice with the microbiota of an obese human with low levels of *Christensenellaceae* amended with *Christensella minuta* reduces adiposity in recipient mice.[15] In 2013, we showed that *Akkermansia muciniphila* counteracts diet-induced obesity and related disorders, such as glucose intolerance, insulin resistance and hepatic steatosis in rodents.[16] Later, we demonstrated that bacterial viability was not required to maintain its health-promoting properties, as pasteurised *A. muciniphila* was as effective as the live bacteria.[17] Noteworthy, we demonstrated that *A. muciniphila* was also beneficial when administered to overweight and obese humans.[18] The aforementioned examples are showing that correlations between the abundance of specific bacteria in human cohorts[19] with clinical variables can then be successfully translated to a beneficial or harmful effect in animal models. Nevertheless, one needs to move from correlation to causality. Indeed, we found that *Subdoligranulum* spp was strongly correlated with *A. muciniphila* and metabolic health, or increased on dietary fibres intervention or metformin administration in numerous human cohorts.[20] However, treating mice with *Subdoligranulum variabile* did not improve diet-induced metabolic disorders,[20] thereby reinforcing the urgent need to directly challenge the real physiological relevance of correlative observations.

We recently isolated and described a novel *Ruminococcaceae* species: *Dysosmobacter welbionis*.[21] This bacterium is closely related to a not yet cultured species that has been consistently associated to leanness: *Oscillospira guillermondii*.[22] In the present study, we aimed to decipher whether *D. welbionis* has an impact on host's metabolic health. First, we measured the relative abundance and prevalence of *D. welbionis* in the faecal microbiota of the general population using several cohorts (ie, human microbiome project (HMP), American Gut Project (AGP), Flemish Gut Flora Project (FGFP) and Microbes4U).[18 23–26] We discovered that *D. welbionis* abundance correlates negatively with body mass index (BMI) and fasting glycaemia. Then, we showed that supplementation of *D. welbionis* strain J115^T to HFD-fed mice reduced body weight and fat mass gain. This was associated with improved glucose homeostasis and increased non-shivering thermogenesis, coupled to a higher number of mitochondria in the brown adipose tissue (BAT).

RESULTS

Prevalence and abundance of *D. welbionis* in the human microbiota

We recently isolated a new species from human stools that belongs to the *Ruminococcaceae* family that we named *D. welbionis*.[21] This is the first species isolated from this new genus.[21] Beyond the taxonomic interest of the description of a novel genus and species, it emerges that *D. welbionis* is closely related to several taxa associated with lower body weight. Indeed, *D. welbionis* has 92% of 16S rRNA gene sequence similarity with the uncultured species *O. guillermondii* that has repeatedly been associated with leanness in human studies based on faecal microbiota sequencing.[22] In addition, the *Anaerotruncus* genus, also belonging to the *Ruminococcaceae* family, is also negatively correlated with body weight in pigs and humans.[27 28] Considering the taxonomic proximity of *D. welbionis* with these taxa, we sought to decipher the association between *Dysosmobacter* abundance in the intestinal microbiota and host health.

We first investigated whether *D. welbionis* was present in the general population. To this aim, we used several independent cohorts such as the HMP,[25] the AGP[23 24] and the FGFP.[26] Based on the 16S rRNA gene sequence of *D. welbionis* J115^T, this sequence variant had a prevalence of 62.7% and a relative abundance range of 0%–3.9% in the HMP cohort (n=161). For the AGP cohort (n=9511) the prevalence was 69.8% with a relative abundance range of 0%–9.2%. Finally, the sequence variant was detected in 65.9% of individuals of the cross-sectional FGFP (n=2259) with a relative abundance ranging between 0% and 0.9%.

We further explored whether this bacterium was correlated with BMI in obese subjects or any specific metabolic markers using a previously recruited cohort of 53 non-diabetic, insulin-resistant and overweight or obese individuals: the Microbes4U cohort.[18] Using *Dysosmobacter* genus-specific primers, we quantified it in the faecal DNA of the Microbes4U cohort. *Dysosmobacter* spp was detected in the stools of all individuals and ranged between 0.00035% and 2.7% of the total microbiota with an average of 0.75 %, corresponding to a range of 1.7×10^5 to 2.0×10^9 with an average of 5.9×10^8 bacteria per gram of stools (figure 1).

Interestingly, in the Microbes4U cohort, the relative and absolute abundance of *Dysosmobacter* spp correlated negatively with BMI, while absolute abundance of *Dysosmobacter* spp correlated negatively with fasting glucose and glycated haemoglobin (HbA1c) (figure 1A, D–G, online supplemental table S1). This suggests that *Dysosmobacter* genus may protect against obesity and obesity-associated glucose metabolism alteration.

D. welbionis J115^T prevents diet-induced obesity in mice

In a first experiment, we found that gavaging high-fat diet (HFD)-fed mice with daily and freshly prepared live *D. welbionis* J115^T (1.0×10^9 cultivable, live bacteria per day and per mouse) for 6 weeks (HFD J115-fresh group) decreased the HFD-induced weight gain by 29% (ie, 1.5 grams) (figure 2A). We then investigated whether the viability of *D. welbionis* J115^T impacted its anti-obesity effects. Killing *D. welbionis* J115^T using pasteurisation (30 min at 70°C) completely abolished its beneficial effects on both body weight and fat mass gain (figure 2B,C). Then, we tested whether treating mice with live *D. welbionis* J115^T for a longer period of time (ie, 13 weeks) could maintain its beneficial effects. We found that live *D. welbionis* J115^T remains active when frozen in trehalose (1.0×10^9 cultivable, live bacteria per day and per mouse) and profoundly decreased

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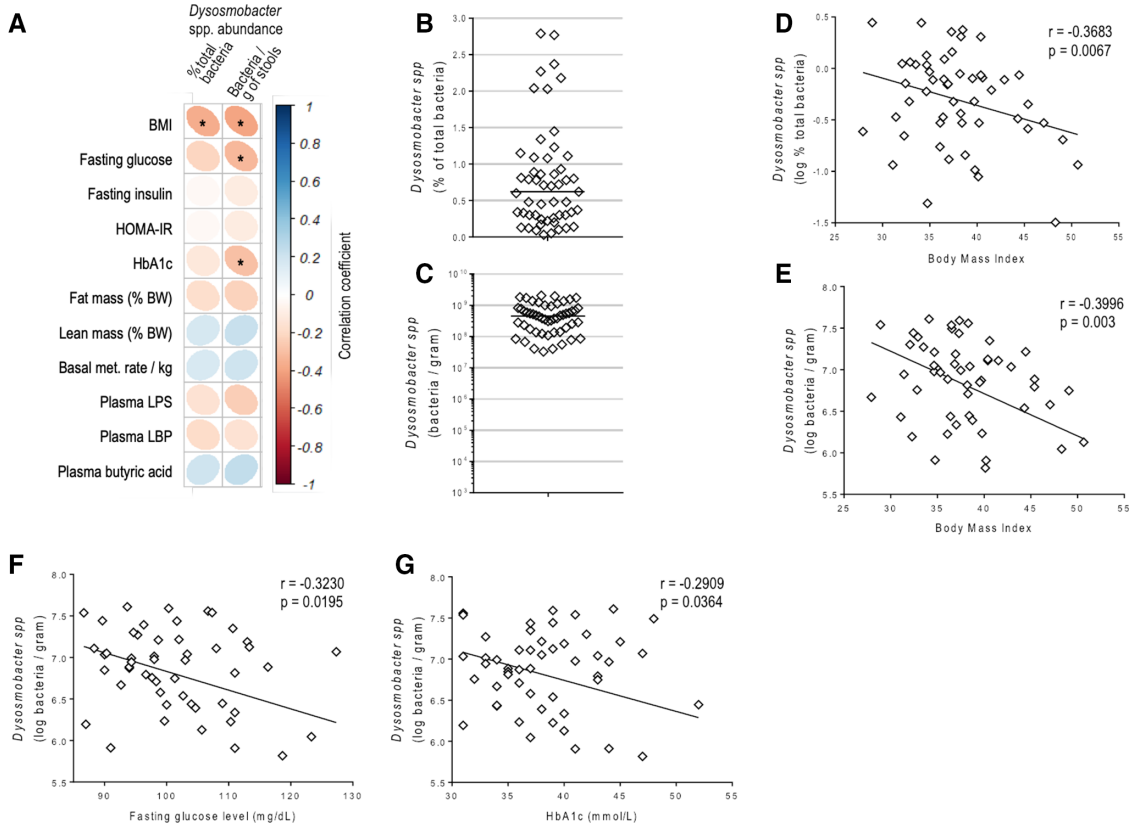


Figure 1 *Dysosmobacter* spp correlates negatively with BMI in humans. (A) Pearson's correlation matrix between *Dysosmobacter* spp abundance in the faecal microbiota and clinical variables in the Microbes4U cohort. *P<0.05. (B) *Dysosmobacter* spp relative abundance in the faecal microbiota of a cohort of overweight and obese humans. (C) *Dysosmobacter* spp concentration in stool samples from a cohort of overweight and obese humans. (D) Pearson's correlation between *Dysosmobacter* spp relative abundance and BMI. (E) Pearson's correlation between *Dysosmobacter* spp absolute concentration and BMI. (F) Pearson's correlation between *Dysosmobacter* spp concentration and fasting blood glucose. (G) Pearson's correlation between *Dysosmobacter* spp. and glycated haemoglobin. Results are represented as dot-plots with median for figure parts B,C. BMI, body mass index; HbA1c, glycated haemoglobin.

HFD-induced weight gain and fat mass gain than HFD-fed mice after 13 weeks of treatment (figure 2D,E). This corresponded to a significant reduction in the weight of mesenteric, subcutaneous (inguinal) and epididymal fat deposits (figure 2F). No impact on the weight of several muscles of the mice was observed (online supplemental figure S1). It is worth noting that treating mice with a dose lower than 1.0×10^9 live bacteria (ie, 10^8) had no beneficial effects (online supplemental figure S2).

D. welbionis J115^T supplementation has minor impact on mouse intestinal microbiota composition

To investigate if the protection against HFD-induced weight gain is a direct effect of *D. welbionis* J115^T or results from the remodelling of the intestinal microbiota ecosystem, we analysed the mouse caecal microbiota composition by 16S rRNA gene amplicon sequencing. Principal coordinates analysis based on generalised UniFrac dissimilarity matrix indicated that HFD profoundly affected the overall composition of the ecosystem. The microbiota of HFD mice and HFD mice that received live *D. welbionis* were very similar (figure 2G). Richness, Simpson's and Shannon's alpha diversity indices were similar between the three groups (online supplemental figure S3). We found that 31 operational taxonomic units (OTUs) had a significantly different relative abundance between two or more mouse groups (figure 2H,I).

Bacteroidaceae family as well as *Alistipes*, *Ruminoclostridium*, *Tyzerella* and unidentified *Lachnospiraceae* genera were increased by the HFD while *Erysipelotrichaceae* family along with *Rikenellaceae* RC9 gut group and *Muribaculum* genus were decreased by the HFD in comparison with the control group (figure 2I). The relative abundance of 2 OTUs was increased by the HFD and restored to control diet mice levels by *D. welbionis* J115^T treatment: OTUs 11 and 16, belonging to *Ruminoclostridium* and *Alistipes* genera, respectively. OTUs 54 and 71, associated to *Bacteroides* and *Ruminoclostridium* genera, were respectively increased and decreased by live *D. welbionis* J115^T treatment but were not affected by the diet. Quantitative PCR (qPCR) indicated that *D. welbionis* was not present in untreated mice and reached 2.3×10^8 bacteria per gram of caecal content (corresponding to 0.76% of the microbiota) in mice force fed with live *D. welbionis* J115^T (figure 2J). *D. welbionis* J115^T did not durably colonise the mouse gut as it was not detected in the faeces of any mouse after a washout period of 3 days (online supplemental figure S3).

