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Changes in the intestinal microbiota of broiler chicken induced by dietary supplementation of the diatomite-bentonite mixture

E. Węsierska[1*], P. Micek[2], M. G. Adamski[3], K. Gondek[4], M. Lis[5], M. Trela[5], D. Wojtysiak[6], J. Kowal[5], A. Wyrobisz-Papiewska[5], G. Kunstman[3], S. Mosiołek[3,7,8] and K. Smoroń[9]

Abstract

Background Diatomite is a source of biologically available silicon but in feed industry its insecticide and anti-caking properties have been also widely recognized. The aim of the study was to evaluate the effect of dietary diatomite-bentonite mixture (DBM) supplementation on the quantitative and qualitative composition of the bacterial microbiome of the broiler chicken gut. The trial was carried out on 960 Ross 308 broiler chickens divided into 2 experimental groups throughout the entire rearing period lasting 6 weeks. The birds were fed complete granulated diets without (group C) or with DBM (group E) in an amount of 1% from the 11 day of life. Two nutritionally balanced diets were used, tailored to the age of the broilers: a grower diet (from day 11 to 34) and a finisher diet (from day 35 to 42 of life).

Results Diatomite used in a mixture with bentonite significantly altered the microbiome. Restricting the description to species that comprise a minimum of 1% of all analyzed sequences, 36 species in group E (with diatomite) and 30 species in group C (without diatomite) were selected. Several bacteria species were identified in intestinal contents of chickens for the first time. Thirteen species occurred only in group E: *Agathobaculum butyriciproducens*, *Anaerobutyricum hallii*, *Anaerobutyricum soehngenii*, *Blautia producta* ATCC 27,340 = DSM 2950, *Gordonibacter pamelaeae* 7-10-1-b, *Helicobacter pullorum* NCTC 12,824, *Lactobacillus crispatus*, *L. helveticus* DSM 20,075 = CGMCC 1.1877, *Mucispirillum schaedleri*, *Phascolarctobacterium faecium*, *Phocaeicola coprocola* DSM 17,136, *P. massiliensis*, and *Ruthenibacterium lactatiformans*.

Conclusions The findings highlight the intricate and potentially consequential relationship between diet, specifically diatomite-bentonite mixture supplementation, and gut microbiota composition.

Keywords Diatomite, Bentonite, Poultry, Health, Intestine, Microbiota

*Correspondence:
E. Węsierska
ewelina.wesierska@urk.edu.pl
Full list of author information is available at the end of the article

Background

The gut microbiota of poultry has been the subject of intensive research over the past 20 years [4, 7, 12, 14, 21, 37, 46, 55, 60, 65, 68, 92, 114]. The continuous development of the broiler chicken industry and its growing importance in ensuring the production of healthy food have stimulated the use of new techniques in this area. Thanks to high-throughput sequencing technologies, aimed at identifying new species and determining their metabolic capacity and function in the host organism, understanding the mechanism of protective activity, and describing the horizontal transmission to hosts of other taxonomic classes became available like never before. In this context, it is noteworthy that sequences originally determined in the gut contents of chickens are often found in samples taken from the intestinal system of humans, other animals, plants, soils, and water reservoirs (Global distribution of the 16 S sequence, https://bacdive.dsmz.de). Therefore, it is not possible to separate knowledge related to animals from that related to human health when exploring this topic, especially since raw materials from animals ultimately serve as food for humans. Furthermore, the taxonomic classification of these microorganisms is continually evolving. For example, the phyla previously known as *Proteobacteria*, *Firmicutes*, *Actinobacteria*, and *Bacteroidetes* have experienced recent changes in their nomenclature, with *Proteobacteria* now sometimes referred to as *Pseudomonadota*, *Firmicutes* as *Bacillota*, *Actinobacteria* as *Actinomycetota*, and *Bacteroidetes* as *Bacteroidota*. Older publications may still use the previous names.

The composition and diversity of the gut microbiota is influenced by many factors, including host genetics [41, 81], long-term diet [14, 19, 39, 58, 81], medication [77, 91], age of the host [65] and several external factors such as ecological conditions of the host environment and laboratory culture of samples [1, 7, 46, 80]. The impact of common parasitic diseases (mainly coccidiosis caused by *Eimeria sp.*) is also worth mentioning [57].

Among many environmental factors, nutrition has the greatest influence on the composition of microorganisms that inhabit the digestive tract of chickens and the quality of their products. In this regard, the use of different feed additives, including minerals such as clays [63] or diatomaceous earth [10] became more and more common. The role of these substances is not only to provide minerals, but also to bind microbiological or toxicological agents from contaminated feed, which can affect the health, productivity and safety of livestock animals. Diatomaceous earth (diatomite DT) is a naturally occurring sedimentary rock which consists of fossilized diatoms [10] and is made up of almost amorphous silicon dioxide (80–90%), with minor contains of alumina (2–4%) and iron oxide (0,5–2%). Diatomite contains a wide range of naturally occurring minerals such as calcium, magnesium, iron, phosphate, sodium, titanium, potassium and organic amorphous silica [106], has the properties of a mycotoxin absorbing agent [43], can inactivate some bacteria like *Staphylococcus aureus* and *Escherichia coli* [17] and prevent the development of ascites in broiler chickens [42]. In feed industry its insecticide and anti-caking proprieties have been widely recognized. Diatomite is also a source of biologically available silicon and has many other positive physiological properties. However, chemical pollution of this material, especially with heavy metals, may limit its nutritional suitability. The earlier work has shown that the mobility and toxicity of heavy metals from DT may be reduced through the use of bentonite especially if a mixture of diatomite and bentonite in a ratio of 75:25% (wt/wt) [36]. Considering the potential of using such a mixture in practical poultry feeding, we decided to evaluate its impact on changes in gut microbiome, which may, in turn, alter the health and performance of broiler chickens.