D. welbionis J115^T slightly affects gut morphology without impacting the absorptive function

As *Dysosmobacter* spp is not detected in the gut microbiota of specific pathogen free mice, we sought to confirm that live

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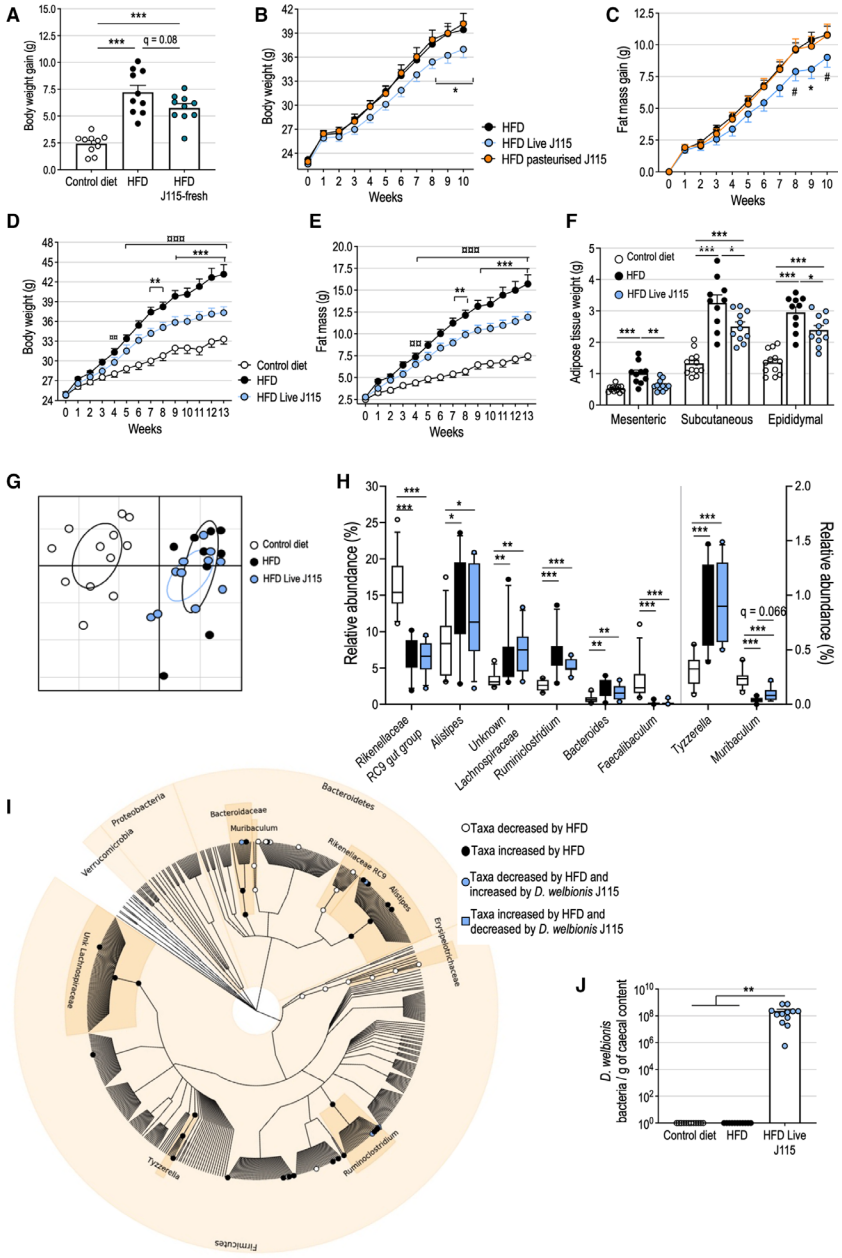


Figure 2 Live *Dysosmobacter welbionis* J115^T prevents diet-induced obesity in mice without major alterations of the faecal microbiota composition. (a) Body weight gain of mice fed a HFD and treated during 6 weeks by daily oral gavage with 1.0×10^9 colony forming units (cfus) of freshly prepared *D. welbionis* J115^T (HFD J115-fresh) and mice fed a control diet or a high-fat diet (HFD) and treated by daily oral gavage with vehicle. (B,C) Body weight and fat mass gain of mice treated during 10 weeks by daily oral gavage with live *D. welbionis* J115^T frozen in trehalose (1.0×10^9 cultivable, live bacteria per day and per mouse) and fed a HFD (HFD Live J115) or pasteurised *D. welbionis* J115^T (HFD pasteurised J115) (1.0×10^9 heat-killed bacteria per day and per mouse) and mice fed a HFD and treated by daily oral gavage with vehicle. (D,E) Body weight and fat mass of mice treated during 13 weeks by daily oral gavage live *D. welbionis* J115^T frozen in trehalose (1.0×10^9 cultivable, live bacteria per day and per mouse) and fed a HFD (HFD Live J115) and mice fed a control diet or a HFD and treated by daily oral gavage with vehicle. (F) Mesenteric, subcutaneous (inguinal) and epididymal fat pads weight at the end of the 13-week period. (G) Principal coordinates analysis of the microbiota composition of experiment 2. Mice microbiota were clustered and the centre of gravity computed for each group. (H) Relative abundance of the bacterial genera significantly altered by HFD or live *D. welbionis* J115^T treatments. (I) Cladogram representing mice microbiota with white clade markers highlighting bacterial groups significantly more abundant in control mice than in HFD mice, black clade markers markers highlighting bacterial groups significantly more abundant in HFD mice than in control mice and light blue clade markers highlighting bacterial groups significantly increased (circle) or decreased (square) by live *D. welbionis* J115^T administration in HFD-fed mice as assessed by figure part H. (J) *Dysosmobacter* spp concentration estimated by quantitative PCR in the caecal content of the mice. Number of mice per group: 10–12. Data were analysed using one-way analysis of variance (ANOVA) followed by Tukey's post hoc test for figure parts A, F and J and two-way repeated measures ANOVA for figure parts B–E. Data were analysed using Kruskal–Wallis test followed by Dunn's pairwise multiple comparison procedure for H–I. *q<0.05; **q<0.01; ***q<0.001. Results are represented as dot plots and bar plots with mean±SEM for figure parts A, F and J, and as boxes and whiskers (first quartile, median and third quartile) for figure part H. In figure parts B–E *q < 0.05; **q<0.01; ***q<0.001 for HFD versus HFD Live J115 comparisons and ¤¤¤q<0.001 for control versus HFD comparisons. In figure part C, #p=0.06. HFD, high-fat diet.

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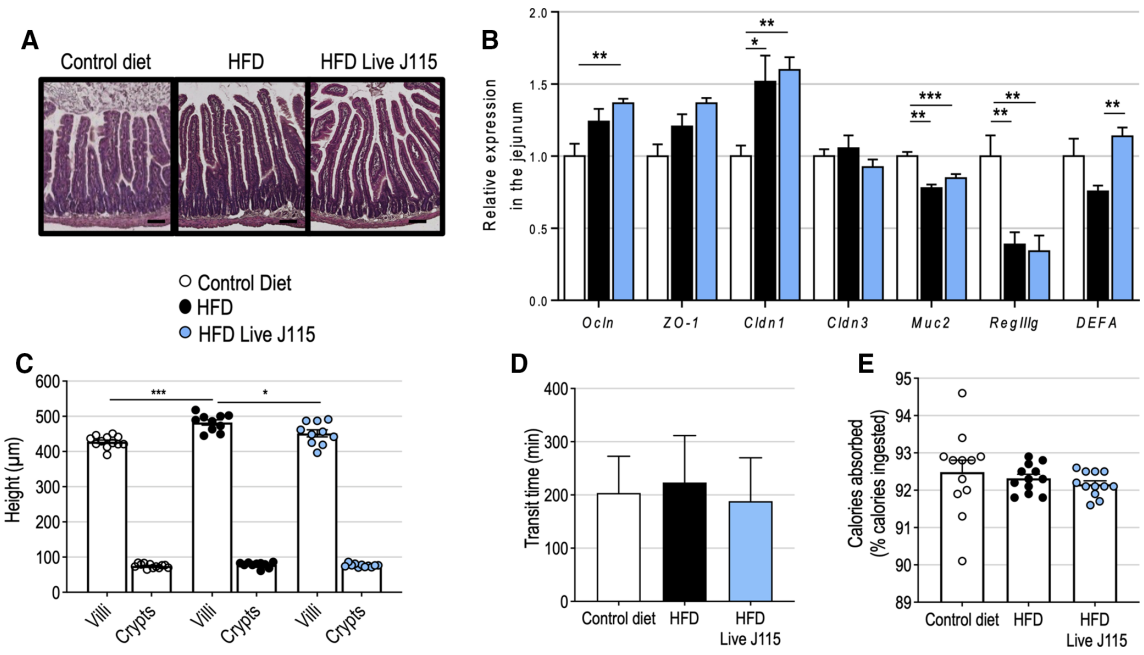


Figure 3 Live *Dysosmobacter welbionis* J115^T moderately alters gut physiology. (A) Representative H&E-stained pictures of the jejunum. Scale bar=100 µm. (B) Relative expression of genes related to gut barrier function in the jejunum. (C) Mean crypts and villi's height in the jejunum. (D) Transit time. (E), Percentage of calories absorbed from the food. Number of mice per group: 10–12. Data were analysed using one-way analysis of variance followed by Tukey's post hoc test for figure part B. *q<0.05; ***q<0.001. Results are represented as bar plots with mean±SEM for figure parts B–D and dot plots and bar plots with mean±SEM for figure parts C–E. HFD, high-fat diet.

D. welbionis J115^T administration was well tolerated by the mice. No sign of inflammation was histologically observed in the jejunum of the mice treated with live *D. welbionis* J115^T (figure 3A). This was supported by the measurement of the relative expression of pro-inflammatory markers in different segments of the gut (online supplemental figure S3) and the absence of deleterious effects on gut barrier markers (eg, antimicrobial peptides, mucus production and tight-junction proteins) (figure 3B). Live *D. welbionis* J115^T administration slightly decreased the height of the villi in the jejunum (542.7 vs 482.3 µm, q=0.024), but the depth of the crypts was not affected (figure 3C). A decrease of the villi's height could potentially result in a reduction of the absorption surface and affect energy absorption, as would an acceleration of the transit time. However, measurement and calculation of both transit time and percentage of dietary calories absorbed from the diet showed that none of these parameters were affected by live *D. welbionis* J115^T administration (figure 3D–E). Our results show that live *D. welbionis* J115^T was well tolerated by the mice and did not alter gut physiology.

D. welbionis J115^T reduces adipose tissue expansion on HFD and improves glucose control

The lower adiposity observed with live *D. welbionis* J115^T administration was associated with better glucose tolerance during an oral glucose tolerance test (OGTT), with faster return to baseline glucose levels after the initial blood glucose peak 15 min after glucose administration (figure 4A,B). This was associated to significantly lower fasting insulin levels and lower insulin resistance index (figure 4C,D). Moreover, mice supplemented with live *D. welbionis* J115^T had significantly lower plasma levels of leptin and resistin than untreated HFD-fed mice (figure 4E,F). A similar trend was observed for plasma glucose-dependent insulinotropic polypeptide (GIP) and plasminogen activator inhibitor-1 (PAI-1) levels (figure 4G,H). Conversely, plasma lipids were not modified by the treatment (online supplemental figure S1).

D. welbionis J115^T supplementation is associated with reduced adipocyte diameter and lower adipose tissue inflammation

Obesity is associated with adipocyte hypertrophy, impaired lipolysis and pro-inflammatory phenotype, which contribute to adverse adipokine secretion, insulin resistance and ectopic fat deposition. Thus, we measured adipocyte diameter in the subcutaneous adipose tissue (SAT) and mesenteric adipose tissue (MAT) by histology and image analysis (figure 4I). *D. welbionis* J115^T treatment significantly increased the proportion of small adipocytes (diameter ≤50 µm) and decreased the proportion of large adipocytes (diameter ≥70 µm) in SAT (figure 4J). This effect was even more pronounced in MAT (figure 4K).

D. welbionis J115^T increases the expression of lipolysis markers in association with altered inflammation markers expression in white adipose tissue

Smaller adipocyte size in live *D. welbionis* J115^T treated mice was associated with an overall lipid metabolism less prone to fat storage. Indeed, the fatty acids transport protein 4 (*Fatp4*), involved in fatty acids uptake from the bloodstream, was two times less expressed in the SAT of treated mice (figure 4L). Conversely, genes involved in lipolysis and fatty acid mobilisation, such as the adipose triglycerides lipase (*Atgl*) and the hormone sensitive lipase (*Hsl*), were more expressed in the SAT of treated mice than in HFD mice. Moreover, the relative expression of the proinflammatory

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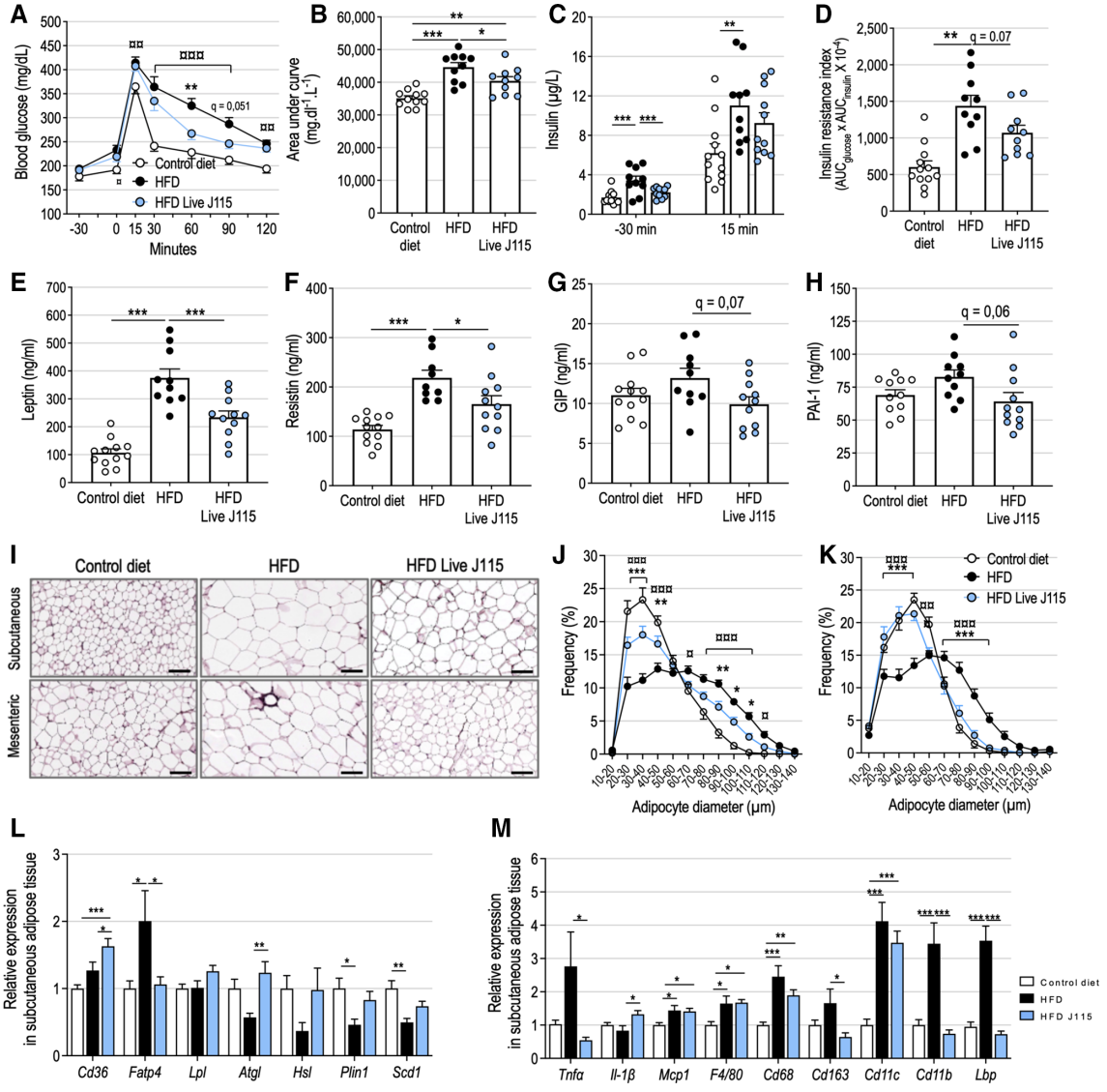


Figure 4 Live *Dysosmobacter welbionis* J115^T reduces adipose tissue expansion and inflammation on high-fat diet (HFD) and improves altered metabolic profile. (A) Plasma glucose profile and (B) mean area under the curve measured during an oral glucose tolerance test (OGTT). (C) Plasma insulin measured 30 min before and 15 min after glucose administration during the OGTT. (D) Insulin resistance index. (E) Leptin, (F) resistin, (G) glucose-dependent insulinotropic polypeptide (GIP) and (H) plasminogen activator inhibitor-1 (PAI-1) plasma levels after a 6 hours fasting period. (I) Representative H&E-stained pictures of subcutaneous and mesenteric adipose tissues (SAT and MAT, respectively). Scale bar=100 µm. (J) Adipocytes diameter (µm) distribution in the SAT. (K) Adipocytes diameter (µm) distribution in the MAT. (L) Relative expression of genes related to lipid metabolism in the SAT. (M) Relative expression of genes related to inflammation and immune system in the SAT. Number of mice per group: 9–12. Results are represented as dot plots and bar plots with mean±SEM for figure parts B–H and as bar plots with mean±SEM for figure parts L and M. Data were analysed using one-way analysis of variance (ANOVA) followed by Tukey's post hoc test for figure parts B–H, L and M and two-way repeated measures ANOVA for figure parts A, J and K. *q<0.05; **q<0.01; ***q<0.001 for HFD versus HFD Live J115 comparisons and ¤¤q<0.01 control versus HFD, ¤¤¤q<0.001 for control versus HFD comparisons. HFD, high-fat diet.

cytokine *Tnfα* and several macrophages infiltration markers such as *Cd68*, *Cd163*, *Cd11b* and *Lbp* was increased by the HFD and decreased by live *D. welbionis* J115^T supplementation, whereas some other markers were not affected (figure 4M).

D. welbionis J115^T counteracts HFD-induced alterations and increases mitochondria number in BAT

The weight of the interscapular BAT of HFD-fed mice supplemented with live *D. welbionis* J115^T was significantly lower than that one of the HFD-fed mice and even slightly lower than that of control diet fed mice (figure 5A). Histology analysis indicated that BAT expansion induced by the HFD was associated with increased lipid droplet size and a unilocular, white-like appearance of the adipocytes (figure 5B). The surface occupied by the lipids droplets in the slices was significantly increased by the HFD (figure 5C). Supplementation of HFD-fed mice with live *D. welbionis* J115^T restored the brown adipocyte morphology and reduced the lipid content. Then, we performed a RNA-seq analysis on a pool of RNA extracted from the BAT of HFD-fed mice treated or not with live *D. welbionis* J115^T (figure 5D). Among the differences between the two pools, it appeared in particular that transcripts belonging to the inflammatory

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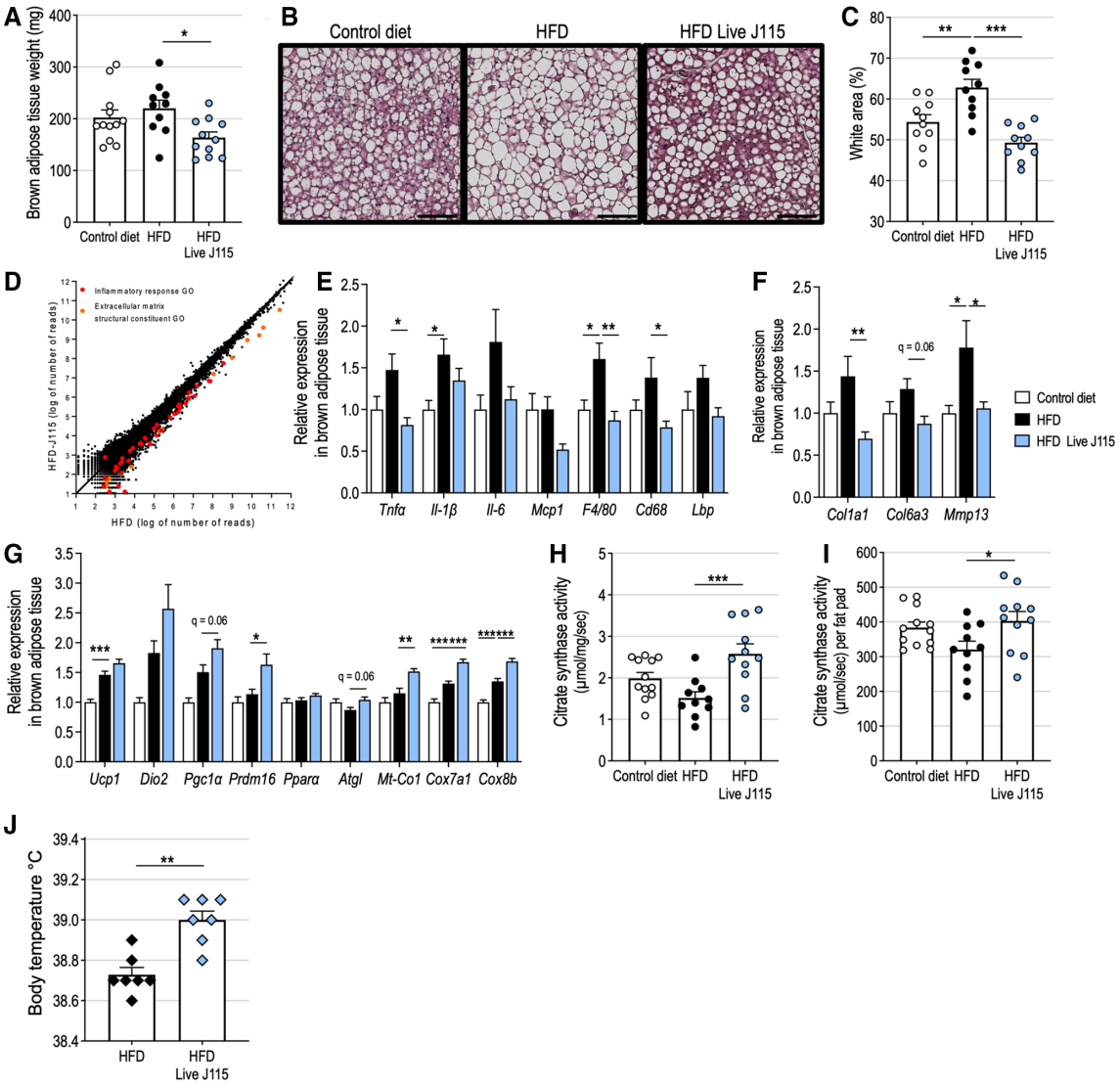


Figure 5 Live *Dysosmobacter welbionis* J115^T reduces high fat diet (HFD)-induced brown adipose tissue (BAT) dysfunction and increases mitochondria number. (A) Interscapular BAT weight of mice treated by daily oral gavage with live *D. welbionis* J115^T frozen in trehalose and fed an HFD (HFD Live J115) or mice fed a control diet or a HFD and treated by daily oral gavage with an equivalent volume of vehicle. (B) Representative H&E-stained pictures of BAT. Scale bar=100 µm. (C) Percentage of white area on the slices, corresponding to lipid droplets, in the BAT. (D) Scatter dot plot between RNA-seq expression data of a pool of RNA from the BAT of HFD mice and a pool of RNA from the BAT of HFD J115 mice. (E) Relative expression of genes related to inflammation and immune system in the BAT. (F) Relative expression of genes related to extracellular matrix and fibrosis in the BAT. (G) Relative expression of genes related to mitochondria number and function in the BAT. (H) citrate synthase activity per mg of BAT. (I) Citrate synthase activity per brown fat pad. (J) Body temperature of mice treated by daily oral gavage with live *D. welbionis* J115^T and fed a high fat-diet (HFD Live J115) or mice fed a high-fat diet (HFD) and gavaged daily with vehicle for 3 weeks (experiment 4, see methods). Number of mice per group: 10–12 in figure parts A, C and E–I). Number of mice per group: 7 in figure part J. Results are represented as dot plots and bar plots with mean±SEM for figure part A, C and H–J and as bar plots with mean±SEM for figure parts E–G. Data were analysed using one-way analysis of variance followed by Tukey's post hoc test for figure parts A, C and E–I and Mann-Whitney test for figure part J. *q<0.05; **p or q<0.01; ***q<0.001.HFD, high-fat diet.

response process and extracellular matrix gene ontologies (GO:0006955 and GO:0030020) were more expressed in the BAT of HFD mice than in that of HFD live *D. welbionis* J115^T treated mice (figure 5D, online supplemental figure S4, online supplemental table S2). Quantitative PCR on several markers of inflammation and macrophage infiltration performed on all mice confirmed that HFD increased inflammation in comparison with control diet-fed mice and that inflammation of the BAT on HFD was completely prevented by live *D. welbionis* J115^T supplementation (figure 5E). In addition, the expression of profibrotic factors such as collagens and matrix metalloproteinases genes was upregulated by the HFD and normalised by live *D. welbionis* J115^T (figure 5F), suggesting a protection against HFD-induced remodelling and/or fibrosis of the BAT.

Inflammation and brown-to-white conversion are associated with mitochondrial dysfunction in the BAT and impaired thermogenesis. The expression of BAT-specific uncoupling protein *Ucp1*, specific BAT markers (*Prdm16* and *Dio2*) and mitochondrial biogenesis marker *Pgc1α* (figure 5G) was increased by *D. welbionis* J115^T supplementation, although statistical significance was reached only for *Prdm16*. To confirm the possible BAT

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activation and higher number of mitochondria, we measured the expression of several genes of the mitochondrial respiratory chain (*Mt-Co1*, *Cox7a1* and *Cox8b*). Their expression was significantly increased by the HFD and was further raised by live *D. welbionis* J115^T (figure 5G).

To further investigate whether the genetic signature observed when investigating mRNA could be linked with specific changes at the metabolic level, we measured citrate synthase activity. This activity (expressed per mg of tissue), a proxy of mitochondria content, was 70% higher in the BAT of HFD live J115 mice than in that of HFD mice (figure 5H). Despite the reduction of the BAT size, the total citrate synthase activity of the HFD live J115 mice fat pads remained 25.7% higher than the activity in fat pads of mice kept on HFD alone (figure 5I), suggesting that live *D. welbionis* J115^T supplementation increases mitochondrial content and activity in the BAT. As the BAT produces heat by non-shivering thermogenesis, we sought to determine if live *D. welbionis* J115^T supplementation increases body temperature. In a separate set of experiments (experiment 4, detailed in Material and methods) during which mice were subjected to HFD or HFD and live *D. welbionis* J115^T supplementation for 3 weeks (online supplemental figure S5), we observed that mice supplemented with live *D. welbionis* J115^T had a rectal temperature on average 0.25°C higher than HFD mice (figure 5J).