Most of the microbiome in chickens caecum is represented by Gram-positive (77%) and Gram-negative rods (14%) as well as Gram-positive cocci (9%) [20]. The predominant bacterial phyla are *Proteobacteria* (2–9%), *Firmicutes* (50–70%), *Actinobacteria* (1–3.5%) and *Bacteroidetes* (approximately 12–40% of the general microbiome) [4, 20]. There are approximately 31 genera described from the *Firmicutes* family, of which 5% are *Eubacterium*, *Ruminococcus* and *Clostridium*. Other genera identified by sequencing include *Riemeralla*, *Paraprevotella*, *Tanneralla*, *Prevotella*, *Phascolarctobacterium*, *Megamonas*, *Faecalibacterium*, *Subdoligranulum* and *Gemmiger*. The predominant genera of *Proteobacteria* include *Neissenia*, *Desulfohalobium*, *Shigella*, *Escherichia*, *Helicobacter* and *Campylobacter* as is the genus *Phocaeicola* in *Bacteroidetes* [14, 60, 68, 107]. Although some studies report that at 3 weeks of age, the bacterial population of the chick changes from *Proteobacteria*, *Bacteroides* and *Firmicutes* to only *Firmicutes* [68], others indicate that anatomically distant sites differ in the qualitative composition of the microbiota for example *Acinetobacter* and *Acidobacteria* predominate in the jejunum as *Bacteroides* and *Clostridium* in the cecum [4]. At least 80% of the total bacterial species present in chicken or human caecum cannot yet be cultured in the laboratory (naturally occurring in quantity 10^{10}–10^{11} cells per gramme) and can only be identified by high-throughput sequencing techniques [2, 4, 60, 91, 107]. Due to a crucial role of microbiota in digestion and protection processes, the aim of the study was to assess the effect of dietary diatomite-bentonite mixture (DBM) supplementation on the quantitative and qualitative composition of chicken

gut bacterial microbiome. The aim of the study was to assess the effect of dietary diatomite-bentonite mixture (DBM) supplementation on the quantitative and qualitative composition of chicken gut bacterial microbiome.

Methods

Animal care and welfare

Animals were treated in a manner according to the principles stated in Directive 2010/63/EU, regarding the protection of animals used for experimental and other scientific purposes, enforced in Poland under Acts 266/2015 and 638/2020 [98]. The practises for animals were equivalent to practices undertaken for the purposes of recognised animal husbandry and not likely to cause pain, suffering, distress, or lasting harm equivalent to, or higher than, that caused by the introduction of a needle in accordance with good veterinary practise. For this reason, an ethics approval by an institutional review board was not necessary according to Directive 2010/63/EU Art 2.5.e-f (OJ L 276, 0.10.2010, p. 33–79) the Act 2015/266/RP Art.1.2. (O.J. 2015 pos. 266). The study reported in the manuscript follows the recommendations of the ARRIVE guidelines [72] and was registered under the number BZ/4240/22/WHBZ. The heating and lighting programmes were in accordance with Ross 308 broiler stock management [6].

Experimental design

The trial was carried out at the Experimental Poultry Farm in Potok, belonging to Ekoplon S.A. Poland. The experiment was conducted on 960 chickens divided into 2 experimental groups throughout the entire rearing period lasting 42 days. Prior to the experiment, the building and equipment were thoroughly cleaned and disinfected in accordance with the principles of veterinary biosecurity. Before the chicks were delivered, the hall was lined with bedding (peat with wood chips) and heated to an air temperature of 34 °C and a floor temperature of 28 °C. The one-day-old broiler Ross 308 chicks (Aviagen EPI ltd, Poland) were randomly divided into two groups of equal weight: control (C) and experimental (E), separated by gender. In each group there were 6 pens (3 for male and 3 for female), with 80 chicks per pen. Sexing the animals and maintaining separate male and female groups was necessary for the production study. For the purposes of this work, only male individuals were used to eliminate factors related to the presence of female hormones. The chicks were fed with the same starter type diet without the addition of experimental diatomite-bentonite mixture (DBM) for 10 days. This procedure aimed to reduce the number of stress-inducing factors during the early stage of rearing while providing highly digestible feed, recommended for the not fully developed digestive tract of chicks. From day 11 of life, the birds were fed complete diets without (C group) or with a 1% addition (10 kg per 1 t of mixture on a fresh matter basis) of DBM (E group) according to the age of the broilers: grower (d 11–34) and finisher (d 35 to 42). Complete nutritionally balanced diets were prepared according to CVB (2018). The DBM consisted of 75% diatomite and 25% bentonite, prepared as described by Gondek et al. [36]. The animals were housed in the same chicken house on both sides of the feeding corridor. Feed and water were given *ad libitum* throughout the entire growing period.

Parasitological analyses

Coproscopical examinations were performed to exclude the impact of *Eimeria* spp. infection on the experiment's results. Fecal samples were collected three times from each pen: after the first, third, and final weeks of the rearing period. The samples were then analyzed using the quantitative McMaster method with centrifugation [73].

Slaughtering and collection of digesta

Immediately after slaughter (5–10 min), the gastrointestinal tract of the males was rapidly removed, and the cecum segment was excised. The cecum content (1 to 1.5 g per bird) was collected into two sterilized tubes (1.5 mL). In total, 36 samples (18 samples per group) were flash-frozen in liquid nitrogen and then stored at −80 °C for sequencing. In each sample, analyses were performed in triplicate, resulting in 54 replicates sequenced within each group. The final body weight at slaughter of the male birds selected for digesta collection was 3067 ± 262 g and 3222 ± 225 g, respectively for the C and E groups.

Sequencing, data calculation, and statistical analysis

Prior to sequencing, the samples were thawed at a controlled temperature. DNA was then isolated using a silica column-based kit (QIAamp PowerFecal Pro DNA Kit, QIAGEN), according to the manufacturer's instructions. Following DNA isolation, polymerase chain reaction (PCR) was performed to amplify the 16 S rRNA gene regions of the bacterial DNA. This amplification was carried out using specific primers provided in the 16 S Barcoding Kit (Oxford Nanopore), following the kit's protocol. After PCR amplification, the samples were prepared for sequencing according to the Oxford Nanopore library preparation protocol. Two 16 S Forward primers (NanoF-1 and NanoF-2) with the sequence AGAGTT TGATCMTGGCTCAG and one 16 S Reverse primer (NanoR) with the sequence CGGTTACCTTGTTAC GACTT were used. Amplification was performed using the following cycling conditions (Table 1). Nanopore sequencing was then carried out using the MinIon device (Oxford Nanopore). Upon completion of the sequencing,

Table 1 PCR amplification cycling conditions

Cycle step	Temperature	Time	Number of cycles
Initial denaturation	95 °C	1 min	1
Denaturation	95 °C	20 s	30
Annealing	55 °C	30 s	
Extension	65 °C	2 min	
Final Extension	65 °C	5 min	1
Hold	4 °C	∞	

the raw data was processed using the MiniKnow software (Oxford Nanopore) to assess the quality of the reads and perform base calling. Further analysis, including taxonomic classification of the sequences, was performed using the Epi2Me platform (Fastq 16s workflow).

The bacterial microbiome dataset, which includes information about different species and their counts, was grouped into diatomit and nondiatomit diet groups (e.g., treatment groups, E and C respectively). The species count data were standardized using the Z score normalization method (StandardScaler) to ensure that each species contributed equally to the analysis. Principal Component Analysis (PCA) was applied to the standardized data to reduce dimensionality and identify the principal components that captured the majority of the variance in the data. A redundancy analysis (RDA) was performed by fitting a linear regression model using the "group" variable as the predictor and the principal components as the response variables. Ordinary least squares (OLS) regression was used to estimate the relationship between the groups and the principal components. Multivariate Analysis of Variance (MANOVA) was applied to test the differences in the first two principal components between the groups, using the formula "PC1 + PC2 ~ group." Additionally, One-Way ANOVA tests were performed separately for the first two principal components to compare the means between the groups.

Visualisation techniques were employed, including the generation of a scatter plot to visualise the distribution of the first two principal components for each group, and a stacked bar plot to display the percentage of the top 10 species for each group. Additionally, a phylogenetic tree was constructed to elucidate the evolutionary relationships among the identified bacterial species in the gut microbiome of both groups. This tree was generated using aligned 16 S rRNA gene sequences and was visualized to highlight the taxonomic classification up to the species level for groups C and E. In the statistical tests and interpretation phase, the RDA results provided information on the relationship between the groups and the composition of the species, as represented by the principal components. The MANOVA test determined whether there were statistically significant differences in the principal components between the groups. The ANOVA tests for PC1 and PC2 assessed differences in the means of these components between the groups, with statistical significance determined using $P > 0.05$.

To identify significant differences in the abundance of bacterial taxa between the diatomit and nondiatomit