MATERIAL AND METHODS

See online supplemental material and methods.

DISCUSSION

In this study, we first discovered that the newly isolated bacterium *D. welbionis* J115^T is highly prevalent in the general population and that this bacterium is inversely associated with BMI, fasting plasma glucose and HbA1c in obese humans suffering from metabolic syndrome. We next demonstrated that supplementation with live *D. welbionis* J115^T partially protects mice against HFD-induced metabolic disorders and low-grade inflammation notably through a mechanism involving the recovery of BAT metabolism and activity.

Although numerous bacteria have been shown to be positively or negatively associated with obesity and cardiometabolic disorders, the vast majority have never been cultured,[7] making it difficult to demonstrate the proof of concept of their causal involvement in adverse or beneficial phenotypes. In this study, we moved from the simple correlation to the demonstration that the newly identified bacteria *D. welbionis* J115^T is a promising candidate. It is important to note that the bacterium has been grown in a well-defined medium suitable for use of the bacterium in humans. This makes it possible to circumvent the difficulties previously faced when investigating *A. muciniphila,* for which all the initial data in mice were obtained using a medium containing animal-derived compounds not suitable for administration to humans.[17]

Interestingly, although *D. welbionis* had initially been isolated from the human gut of one healthy subject,[21] the presence of this bacterium is widely spread into the general population. Indeed, by using several cohorts such as the HMP, the AGP and the FGFP (ie, 11 984 subjects in total), we discovered that at least two-thirds of the general population harbour this newly discovered bacterium in their intestine.

As this bacterium abundance correlates negatively with metabolic parameters and BMI in obese humans suffering from metabolic syndrome, we tested whether the bacterium could affect host metabolism on HFD feeding. To do so, we treated mice with fresh daily prepared live *D. welbionis* J115^T (1.0×10^9 cultivable, live bacteria per day and per mouse) or using bacteria that were alive but that had been frozen in trehalose (1.0×10^9 cultivable, live bacteria per day and per mouse) or pasteurised *D. welbionis* J115^T (ie, heat-killed bacteria). We found that both treatment of mice with the live bacteria, either obtained from a fresh culture or frozen in a cryoprotectant, reduced the body weight and the fat mass gain of HFD-treated mice. However, killing the bacteria by using pasteurisation completely abolished its beneficial effects. We found that treating the mice for a longer period of time (ie, 13 weeks) was associated with a stronger effect and further reduced fat mass gain, improved glucose tolerance and reduced insulin resistance. Nevertheless, when treated with a lower dose of *D. welbionis* J115^T (ie $<1.0\times10^9$ cultivable and viable cells), the mice did not respond to the beneficial effects of the bacteria (online supplemental figure S2).

The viability of probiotics and beneficial bacteria has often been considered as a prerequisite for their health-promoting properties. While it is known to be true for certain species, for example, *A. soehngenii* whose beneficial effect is associated with its capacity to replicate in the gut,[14] it has also been shown that heat-killed *A. muciniphila* and several *Lactobacillus* and *Bifidobacterium* species are as potent as their live form.[17 29] In the present study, we found that pasteurised *D. welbionis* J115^T was inefficient. We also found that the live bacterium was unable to permanently colonise the gastrointestinal tract of the mice. Indeed, after 72 hours of wash-out, the faecal content of *D. welbionis* J115^T was below qPCR detection limit (online supplemental figure S3). Whether the beneficial effects of *D. welbionis* J115^T are mediated by constitutive components or metabolites present both in the fresh and frozen preparation but not by metabolites produced in the gut warrants further investigation. Altogether, this study provides a proof of concept that the correlation observed in obese humans is fully supported by mouse experiments showing beneficial effects of *D. welbionis* J115^T.

To further explore the mechanisms underlying how live *D. welbionis* J115^T improves metabolic parameters, we sequenced the gut microbiota of mice and confirmed that HFD changes the gut microbiota composition.[30 31] However, we observed only subtle shifts in the gut microbiota composition between treated and untreated groups, thereby suggesting a direct effect of the bacteria on host metabolism rather than through the modulation of the whole gut ecosystem. This is a finding that we previously observed for *A. muciniphila*.[16 18] Hence, we investigated whether the lower body weight and fat mass gain observed on live *D. welbionis* J115^T treatment could be the consequence of acute inflammation or decreased energy absorption. We found that the chronic administration of live *D. welbionis* J115^T did not affect intestinal inflammation, transit time and energy absorption therefore suggesting that bacterium administration is well tolerated and that the metabolic improvements did not result from decreased energy absorption. We found that live *D. welbionis* J115^T completely normalised visceral fat cell morphology, as well as several markers of inflammation known to contribute to the development of insulin resistance and glucose intolerance. These data are also supported by lower circulating levels of resistin and, to a lower extent, of PAI-1. Both were shown to be involved in the onset of insulin resistance.[32 33]

Besides the white adipose depots, the brown adipose tissue (BAT) is of utmost importance in the control of energy and glucose metabolism. It has been largely described that

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HFD feeding induces alteration of BAT, with a brown-to-white conversion of the morphology and functionality of the adipocytes, a process referred to as whitening of the brown adipose tissue that eventually leads to lower BAT thermogenesis and energy expenditure.[34] We found that live *D. welbionis* J115^T completely prevented high-fat diet-induced brown adipose tissue whitening, characterised by a lower weight and lower abundance of white adipocytes. In addition, RNAseq and qPCR analyses showed that the administration of live *D. welbionis* J115^T reduced macrophages infiltration, expression levels of several markers of inflammation and profibrotic markers, the latter being associated with a dysfunctional adipose tissue and impaired energy production through substrate oxidation.[35] Transcriptomic data suggesting an increased number of mitochondria were substantiated by a higher activity of the citrate synthase, an exclusive marker of the mitochondrial matrix.[36] This increase in the number of mitochondria is triggered by *D. welbionis* and leads to higher body temperature, associated to a better energy metabolism and a higher energy expenditure in live *D. welbionis* J115^T treated mice as compared with HFD-treated mice. Although our experiments strongly suggest important effects of live *D. welbionis* J115^T on energy metabolism, it would be interesting to further investigate whether live *D. welbionis* J115^T could induce even stronger effects on metabolism when exposed to thermoneutrality.[37]

The exact mechanisms of action, however, remain to be deciphered. Among the potential candidate-mediators, we can mention butyrate, which is produced by *D. welbionis* J115^T from myo-inositol and known to increase BAT thermogenesis,[38] but also other specific bioactive lipids controlling glucose metabolism and inflammation.[39 40] However, we did not find any increase in the levels of butyrate in the plasma or in the caecal content (online supplemental figure 6).

Altogether, our data strongly support that the human gut commensal *D. welbionis* J115^T is a bacterium contributing to the regulation of host's metabolism in response to an obesogenic diet. Using different complementary in vivo approaches, we demonstrate that *D. welbionis* J115^T regulates host's energy metabolism likely through the modulation of fat mass development and BAT metabolism. As for other next-generation beneficial bacteria, the final mechanisms explaining how the bacterium is dialoguing with the host deserve additional exploration.[41 42] In the present study, although we found that the bacterium is a butyrate producer, we cannot rule out that other specific secreted factors might be involved. Finally, we found that the adminstration of *D. welbionis* J115^T at the dose of 1.0×10^9 cultivable, viable cells to genetically and severely obese *ob/ob* mice for 6 weeks did not significantly reduce body weight and fat mass gain (online supplemental figure S7). Altogether, our data strongly support the beneficial effects of live *D. welbionis* J115^T on diet-induced obesity and diabetes. However, whether higher doses of live *D. welbionis* J115^T and/or longer duration of treatment are required to observe a beneficial effect in a specific model such as *ob/ob* (also known as a hyperphagic model) warrants further investigation. Moreover, we may not exclude that the administration of live *D. welbionis* J115^T induces beneficial effects on insulin resistance independently from changes in adiposity in these mice. Indeed, it has been shown that host exposure time to microbiota is a critical factor to contribute to change insulin sensitivity.[43] Therefore, exposure time is an important concern in bacteria targeted strategies aimed at attenuating diabetes versus overweight and obesity.

In conclusion, *D. welbionis* J115^T is a newly isolated human bacterium, which is highly prevalent in the general population and inversely associated with BMI, fasting plasma glucose and HbA1c in overweight or obese subjects suffering from a metabolic syndrome. The daily administration of live *D. welbionis* J115^T to mice for at least 6 weeks and up to 13 weeks blunted the high-fat diet induced metabolic disorders, by mechanisms independent of specific changes in the gut microbiota, but rather acting on both white and brown adipose tissue metabolism.

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Contributors PDC, TLR and EMdH conceived the project. PDC supervised all the preclinical and clinical part. PDC, AE, CDr, CDe, MdB, JPT, AL, DM and MPH contributed to the clinical study Microbes4U. SV, GF and JR contributed to the analysis of the bacterium in the cohort FGFP. RP analysed the human microbiome project and American Gut Project cohort. AP and GGM performed short chain fatty acids measurements. TLR, EMdH, MVH and PDC performed experiments and interpreted all the results. TLR and EMdH generated figures and tables. NMD, LBB, MR and JR contributed to scientific discussions. PDC, TLR, EMdH and MVH wrote the manuscript. All authors discussed the results and approved the manuscript.

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Competing interests PDC is cofounder of A-Mansia biotech. TLR and PDC are inventors on patent applications dealing with the use bacteria in the treatment of obesity and related disorders.

Patient consent for publication Not required.

Ethics approval The mouse experiments were approved by and performed following the guidelines of the local ethics committee for animal care of the Health Sector of the Université catholique de Louvain under the specific agreement number 2017/UCL/MD/005. Animal housing conditions were as specified by the Belgian Law of 29 May 2013 regarding the protection of laboratory animals (Agreement number LA 1230314). FGFP procedures were approved by the Medical Ethics Committee UZ Brussels-VUB (BUN 143201215505) and the Commissie Medische Ethiek, UZ/KU Leuven (S58125). The cohort Microbes4U was registered at https://clinicaltrials.

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gov as trial number NCT02637115. Written informed consent was obtained from each participant, and the study protocol was approved by the Commission d'Ethique Biomédicale Hospitalo-facultaire of the Université catholique de Louvain.

Provenance and peer review Not commissioned; externally peer reviewed.

Data availability statement Data are available in a public, open access repository. Data are available on reasonable request. All data relevant to the study are included in the article or uploaded as supplementary information. All datasets and raw data generated and/or analysed during the current study are available from the corresponding author on reasonable request. The 16S rRNA gene sequencing raw sequences of the mouse study can be accessed in Sequence Read Archive database with accession code PRJNA606762. The raw 16S data of the FGFP cohort are available at European Genome-Phenome Archive (https://ega-archive.org/) under accession no. EGAS00001004420, and for the Microbes4U cohort under accession no. EGAS00001003585. For the HMP, healthy human subjects cohort was downloaded from the human microbiome project data portal (https://portal.hmpdacc.org/).