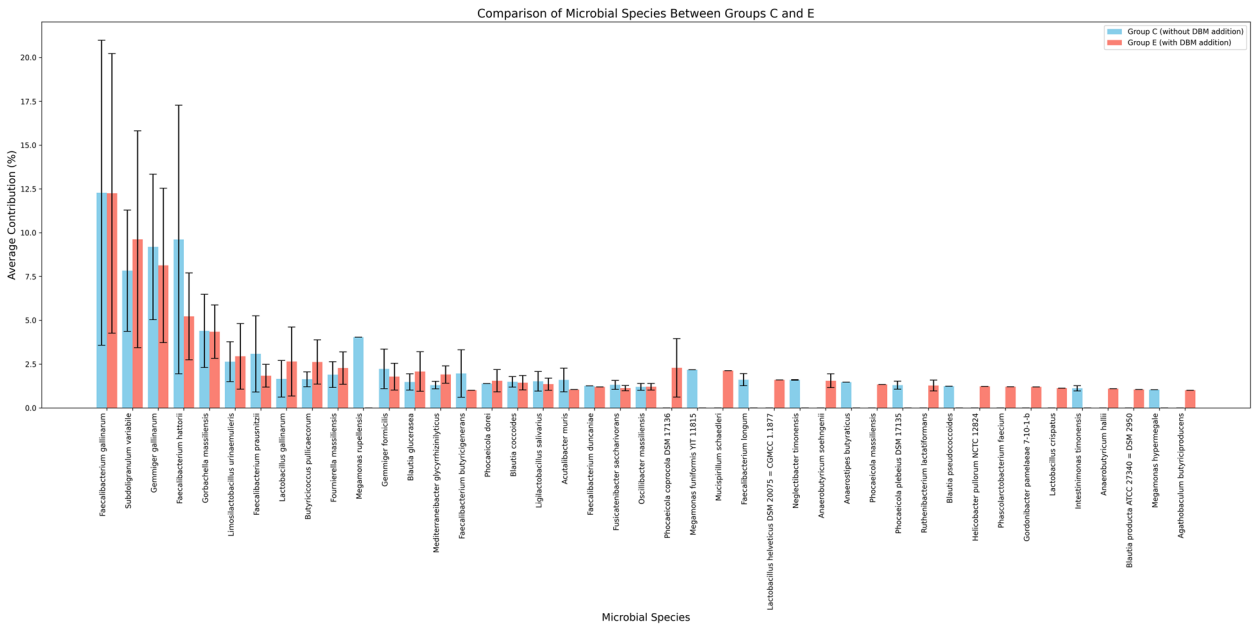

Fig. 1 Average contribution with standard deviation of species specific to all identified sequences in group E with DBM addition and in group C without DBM addition

diet groups, a series of univariate statistical analyses were conducted at the phylum, genus, and species levels. For each taxonomic level, Fisher's Exact Test was employed to determine whether there were statistically significant differences in the abundance of each taxon between the two diet groups. To mitigate increased risk of Type I errors (false positives) due to multiply comparisons, p-values obtained from Fisher's Exact Tests were adjusted using the False Discovery Rate (FDR) method, specifically the Benjamini-Hochberg procedure.

The analysis was conducted using the Python programming language, leveraging several widely used libraries for data manipulation, statistical modeling, and visualization. This included Pandas for data manipulation and analysis, Scikit-learn for normalization and PCA, Statsmodels for conducting RDA, MANOVA, and ANOVA tests, and Matplotlib for generating scatter plots and bar plots. For the univariate taxonomic level comparisons, the scipy.stats library was utilized to perform Fisher's Exact Tests, while statsmodels.stats.multitest was employed to apply the Benjamini-Hochberg FDR correction to the resulting p-values.

Results

Parasite analyses did not reveal any infection caused by coccidia (*Eimeria sp.*) or helminths, during the whole rearing period. In turn, the samples obtained from cecal chicken feces from both research groups, with (E) or without the addition of DBM (C), differed in the presence of several species characteristic of each other. Sequences assigned isolates to well-known and relatively new species. Library coverage ranged from 85 to 99.8% for both groups. Limiting the description to species with ≥1% share among all analysed sequences, 36 species in group E and 30 species in group C were selected (Fig. 1). The specific phyla and genus composition of identified sequences is presented in Tables 2, 3, and 4.

Thirteen species occurred only in Group E (*Agathobaculum butyriciproducens*, *Anaerobutyricum hallii*, *(A) soehngenii*, *Blautia producta* ATCC 27340 = DSM 2950, *Gordonibacter pamelaeae* 7–10-1-b, *Helicobacter pullorum* NCTC 12824, *Lactobacillus crispatus*, *L. helveticus* DSM 20075 = CGMCC 1.1877, *Mucispirillum schaedleri*, *Phascolarctobacterium faecium*, *Phocaeicola coprocola* DSM 17136, *P. massiliensis*, *Ruthenibacterium lactatiformans*), and 7 in Group C (*Anaerostipes butyraticus*, *Blautia pseudococcoides*, *Intestinimonas timonensis*, *Megamonas funiformis YIT 11815*, *M. hypermegale*, *Neglectibacter timonensis*, *Phocaeicola plebeius DSM 17135*). The remaining 23 species were confirmed in both groups (*Acutalibacter muris*, *Blautia coccoides*, *(B) glucerasea*, *Butyricicoccus pullicaecorum*, *Faecalibacterium butyricigenerans*, *F. duncaniae*, *F. gallinarum*, *F. hattorii*,

Table 2 Taxonomic composition of identified sequences

Taxon	Cumulative Reads
Bacillota (previously *Firmicutes*)	962 342
Bacteroidota (previously *Bacteroidetes*)	39 756
Actinomycetota (previously *Actinobacteria*)	7 110
Campylobacterota (previously *Proteobacteria*)	5 785
Pseudomonadota (previously *Proteobacteria*)	4 468
Deferribacterota	3 323
Thermodesulfobacteriota	408
Lentisphaerota	75
Cyanobacteriota (previously *Cyanobacteria*)	19
Candidatus Melainabacteria	10
Mycoplasmatota (previously *Tenericutes*)	7
Synergistota	6

Table 3 The percentage distribution of the cecal microbial community the genus level

Genus	Group C without diatomite (%)	Group E with diatomite (%)	*p*-value	Adjusted *p*-value
Faecalibacterium	46.44	33.17	< 0.0001	< 0.0001
Gemmiger	16.03	15.81	0.0357	0.0371
Subdoligranulum	11.71	16.92	< 0.0001	< 0.0001
Gorbachella	6.66	7.13	< 0.0001	< 0.0001
Blautia	3.56	3.59	0.6724	0.6724
Allofournierella	3	3.26	< 0.0001	< 0.0001
Lactobacillus	0.95	3.95	< 0.0001	< 0.0001
Phocaeicola	1.38	3.48	< 0.0001	< 0.0001
Limosilactobacillus	1.38	3.04	< 0.0001	< 0.0001
Mediterraneibacter	1.42	2.35	< 0.0001	< 0.0001
Butyricicoccus	0.99	2.6	< 0.0001	< 0.0001
Ligilactobacillus	1.34	0.53	< 0.0001	< 0.0001
Acutalibacter	1.5	0.29	< 0.0001	< 0.0001
Megamonas	1.26	0	< 0.0001	< 0.0001
Fusicatenibacter	0.65	0.48	< 0.0001	< 0.0001
Oscillibacter	0.39	0.52	< 0.0001	< 0.0001
Ruthenibacterium	0	0.84	< 0.0001	< 0.0001
Anaerobutyricum	0	0.81	< 0.0001	< 0.0001
Neglectibacter	0.69	0	< 0.0001	< 0.0001
Intestinimonas	0.43	0	< 0.0001	< 0.0001
Mucispirillum	0	0.35	< 0.0001	< 0.0001
Gordonibacter	0	0.26	< 0.0001	< 0.0001
Helicobacter	0	0.23	< 0.0001	< 0.0001
Phascolarctobacterium	0	0.23	< 0.0001	< 0.0001
Anaerostipes	0.23	0	< 0.0001	< 0.0001
Agathobaculum	0	0.17	< 0.0001	< 0.0001

Table 4 The percentage distribution of the cecal microbial community at the phylum level

Phyllum	Group C without diatomite (%)	Group E with diatomite (%)	*p*-value	adjusted *p*-value
Bacillota	98.62	95.68	< 0.0001	< 0.0001
Bacteroidota	1.38	3.48	< 0.0001	< 0.0001
Deferribacterota	0	0.35	< 0.0001	< 0.0001
Actinomycetota	0	0.26	< 0.0001	< 0.0001
Campylobacterota	0	0.23	< 0.0001	< 0.0001

F. longum, *F. prausnitzii*, *Fournierella massiliensis*, *Fusicatenibacter saccharivorans*, *Gemmiger formicilis*, *G. gallinarum*, *Gorbachella massiliensis*, *Lactobacillus gallinarum*, *Ligilactobacillus salivarius*, *Limosilactobacillus urinaemulieris*, *Mediterraneibacter glycyrrhizinilyticus*, *Megamonas rupellensis*, *Oscillibacter massiliensis*, *Phocaeicola dorei*, *Subdoligranulum variabile*).

In Figs. 2 and 3, the taxonomy trees for Group C and Group E are respectively presented, extending down to the species level. These trees provide a comprehensive visual representation of the bacterial communities in each group, highlighting the diversity and relative abundance of bacterial taxa. The hierarchically organized percentage compositions illustrate differences in dominant and less abundant taxa, allowing for a direct comparison of the microbial communities between the two groups and showcasing how variations in species composition impact the overall structure of the microbiome.

Principal Component Analysis (PCA) was conducted to understand how the samples differentiate from each other based on the presence of various microbial species. The two main components (PC1 and PC2) explained a significant proportion of the variability in the data (Fig. 4). The plot illustrates the pronounced separation between the two dietary treatments, particularly along the PC1 axis, highlighting the influence of diatomite on the gut microbiome. Group C (red) represents the diet without DBM, and group E (blue) represents the diet with DBM. Individual data points are depicted for each group and the corresponding ellipses represent the spread of the data within each group. PC1 explains 56.47% of the total variance and significantly differentiates the two groups (ANOVA, F-value: 7.33, P-value: 0.017), indicating a distinct effect of DBM on microbial composition. PC2 accounts for 19.85% of the variance but does not differentiate significantly between the groups (ANOVA, F-value: 0.35, P-value: 0.565). The highest positive correlations with PC1 were observed for the following 10 species: *Akkermansia muciniphila*, *Bacteroides thetaiotaomicron*, *B. vulgatus*, *Bifidobacterium longum*,