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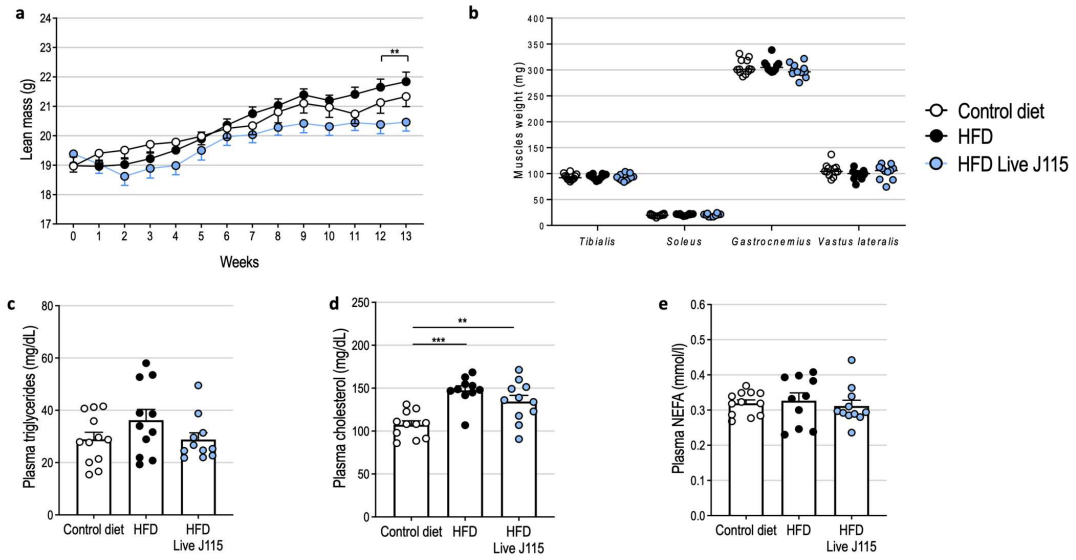
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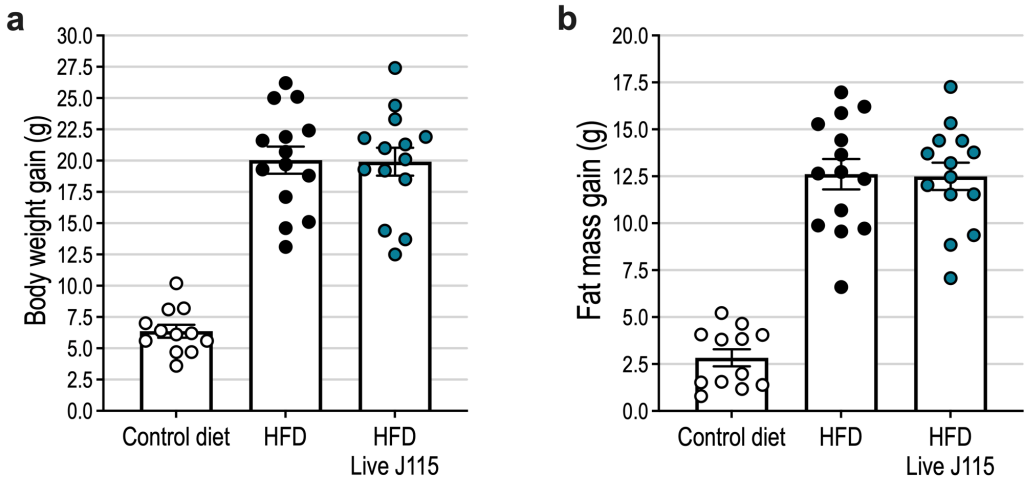
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Supplementary Table S1: Separate excel spreadsheet. Correlation coefficients and p-values (Pearson correlations) between clinical variables and the absolute and relative abundance of *Dysosmobacter* spp. assessed by qPCR in the stools of the Microbes4U cohort.

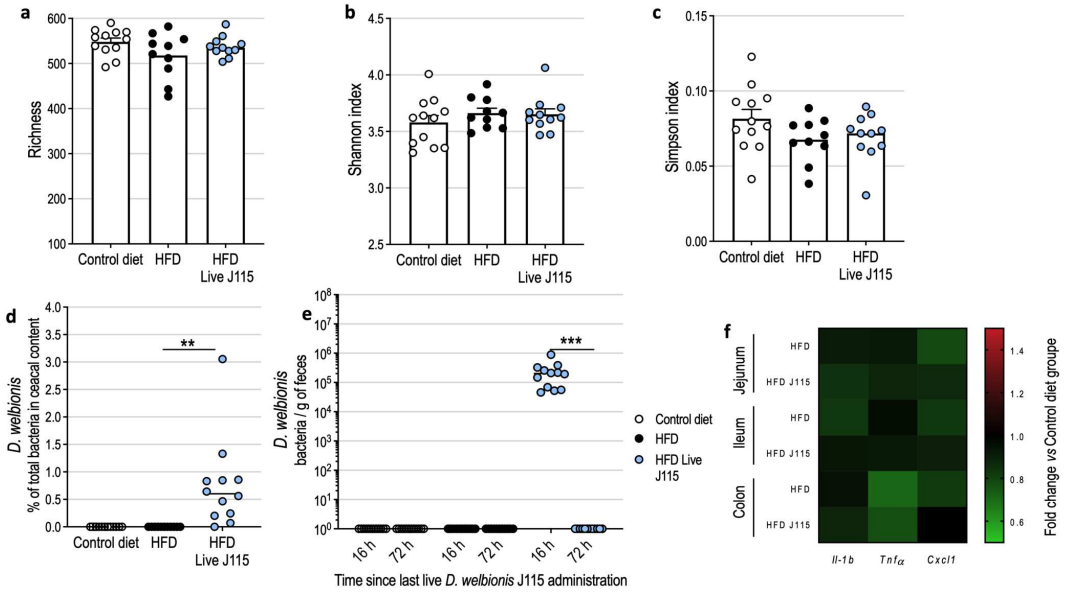
	Dysosmobacter spp (percentage of total bacteria)		*Dysosmobacter spp* (bacteria per gram of stools)	
	Correlation coefficient	p value	Correlation coefficient	p value
Body mass Index	-0,3683	0,0067	-0,3996	0,0030
Fasting plasma glucose	-0,2112	0,1328	-0,3230	0,0195
Fasting plasma insulin	-0,0384	0,7890	-0,1090	0,4466
HbA1c (mmol per L)	-0,1230	0,3851	-0,2909	0,0364
Fat mass as percentage of body weight	-0,1752	0,2095	-0,2238	0,1072
Lean mass as percentage of body weight	0,1786	0,2008	0,2295	0,0983
Basal metabolic rate (kcal per kg)	-0,1067	0,4561	-0,0423	0,7681
Plasma LPS	-0,1557	0,2655	-0,2401	0,0834
Plasma Lipid Binding protein	-0,1864	0,1814	-0,1502	0,2832
Plasma butyric acid	0,2018	0,1514	0,2408	0,0855



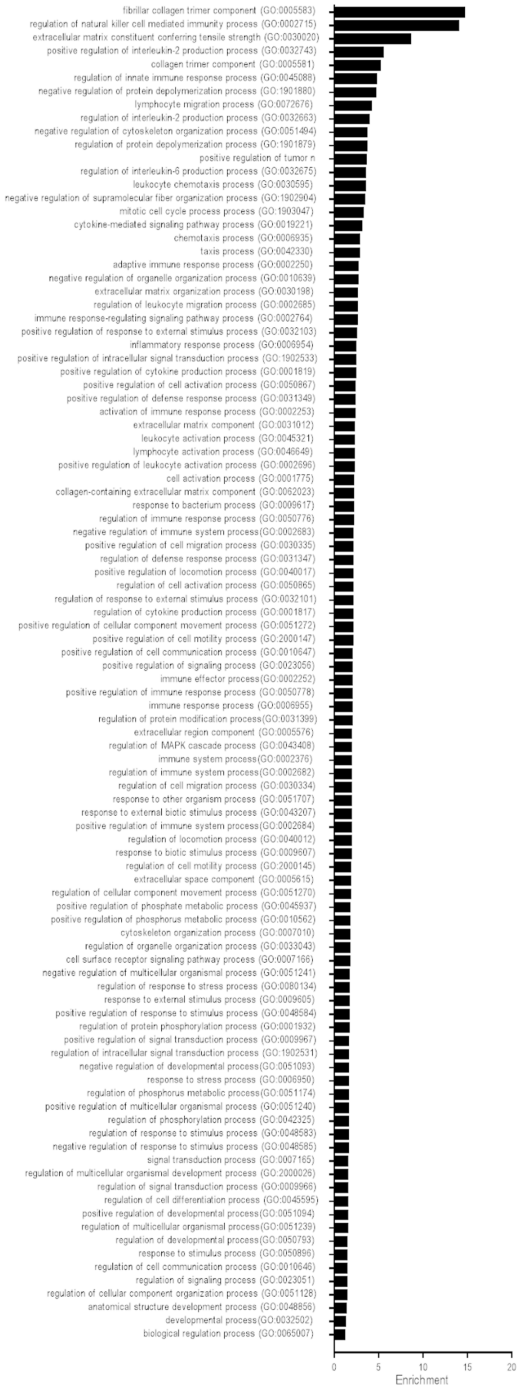
Supplementary Figure S1. Live *D. welbionis* J115^T has no impact on lean mass and plasma lipids levels. a, Lean mass evolution of mice treated during 13 weeks by daily oral gavage with live *D. welbionis* J115^T frozen in trehalose and fed a HFD (HFD J115) and mice fed a control diet or a HFD and treated by daily oral gavage with vehicle. **b**, *Tibialis*, *soleus*, *gastrocnemius* and *vastus lateralis* weight at the end of the 13-weeks period. **c**, Triglycerides, **d**, Total cholesterol and **e**, Non-esterified fatty acids (NEFA) levels in the plasma after a 6-hour fasting period. Number of mice per group: 10 to 12. Results are represented as dot-plots with mean for **b-e** and as bar-plots with mean ± SEM for **a.** Data were analysed using 2-way repeated measures ANOVA for **a** and one-way ANOVA followed by Tukey's post hoc test for **b-e**. * $q < 0.05$; ** $q < 0.01$; *** $q < 0.001$.



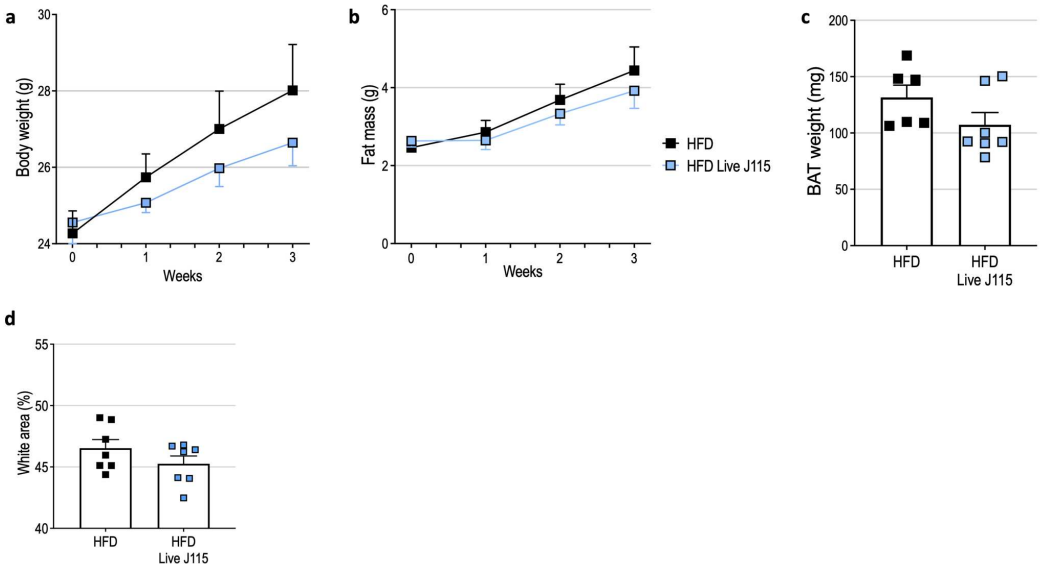
Supplementary Figure S2. Low dose of live *D. welbionis* J115^T did not impact on body weight gain and fat mass gain after 13 weeks of treatment (experiment 5). **a**, Body weight, **b**, fat mass of mice fed a HFD and treated during 13 weeks by daily oral gavage with 1.0 × 10^8 cells of live *D. welbionis* J115^T frozen in trehalose and mice fed a HFD and treated by daily oral gavage with vehicle (experiment 4). Number of mice per group: 12 to 14. Results are represented as dot-plots and bar-plots with mean +/- SEM.