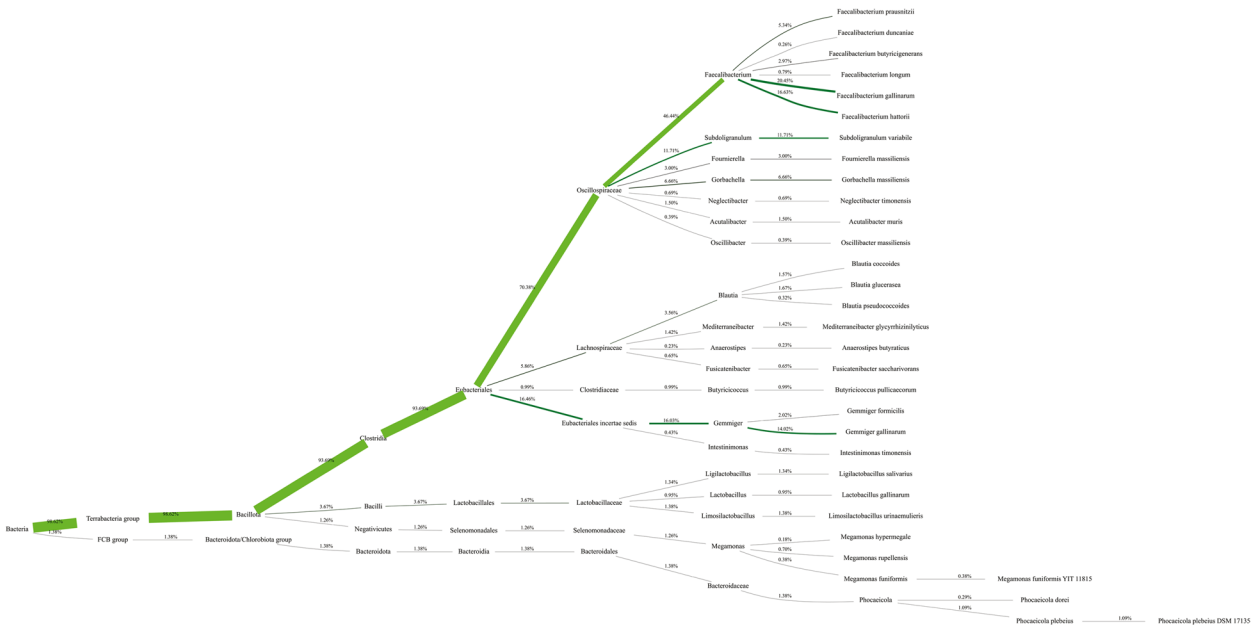

Fig. 2 Graphical representation of the bacterial communities in Group E with DBM addition, illustrating the taxonomic breakdown and respective percentage composition for each branch

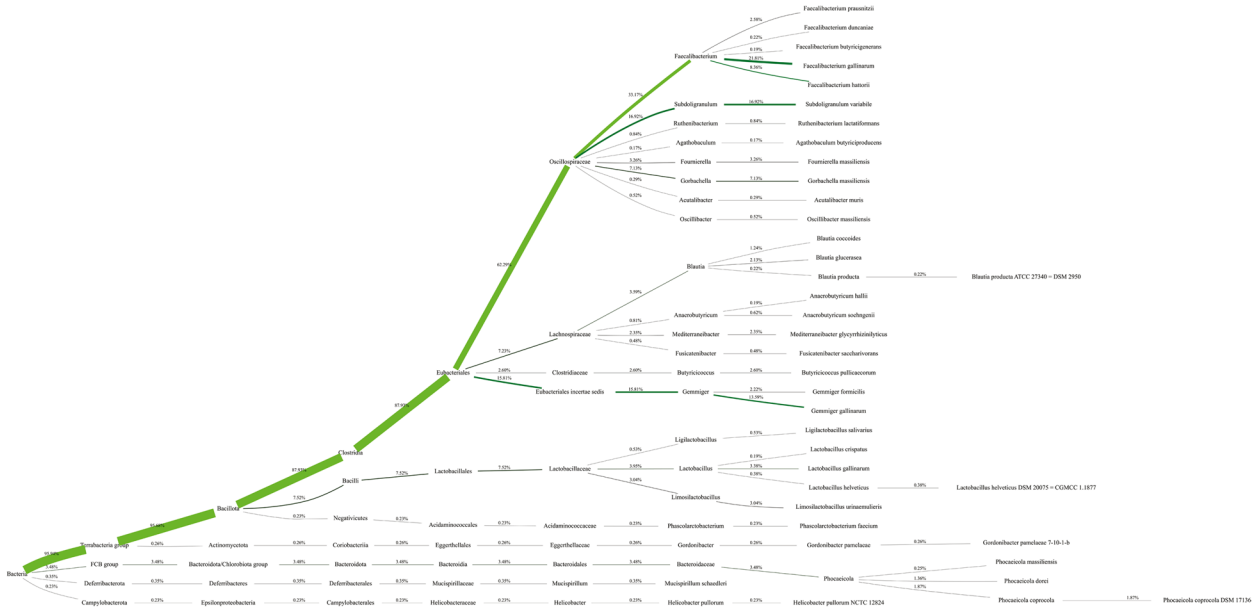

Fig. 3 Graphical representation of the bacterial communities in Group C without DBM addition, illustrating the taxonomic breakdown and respective percentage composition for each branch

Escherichia coli, *Eubacterium rectale*, *Faecalibacterium prausnitzii*, *Lactobacillus rhamnosus*, *Roseburia intestinalis* and *Ruminococcus bromii*. These findings suggest that the presence of DBM has a significant impact on the composition of microbiome in the samples. PC2 did not show a significant difference between groups.