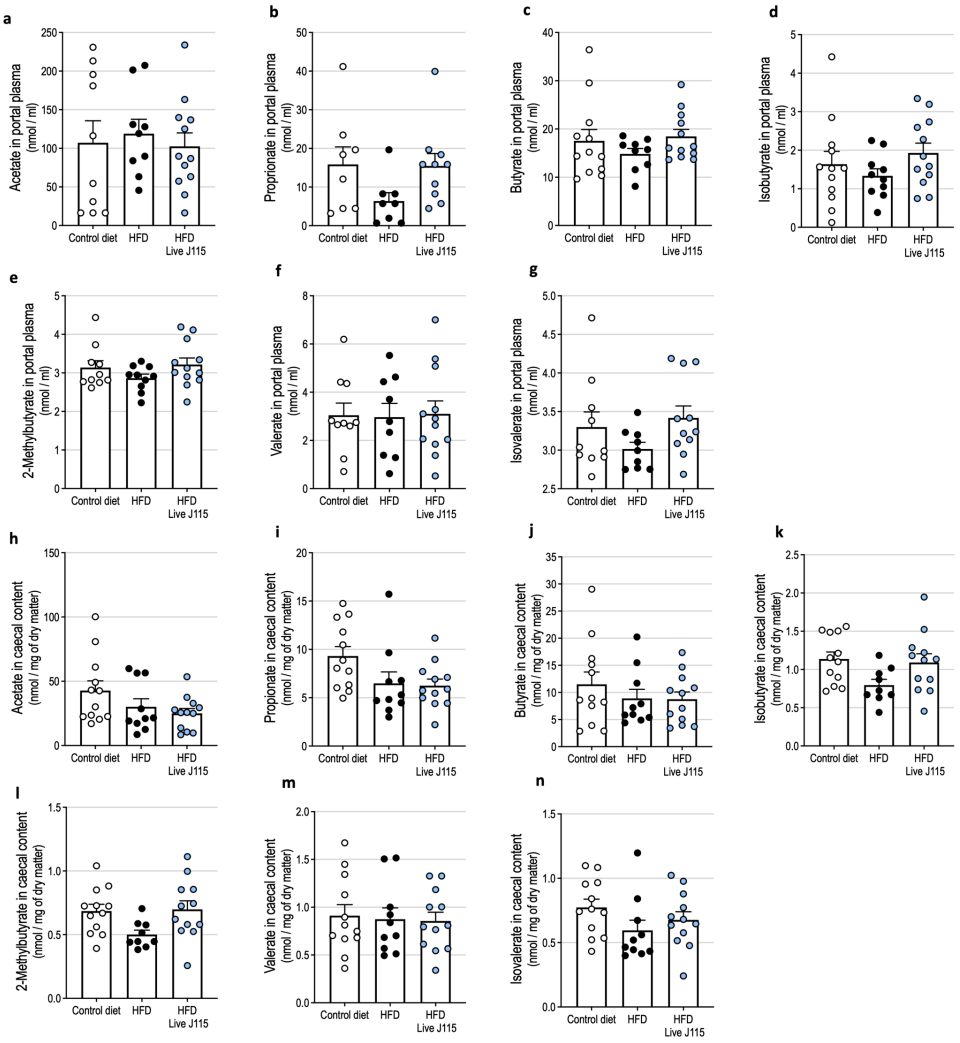
Supplementary Figure S3. **Live *D. welbionis* J115^T does not persist in the mouse gut and has little effect on intestinal microbiota and gut inflammation. a**, Richness of the caecal microbiota based on V3-V4 16S rRNA gene sequences analysis. **b**, Shannon index of the caecal microbiota. **c**, Simpson index of the caecal microbiota. **d**, *D. welbionis* relative abundance estimated by quantitative PCR in the caecal microbiota of mice treated during 13 weeks by daily oral gavage with live *D. welbionis* J115^T frozen in trehalose (HFD Live J115) and mice fed a control diet or a HFD and treated by daily oral gavage with vehicle. **e**, *D. welbionis* concentration estimated by quantitative PCR in the faeces of mice 16 and 72h after the last oral force feeding with live *D. welbionis* J115^T frozen in trehalose or with vehicle. **f**, Heatmap of the relative expression measured by qPCR of 3 inflammation markers (*Il-1b*, *Tnfα* and *Cxcl1*) in the jejunum, the ileum and the colon of the mice. Number of mice per group: 10 to 12. Results are represented as dot-plots with mean for **a-e** and as heatmap (mean of fold-change *vs* control diet group) for **f**. Data were analysed using one-way ANOVA followed by Tukey's post hoc test. ** q < 0.01; ***q < 0.001.



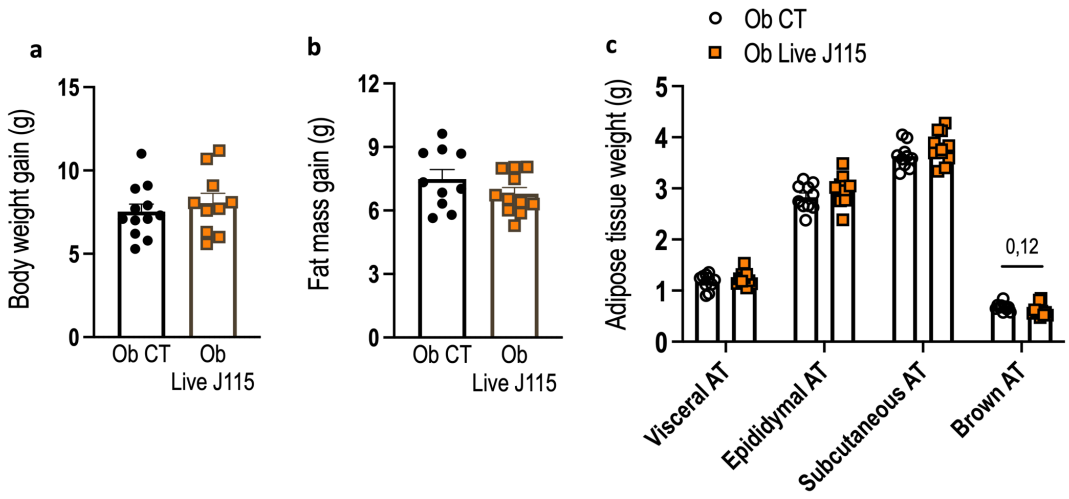
Supplementary Figure S4. Gene ontologies with an upregulated number of transcripts (RNAseq) in the interscapular brown adipose tissue of HFD-fed mice in comparison with HFD-fed mice supplemented with live *D. welbionis* J115^{T} frozen in trehalose during 13 weeks. False discovery rate (FDR) < 0.01.



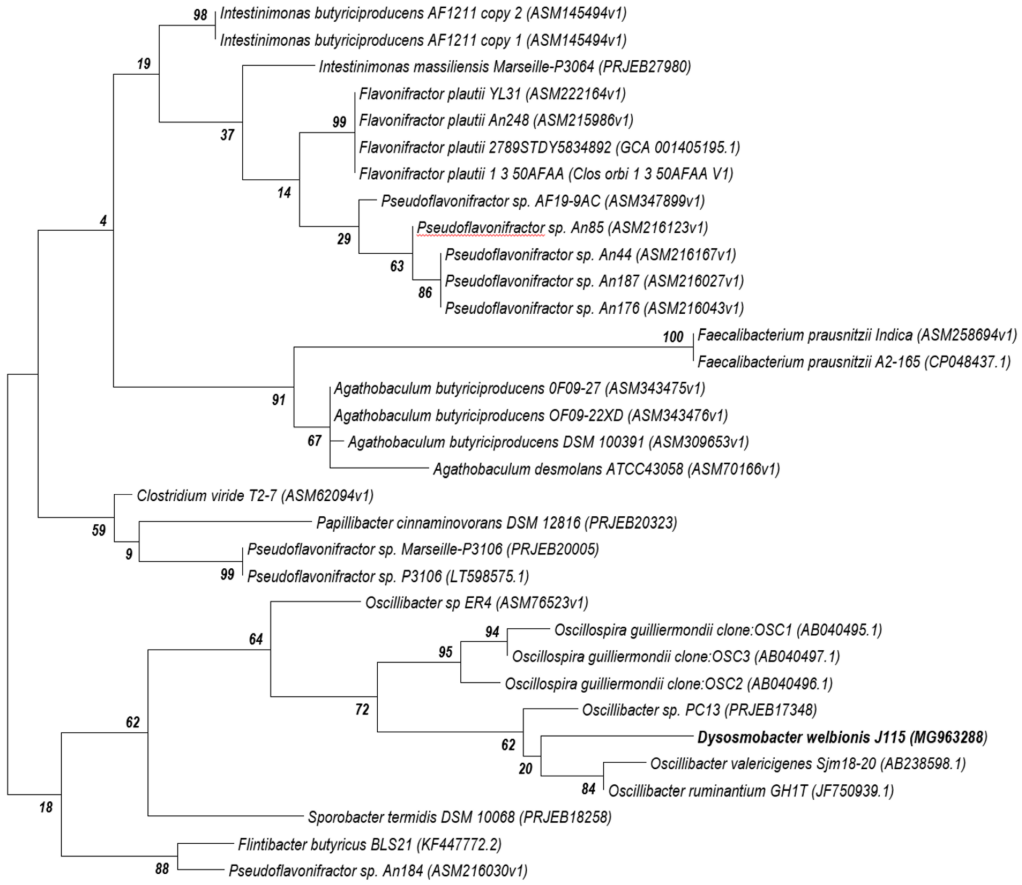
Supplementary Figure S5. Live *D. welbionis* J115^T impact on body weight, body composition and brown adipose tissue characteristics after 3 weeks of treatment (experiment 4). **a**, Body weight, **b**, fat mass, **c**, interscapular brown adipose tissue weight of mice fed a HFD and treated during 3 weeks by daily oral gavage with live *D. welbionis* J115^T frozen in trehalose (HFD Live J115) and mice fed a HFD and treated by daily oral gavage with vehicle (experiment 4). **d**, Percentage of white area on the slices, corresponding to lipid droplets, in the BAT. Number of mice per group: 7. Results are represented as bar-plots and dot-plots with mean ± SEM for **c-d.**



Supplementary Figure S6. Live *D. welbionis* J115^T does not affect short-chain fatty acids levels in portal blood and in caecal content 20 to 24 hours after last administration. **a**, Acetate, **b**, Propionate, **c**, Butyrate, **d**, Isobutyrate, **e**, 2-Methylbutyrate, **f**, Valerate, and **g**, Isovalerate concentrations in the portal plasma of mice treated during 13 weeks by daily oral gavage with live *D. welbionis* J115^T frozen in trehalose and fed a HFD (HFD Live J115) and mice fed a control diet. Last gavage was performed at 5 pm the day before the sacrifice. **h**, Acetate, **i**, Propionate, **j**, Butyrate, **k**, Isobutyrate, **l**, 2-Methylbutyrate, **m**, Valerate, and **n**, Isovalerate concentrations in the caecal content. Number of mice per group: 8 to 12. Results are represented as dot-plots with median. Data were analysed using one-way ANOVA followed by Tukey's post hoc test.



Supplementary Figure S7. Live *D. welbionis* J115^T did not impact on body weight gain and fat mass gain after 6 weeks of treatment in *ob/ob* mice (experiment 6). **a**, Body weight gain, **b**, fat mass gain, **c**, Visceral (mesenteric), epididymal, subcutaneous (inguinal) and brown adipose tissue (AT) weight of genetically obese *ob/ob* mice fed a CT diet and treated during 6 weeks by daily oral gavage with 1.0 × 10^9 cells of live *D. welbionis* J115^T frozen in trehalose (Ob Live J115) and mice fed a treated by daily oral gavage with vehicle (Ob CT) (experiment 6). Number of mice per group: Ob CT (n = 10) and Ob Live J115 (n = 11). Results are represented as dot-plots and bar-plots with mean +/- SEM.



Supplementary Figure S8. Phylogenetic tree based on 16S rRNA gene sequences, showing the connections between *D. welbionis* and related taxa used to design specific qPCR primers. Bootstrap values based on 1000 replicates are indicated on branch points. Bars, 0.02 substitutions per nucleotide position.

Supplementary Table S2: Expression fold change of the genes detected in the RNAseq analysis in pools of RNA extracted from the interscapular brown adipose tissue of mice treated by daily oral gavage with live *D. welbionis* J115^T frozen in trehalose and fed a high fat-diet (HFD Live J115) and mice fed a high-fat diet (HFD) and treated by daily oral gavage with an equivalent volume of vehicle (experiment 3).

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NR_028304.1	0,872958938
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NR_028307.1	2,59393513
NR_028313.1	0,563898941
NR_028329.1	1,108519286
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XR_378845.3	0,948868411
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XR_379029.3	0,60572661
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XR_379050.2	0,914528411
XR_379064.2	0,920923715
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XR_379082.3	1,224409939
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XR_379162.3	0,882891467
XR_379174.1	0,623542099
XR_379185.3	0,427571725
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XR_379336.2	0,748250518
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XR_379341.3	0,997667358
XR_379369.2	1,541849553
XR_379371.1	1,006342726

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XR_379512.2	0,399066943
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XR_379591.3	0,764878308
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XR_379717.3	0,831389465
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XR_379891.3	1,28865367
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XR_380167.3	1,097434093
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XR_380351.1	1,363478722
XR_380395.3	0,36278813
XR_380439.3	0,581972625
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XR_380565.1	1,08836439
XR_380597.2	1,140191266
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XR_882356.2	1,546384404

Online MATERIALS AND METHODS

Dysosmobacter spp. quantification by qPCR.