A graph of side-by-side horizontal bar charts was created to display the percentage of the top 10 species for each group (with and without DBM; Fig. 5). Each bar represents a single sample, and the colours within the bar denote distinct species. The percentage contribution of the species was calculated based on the normalized

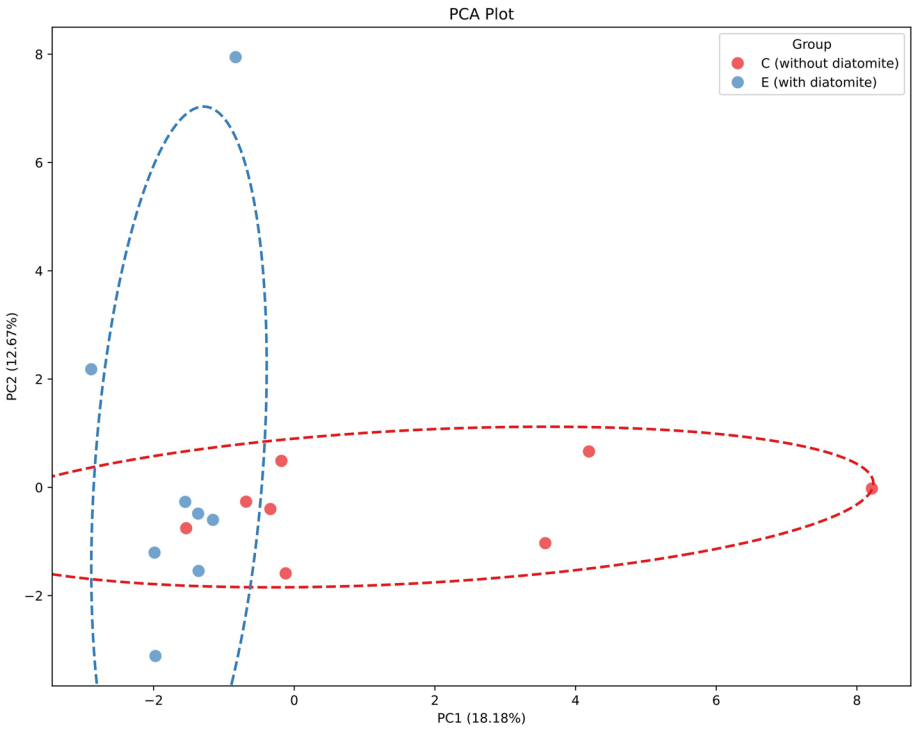

Fig. 4 Principal Component Analysis (PCA) of Microbial Composition Between Diets with and without Diatomite. Group C (without diatomite) and Group E (with diatomite)