The qPCR target DNA region was the 16S rRNA gene. To design specific primers, the 16S rRNA gene sequences of *Dysosmobacter welbionis* J115^T and 32 closely related species or strains (highest hits during Blast), cultivated or not, was collected from public databases (NCBI accession numbers are ASM343475v1, ASM309653v1, ASM343476v1, ASM70166v1, ASM62094v1, ASM258694v1, Clos_orbi_1_3_50AFAA_V1, GCA_001405195.1, ASM215986v1, ASM222164v1, ASM145494v1, PRJEB27980, PRJEB20323, ASM216167v1, ASM216123v1, ASM216043v1, ASM216030v1, ASM216027v1, PRJEB18258, PRJEB17348, ASM76523v1, KF447772.2, LT598575.1, ASM347899v1, ASM216123v1, CP048437.1, AB238598.1, JF750939.1, AB040496.1, AB040497.1, AB040495.1, MG963288). Multiple alignment of the sequences was performed using MUSCLE [1], Distances were computed using the maximum composite likelihood method and the phylogenetic trees were reconstructed using maximum-likelihood method in MEGA 7.0 after gaps and unknown bases were eliminated [2]. The tree was reconstructed with 1000 bootstrap replications (Supplemental figure S8). Then, we determined the positions of the bases that differed between *D. welbionis* J115^T 16S rRNA sequence and the 32 other 16S rRNA gene sequences and designed primers on these regions using Primer-Blast [3]. The specificity of the obtained primers was first checked by performing Blast on NCBI Nucleotide collection (nr/nt), then by checking the absence of amplification in qPCR using *Oscillibacter valericigenes* Sjm18-20 and *O. ruminantium* GH1 genomic DNA as template. The fragment between the positions 184 and 239 of the 16S rRNA gene is amplified and the sequences of the primers are ***Dysosmobacter* spp:** Forward: ATGACGCATGACGCATGACC, Reverse:

CCAGCGATAAAATCTTTGACATGCC. Genomic DNA was extracted from mouse faeces, mouse caecal content or human stools using the QIAamp DNA Stool Mini Kit (Qiagen, Germany), including a bead-beating step. Quantified standard DNA for *Dysosmobacter* spp. qPCR was obtained by extracting genomic DNA with the same DNA extraction protocol than for the faeces/stools from a *Dysosmobacter welbionis* J115^T culture in exponential growing phase of known concentration in colony forming units (cfu) determined by plating. DNA concentration was determined, and purity (A260/A280) was checked using a NanoDrop2000 (Thermo Fisher Scientific, USA). Samples were diluted to an end concentration of 10 and 0.1 ng/µl in TE buffer pH 8. Total bacteria qPCR was performed on the 0.1 ng/µl dilution and the *Dysosmobacter* spp. qPCR was performed on the 10 ng/µl dilution. Real-time PCRs were performed with the StepOnePlus real-time PCR system and software (Applied Biosystems, Den Ijssel, The Netherlands) using Mesa Fast qPCR sybr green mix (Eurogentec, Seraing, Belgium) for detection according to the manufacturer's instructions. A standard curve was included on each plate by diluting genomic DNA from pure culture. *Dysosmobacter* spp. Standard curve ranged between 3.2 10^3 and 1.0 10^7 cfu per well for *Dysosmobacter* spp. and between 6.4 10^2 and 2.0 10^6 cfu per well for total bacteria. Bacteria quantity in caecal content and faeces was expressed as percentage of total bacteria and as cfu per gram of faeces.

Primer sequences for total bacteria are ***Total Bacteria*** Forward: ACTCCTACGGGAGGCAGCAG Reverse: ATTACCGCGGCTGCTGG.

Culture and preparation of *Dysosmobacter welbionis* for mice experiments. *D. welbionis* J115^T was cultured anaerobically in a modified YCFA medium supplemented with 10 g/L inositol. Cultures were centrifuged at 5000g during 20 min and the supernatant was removed. For fresh bacterial suspension preparation, cells were

resuspended in anaerobic PBS-carbonate buffer and immediately administered to the mice by oral gavage. For frozen bacterial suspension preparation, cells were resuspended in anaerobic PBS-carbonate buffer supplemented with 15 % (vol/vol) trehalose then immediately frozen in anaerobic vials and stored at -80°C. The number of total and cultivable bacteria administered to the mice was calculated by plating the bacterial culture before preparation and the bacterial suspension after preparation for mice administration.

Mice experiments. Sets of 10-week-old C57BL/6J male mice (Janvier Laboratories, Le Genest-Saint-Isle, France) were housed in pairs in SOPF (specific opportunistic and pathogen free) conditions and in a controlled environment (room temperature of 22 ± 2°C, 12h daylight cycle) with free access to sterile food (irradiated) and sterile water. Upon arrival, all mice underwent a 1-week acclimatization period, during which they were fed a control diet (ND) (AIN93Mi, Research Diet, New Brunswick, NJ, USA). During the experiments, food and water intake were recorded once a week. Body composition was assessed by using a 7.5 MHz time domain-nuclear magnetic resonance machine (TD-NMR) (LF50 minispec, Bruker, Rheinstetten, Germany). In the experiment 6, male homozygous *ob/ob* mice (B6.V-Lepob/ob/JRj) were used as genetically obese model (leptin-deficient mice with severe obesity). Mice were purchased at the age of 6 weeks (Janvier Laboratories, Le Genest-Saint-Isle, France) and housed in the same condition as described here above.

Experiment 1. The purpose of this first mice experiment was to assess the impact of freshly prepared, daily cultured *D. welbionis* J115^T on diet-induced obesity. A set of 30 mice was divided in 3 groups of 10 mice. The mice were fed a control diet (AIN93Mi; Research diet, New Brunswick, NJ, USA) or a high-fat diet (60% fat and 20%

carbohydrates (kcal/100g), D12492, Research diet, New Brunswick, NJ, USA). One group of HFD-fed mice was treated with an oral administration of daily prepared fresh cultures of *Dysosmobacter welbionis* J115^T by oral gavage at the dose 1.0 10^9 cfu /0.2 ml of cultivable, live bacteria per day and per mice (HFD J115 fresh) and control groups were treated with an oral gavage of an equivalent volume of PBS-carbonate buffer. Treatment continued for 6 weeks. Mice were euthanized after a 6-hour fasting period.

Experiment 2. The aim of this second experiment was to investigate whether heat-killed *D. welbionis* J115^T was still effective on diet-induced obesity. Moreover, we used live *D. welbionis* J115^T not coming from a fresh culture but frozen in anaerobic PBS-carbonate buffer supplemented with 15 % (weight/vol) of the cryoprotectant trehalose. A set of 30 mice was divided in 3 groups of 10 mice. The mice were fed a high-fat diet. One group of HFD-fed mice was treated with live *D. welbionis* J115^T frozen in trehalose by oral gavage at the dose of 1.0 10^9 cfu /0.2 ml of cultivable, live bacteria per day and per mice (HFD Live J115). One group of HFD-fed mice was treated with 1.10^9 cells/0.2 ml of *D. welbionis* J115^T pasteurised by heating procedure (30 min at 70°C) (HFD pasteurised J115), the control HFD groups was treated with an oral gavage of an equivalent volume of PBS-carbonate buffer supplemented with 15 % (weight/vol) trehalose (HFD). Mice have been treated for 10 weeks. Mice were euthanized after a 6-hour fasting period.

Experiment 3. The aim of this third experiment was to confirm the impact of live *D. welbionis* J115^T on diet-induced obesity obtained during experiment 1 and to determine the impact of longer period of treatment (i.e., 13 weeks) using the frozen bacterial preparation. A set of 36 mice was divided in 3 groups of 12 mice. The mice were fed a control diet or a high-fat diet. One group of HFD-fed mice was treated with live *D. welbionis* J115^T frozen in anaerobic PBS-carbonate buffer supplemented with 15 %

trehalose (weight/vol); each mouse received 1.0 10^9 cfu /0.2 ml of cultivable, live bacteria per day (HFD Live J115). HFD and control groups were given an oral gavage of an equivalent volume of PBS-carbonate buffer supplemented with 15 % (weight/vol) trehalose (Control and HFD). At week 10, faeces were collected in the morning, that is to say 16hour after last *D. welbionis* administration. Then, bacteria administration was discontinued for three days, then faeces were collected again, and daily bacteria administration resumed until the end of the experiment. Mice were euthanized after a 6-hour fasting period.

Experiment 4. The purpose of this fourth experiment was to measure the temperature of the mice after a shorter treatment than during experiments 1 and 2. A set of 14 mice was divided in two groups of 7 mice that were housed individually, with free access to food and water. The mice were fed a high-fat diet (HFD). A group of mice was treated by oral gavage with live *D. welbionis* J115^T frozen in anaerobic PBS-carbonate buffer supplemented with 15 % trehalose (weight/vol); each mouse received 1.0 10^9 cfu /0.2 ml of cultivable, live bacteria per day (HFD Live J115). HFD groups was treated with an oral gavage of an equivalent volume of PBS-carbonate buffer supplemented with and 15 % trehalose (HFD). Treatment continued for 3 weeks. On the last day of the experiment, the temperature of the mice was measured using a rodent rectal thermometer. Mice were euthanized in the morning with no fasting period.

Experiment 5. The purpose of this experiment was to assess if gavaging with lower numbers of *D. welbionis was as effective.* A set of 40 mice was divided in 3 groups of mice (n=12 control, n=14 HFD, n=14 HFD Live J115). The mice were fed a control diet or a high-fat diet. One group of HFD-fed mice was treated for 13 weeks with live *D. welbionis* J115^T frozen in anaerobic PBS-carbonate buffer supplemented with 15 % trehalose (weight/vol); each mouse received 1.0 10^8 cfu /0.2 ml of cultivable, live

bacteria per day (HFD Live J115). This experiment led us to discover that a low abundance of *D. welbionis* J115^T that is <1.0 10^9 cfu /0.2 ml of cultivable, live bacteria per day is not associated with any improvement of the metabolism (Supplemental figure S2).

Experiment 6. The aim of this sixth experiment was to study the impact of live *D. welbionis* J115^T in a model of severe obesity, therefore, the genetically induced obese *ob/ob* mice (B6.V-Lepob/ob/JRj) have been used. The mice were fed a control diet. One group was treated with live *D. welbionis* J115^T frozen in anaerobic PBS-carbonate buffer supplemented with 15 % trehalose (weight/vol); each mouse received 1.0 10^9 cfu /0.2 ml of cultivable, live bacteria per day (Ob Live J115) (n = 11), the control group was treated with an oral gavage of an equivalent volume of PBS-carbonate buffer supplemented with and 15 % trehalose (Ob CT) (n = 10). The treatment continued for 6 weeks (Supplemental figure S7).

Oral glucose tolerance test (OGTT). One week before the end of experiment 3, the mice were fasted for 6 hours before being given an oral gavage glucose load (2 g glucose per kg body weight). Blood glucose was measured 30 minutes before (time point -30), just prior the oral glucose load (time point 0) and then after 15, 30, 60, 90 and 120 min. Blood glucose was determined with a glucose meter (Accu Check, Roche, Switzerland) on blood samples collected from the tip of the tail vein. Plasma insulin concentration was determined using an ELISA kit (Mercodia, Uppsala, Sweden) according to the manufacturer's instructions.

Tissue sampling. The animals were anesthetized with isoflurane (Forene®, Abbott, Queenborough, Kent, England) and blood was collected from the portal and cava veins. Then mice were immediately euthanized by cervical dislocation. Tissue samples (liver, brown adipose tissue, subcutaneous adipose tissue, mesenteric adipose tissue,

jejunum, ileum and proximal colon, muscles) were dissected, immersed in liquid nitrogen, and stored at –80 °C for further analysis. A part of the adipose tissues and intestines was fixed in 4 % paraformaldehyde in PBS for histological analysis.

Short chain fatty acids assay

Portal plasma (50µL) and caecal content (50mg) were used short chain fatty acids determination by high performance liquid chromatography associated to mass spectrometry (HPLC-MS). Briefly, samples were added to 200 µL of acetonitrile containing valproic acid (used as internal standard). Tubes were mixed vigorously and incubated in an ultrasound water bath (10 min, 4°C) before being incubated 1 h at -20°C to allow protein precipitation. Following centrifugation (10 min, 13000 g) supernatants were transferred in glass tubes for the derivatization reaction. 100 µL of 3-nitrophenylhydrazine solution (0.14 M, in acetonitrile-water (1:1, v/v)) and 200 µL of an EDC solution (0.06 M, in acetonitrile-water (1:1, v/v)) containing 3% (v/v) of pyridine were added to the supernatants. After incubation (1 h, 40°C) under regular mixing, the tubes were placed in ice-cold water, and water (750 µL containing 50 µL of 2 N HCl) and chloroform (1.5 mL) were added to extract the derivatized SCFA. Following removal of the organic layer, the samples were reconstituted in methanol for the HPLC-MS analysis using a LTQ-Orbitrap mass spectrometer coupled to an Accela HPLC (ThermoFischer Scientific). Separation was achieved on a Hypersil GOLD PFP (100x2.1 mm; 1.9 µm) column maintained at 40°C. A gradient (200 µL/min) using water-acetonitrile-acetic acid 94.9:5:0.1 (v/v/v) and acetonitrile-acetic acid 99.9:0.1 (v/v) allowed for the separation of the different SCFA. An APCI source operated in positive mode was used for the MS analysis. For the quantification, calibration curves were obtained in the same conditions using increasing amount of SCFA and a constant

amount of internal standard. SCFA levels in the caecal content were normalized to the dry weight.

Caecal microbiota analysis by 16S rRNA gene sequencing. Genomic DNA extracted from the caecal content of the mice (extracted as described in *Dysosmobacter* spp. quantification by qPCR section) was diluted at 20 ng/µl. Sequencing was performed at MR DNA (www.mrdnalab.com, Shallowater, TX) on a MiSeq instrument following the manufacturer's guidelines. The V1-V3 region was amplified from purified DNA with the primers ill27Fmod (AGRGTTTGATCMTGGCTCAG) and ill519Rmod (GTNTTACNGCGGCKGCTG), using 30 amplification cycles with an annealing temperature of 65°C. Because MiSeq sequencing enables paired 300-bp reads, the ends of each read overlap and can be stitched together to generate extremely high-quality, full-length reads covering the entire V1-V3 region. The resulting PCR products were purified and loaded onto the Illumina MiSeq cartridge, according to the manufacturer instructions. The sequences were analysed using FROGS pipeline [4] implemented on a galaxy instance (http://migale.jouy.inra.fr/galaxy/). Briefly, reads were demultiplexed and clustered. After dereplication, the clusterisation tool ran with SWARM [5]. Chimeras were then removed using VSEARCH [6] and sequences were filtered to keep clusters (also called OTUs) accounting for at least 0.005% of all sequences. Taxonomic affiliation was performed with both RDP Classifier and Blastn+ against the SILVA 132 pintail 100 database [7]. The average number of sequences per sample was 40 418 ± 7 203 sequences. Then, we normalized the dataset to the number of sequences of the sample with the lowest sequencing depth, that is to say 26 881 sequences, using Rhea script without random subsampling [8].

Human cohort analyses

To gain insight into the prevalence and relative abundance of *Dysosmobacter welbionis* across a human population, data of the human microbiome project (HMP) was investigated (The Human Microbiome Project Consortium, 2012) [9]. Already trimmed 16S rRNA gene sequence data generated from faeces samples of the healthy human subjects (HHS) cohort was downloaded from the human microbiome project (HMP) data portal (https://portal.hmpdacc.org/). The 16S data set was split based on the amplified region of the 16S gene, the V3-V5 data subset was chosen for further analysis as it contained the most samples (N=216). The USEARCH v11 tool was used for 16S analysis [10, 11]. Reads were globally trimmed to 350 bp and denoised using the unoise3 command with default parameters [12]. Original reads were mapped to the resulting set of ZOTUs (zero-radius operational taxonomic units) to obtain a count table that was converted into the standard BIOM format [13]. The ZOTU table was imported in R version 3.6.3 using the phyloseq 1.30.0 package and further analysed. Samples with sequence library sizes within the first quartile (9057.5) were omitted as these were deemed too low (N=161). Taxonomy of the ZOTU sequences was predicted using SINTAX [11], with a bootstrap cutoff value of 0.8 and the Ribosomal Database Project training set v16 with the reference *Dysosmobacter welbionis* J115^T 16S gene sequence (Genbank accession MG963288.1) added at the database. Two ZOTU sequences with exact matches to the reference *Dysosmobacter welbionis* J115^T 16S gene sequence were retrieved. The relative abundance of these ZOTUs was summed to obtain a better estimate of the relative abundance of *D. welbionis.* For the FGFP the sequence variant was also corresponding to 100% homology to the 16SrRNA sequence on its full length (232 bp) with 0 gaps introduced. The sequencing methods used the V4 region of the 16S rRNA amplified by using the 515F/806R primer pair

(GTGYCAGCMGCCGCGGTAA and GGACTACNVGGGTWTCTAAT). The DADA2 pipeline was used to partition rarefaction counts (10,000) into taxonomic units, and as extensively detailed here [14]

For the American Gut Project (AGP), the relative abundance sOTU table obtained by Deblur processing on 16S V4 sequence data, following trimming to 125 bp and bloom removal, was downloaded in the standard BIOM format [15]. The table contained 32,954 sOTUs and 9,511 samples. The sOTU sequences were extracted from the table and BLASTn was performed with the *Dysosmobacter welbionis* J115^T MG963288.1 gene sequence. One sOTU sequence with exact match to the reference *Dysosmobacter welbionis* J115^T 16S gene sequence was retrieved

Histological analyses. Subcutaneous adipose tissue (SAT), mesenteric adipose tissue (MAT), brown adipose tissue (BAT) depots and jejunal tissue were fixed in 4 % paraformaldehyde for 24 h at room temperature. Samples were then dehydrated by immersion in ethanol 100% for 24 h and processed for paraffin embedding. Paraffin sections of 5 µm were stained with haematoxylin and eosin. Images were obtained using a SCN400 slide scanner and Digital Image Hub software (Leica Biosystems, Wetzlar, Germany). Adipocytes size and distribution in white adipose tissues were calculated from 3 fields per sample for mesenteric adipose tissue and from 5 fields per sample for subcutaneous adipose tissue using Fiji and Adiposoft softwares [16]. White area in brown adipose tissue corresponds to the lipid droplets and was quantified from 5 fields per sample using Fiji software. Crypts and villi length in the jejunum were measured using Digital Image Hub from Slidepath (Leica) on an average of 20 crypts/villus (10 crypts/villus on 2 different slices) per sample.

Transit time measurement. Mice were force-fed with 200 µl of carmine red dissolved in drinking water at a concentration of 10 mg/ml. The transit time was the time elapsed between the force-feeding and the emission of the first red pellet.

Energy intestinal absorption. Six weeks after the beginning of the experiment, the faeces of two 7-days periods were collected. During the same time the food intake was monitored (the food was weighed before and after the faeces collection period). The faeces were dried at 60°C for 2 hours and weighted. Total energy of the diet and the faeces was determined by bomb calorimetry (C1, IKA, USA). The net intestinal absorption is calculated based on the ingested and excreted energy and represented the proportion of ingested energy that was not recovered in faeces output.

Fasting concentration of hormones. Circulating leptin, resistin, glucose-dependent insulinotropic polypeptide (GIP) and plasminogen activator inhibitor-1 (PAI-1) concentrations were determined using a multiplex immunoassay kit (Mouse diabetes assay, Bio-Plex Pro, Bio-Rad, Belgium) and measured using Luminex technology (Bioplex, Bio-Rad, Belgium) according to manufacturer's instructions.

Gene expression analysis by real-time qPCR analysis and RNAseq analysis. Total RNA was prepared from tissues using TriPure reagent (Roche). Quantification and integrity analysis of total RNA was performed by running 1 µl of each sample on an Agilent 2100 Bioanalyzer (Agilent RNA 6000 Nano Kit, Agilent).

For qPCR analysis, cDNA was prepared by reverse transcription of 1 µg total RNA using a Reverse Transcription System kit (Promega, Leiden, The Netherlands). Real-time PCRs were performed with the StepOnePlus real-time PCR system and software (Applied Biosystems, Den Ijssel, The Netherlands) using Mesa Fast qPCR sybr green mix (Eurogentec, Seraing, Belgium) for detection according to the manufacturer's

instructions. RPL19 was chosen as housekeeping gene. All samples were run in duplicate in a single 96-well reaction plate, and data were analysed according to the $2^{-\Delta\Delta Ct}$ method. The identity and purity of the amplified product was checked through analysis of the melting curve carried out at the end of amplification. Primer sequences for the targeted mouse genes are available in Supplemental Table S3.

For RNAseq analysis, the integrity of RNA from brown adipose tissue (BAT) was determined using the Agilent bioanalyzer 2100 system with the RNA 6000 Nano LabChip kit. BAT RNA samples with an RNA integrity number inferior to 8 on a scale ranging from 0 to 10 were eliminated. Then, samples were pooled for each group (HFD pool and HFD-J115 pool) to an end concentration of 50 ng/µl. The samples were then sequenced by Eurofins Genomics, which consisted in purification of poly-A containing mRNA molecules, then mRNA fragmentation, random primed cDNA synthesis (strand specific), adapter ligation and adapter specific PCR amplification and finally paired-end Illumina sequencing with a read length of 2 x 150 bp. Eighty to 90 million read pairs were obtained and analysed on Galaxy server using RNA-STAR and htseq modules.

Citrate synthase activity. Around 10 mg of brown adipose tissue was weighed and lysed in 20 volumes of CelLytic MT Cell Lysis containing 1 % (vol/vol) of protease inhibitor cocktail P8340 (Sigma) by bead-beating. The lysate was centrifuged at 10 000g during 10 min at 4°C two times in order to remove the lipids and the tissue debris. Tissue extract was diluted 1:10 in a 100mM phosphate buffer (pH 7.1) containing 10 mM 5,5'-dithiobis-(2-nitrobenzoic acid) (DTNB) and 30 mM acetyl-CoA. After the addition of 10 mM oxaloacetate, free coenzyme A produced from the condensation of acetyl-CoA and oxaloacetate was bound to DTNB, and resulting change in light absorbance detected spectrophotometrically at 412 nm was used to determine the activity of citrate synthase (µmol/mg/s).

Statistical analyses. Statistical analyses were performed using GraphPad Prism version 7.00 for Windows (GraphPad Software, San Diego, CA, USA) and R 3.5.1. Comparison between two groups was performed by Mann–Whitney–Wilcoxon test, comparison between three or more groups on one time-point was performed by one-way ANOVA followed by Tukey correction and comparison between 3 or more groups at different time-points was performed by 2-way repeated measures ANOVA. Probability value was referred as p value for uncorrected tests and as value for tests followed by a correction. p or q < 0.05 was considered statistically significant. Principal coordinates analyses (PCoA) were performed using R program and Rhea scripts. The cladogram generator GraPhIAn was used for 16S rRNA gene sequencing data visualization. Data from the Microbes4U cohort deemed not normal using the Shapiro test were log transformed. We used R program and the Hmisc and corrplot packages to produce Pearson correlations matrix.

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Supplementary Table S3. Primers sequences for relative genes expression analysis by qPCR.

Primers		Sequence
Rpl-19	Forward	GAAGGTCAAAGGGAATGTGTTCA
	Reverse	CCTGTTGCTCACTTGT
Cd36	Forward	ATCTCAATGTCCGAGACTTTTCAAC
	Reverse	CTCGTTGATTTCTGGGGAAC
Fatp4	Forward	GGCTCTCATCAACACCAACC
	Reverse	CCAGGATCCAGAGCAGAAGA
Lpl	Forward	TCTGTACGGCACAGTGG
	Reverse	CCTCTCGATGACGAAGC
Atgl	Forward	ACAGCTCCAACATCCAC
	Reverse	AGCCCTGTTTGCACATCTCT
Hsl	Forward	GCTAGCCAGGCTCATCTCCT
	Reverse	GTTCTTGAGGTAGGGCTCGT
Plin1	Forward	GATGCCCTGAAGGGTGTTAC
	Reverse	CCTCTGCTGAAGGGTTATCG
Scd1	Forward	CCTCTTCGGGATTTTCTACTACATG
	Reverse	GCCGTGCCTTGTAAGTTCTGT
Tnfα	Forward	TCGAGTGACAAGCCTGTAGCC
	Reverse	TTGAGATCCATGCCGTTGG
Il-1β	Forward	TCGCTCAGGGTCACAAGAAA
	Reverse	CCTCTCGATGACGAAGC
Mcp1	Forward	GCAGTTAACGCCCCACTCA
	Reverse	TCCAGCCTACTCATTGGGATCA
F4/80	Forward	TGACAACCAGACGGCTTGTG
	Reverse	GCAGGCGAGGAAAAGATAGTGT
Cd68	Forward	CTTCCCACAGGCAGCACAG
	Reverse	AATGATGAGAGGCAGCAAGAGG
Cd163	Forward	TCCACACGTCCAGAACAGTC
	Reverse	CCTTGGAAACAGAGACAGGC
Cd11c	Forward	ACGTCAGTACAAGGAGATGTTGGA
	Reverse	ATCCTATTGCAGAATGCTTCTTTACC
Cd11b	Forward	GTCAGAGTCTGCCTCCGTGT

	Reverse	CCTGCGTGTGTTGTTCTTTG
Lbp	Forward	GTCCTGGGAATCTGTCCTTG
	Reverse	CCGGTAACCTTGCTGTTGTT
Col1a1	Forward	CCTCAGGGTATTGCTGGACAAC
	Reverse	ACCACTTGATCCAGAAGGACCTT
Col6a3	Forward	TCAAGAGCCTGCAGTGGATG
	Reverse	TGGACACTTCTTGTCTATGCAG
Mmp13	Forward	GTTTACCTTCGCCTCACTAG
	Reverse	TCTCTCCTTCCCAGGGCAAGCAT
Ucp1	Forward	GCTACACGGGGACCTACAATG
	Reverse	CGTCATCTGCCAGTATTTTGTT
Dio2	Forward	AATTATGCCTCGGAGAAGACCG
	Reverse	GGCAGTTGCCTAGTGAAAGGT
Pgc1-α	Forward	AGCCGTGACCACTGACAACGAG
	Reverse	GCTGCATGGTTCTGAGTGCTAAG
Prdm16	Forward	CAGCACGGTGAAGCCATTC
	Reverse	GCGTGCATCCGCTTGTG
Ppar-α	Forward	TGACAACCAGACGGCTTGTG
	Reverse	GCAGGCGAGGAAAAGATAGTGT
Mt-Co1	Forward	CAACGGCGTCGAAGACAAA
	Reverse	TGACGGTCTCCACGGACAT
Cox7a1	Forward	CCGACAATGACCTCCCAGTA
	Reverse	TGTTTGTCCAAGTCCTCCAA
Cox8b	Forward	GGACATTCAGGGTGCCTCTT
	Reverse	GAAGTGGGAGTTTTGGCTGG