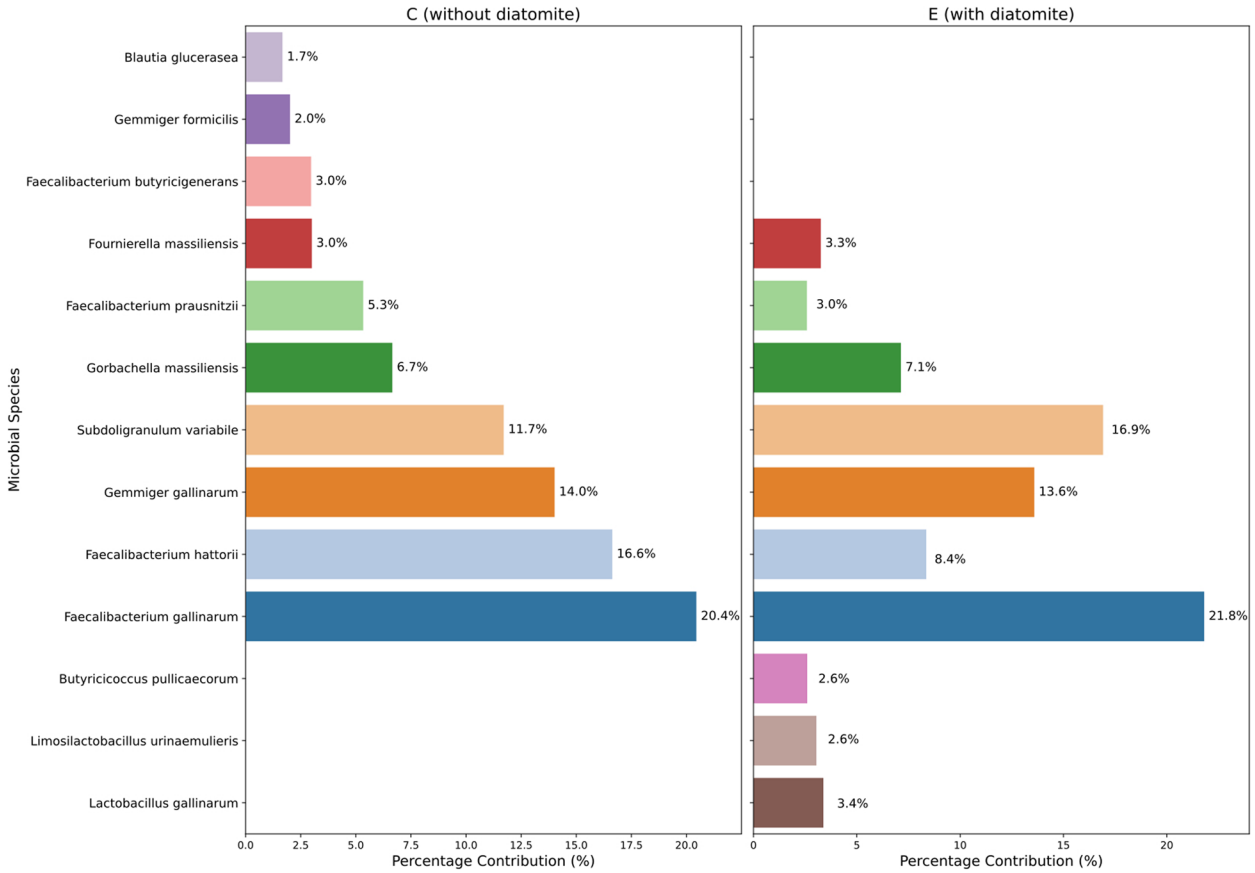

Fig. 5 Percentage contribution of the Top 10 Microbial Species in each sample. Group C (without diatomite) and Group E (with diatomite)

read count for each species relative to the sum of the read counts. Differences in the structure of the microbiome allow the identification of species that may have a particular impact on the differentiation of groups of chickens with and without the addition of DBM. Until now, in poultry, mainly *Blautia coccoides*, *Faecalibacterium prausnitzii*, *Helicobacter pullorum*, *Lactobacillus gallinarum* and *Ligilactobacillus salivarius*, identified in this work, have been described in the literature due to their high frequency or pro-health or disease-promoting properties. Most of the species identified and presented in this work are described in poultry for the first time.

Discussion

Identified species are not insignificant for the health of poultry or humans. The human microbiota is correlated with the microbiota of raw materials, also of animal origin. Poultry health is closely related to the quantitative and qualitative composition of the gut microbiota [70, 91]. Functions of the bacteria include host metabolic and immune response and thereby influence the development and treatment of infections and chronic diseases, as well as absorption of nutrients [2, 4, 114]. Young chickens are very sensitive to enteropathogen infections because their intestinal microbiota is not fully established [18]. The health of gastrointestinal tract (GIT) impacts therefore animal productivity [4]. Short-chain fatty acids (SCFAs), produced by fermentation of dietary fibre by several abundant genera of the intestinal microbiota, have been reported to induce beneficial effects on energy metabolism [21, 74, 76, 90, 11378]. Butyrate is the main energy source for colonocytes, and it has protective properties against colorectal cancer and inflammatory bowel diseases inter alia by inhibiting NF-κβ activation and interferon-γ expression [11, 12, 47, 59, 76, 93, 104, 114]. A potential protective role of gut bacteria was found through the reduction of inflammatory cytokines [13, 67, 68, 90, 101]. *Subdoligranulum variabile* and *Faecalibacterium* genus are e.g. currently recognized as one of the most important gut bacteria for human and animals health [31, 53, 65, 78, 104] (Table 5). Several authors have demonstrated the antimicrobial activity of human and avian strains against bacterial pathogens, including *Campylobacter* spp., *Clostridium perfringens*, *Pasteurella*

Table 5 Characteristics of the morphology, habitat and beneficial/adverse effects on the host organism of selected intestinal bacteria, determined based on 16s sequence

Name	Morphology and growth conditions	Global distribution of 16s sequence	Selected activity	Beneficial/non-beneficial impact for human and animal health (literature)
Acutalibacter muris	Anaerobic, no-spore-forming, no-motile but motility-associated proteins are encoded in the genome, rod-shaped, long rods with tapered ends, mesophilic, Gram (+)	Gastrointestinal tract (GIT) of animals. Plant, soil and aquatic samples	Catalase (-)	(https://bacdive.dsmz.de)
Agathobaculum butyriciproducens	Anaerobic, no spore-forming, no-motile, plump rods, mesophilic, Gram (+)	GIT of human and animal. Plant, soil and aquatic samples	Catalase (-), oxydase (-), butyric acid (+), acetic acid (+), ethanol (+), butanol (+)	*A.b.* phylogenetically, belongs to the family *Ruminococcaceae* [3]. As a result of the ability to produce short-chain fatty acids (SCFAs), *A.b.* induces cognitive improvement, reduces Alzheimer's disease pathologies in a mouse model, and plays a key role in the activation of microglia. *AB* is considered as a therapeutic strategy in Parkinson's disease [51]
Anaerobutyricum hallii, *A. soehngenii*	Anaerobic, no-spore-forming, no-motile, rod-shaped, mesophilic, Gram (+)	GIT of human (*A.h.*) as well as GIT of human and pig (*A.s.*)	Catalase (-), oxydase (-), butyric acid (+), formic acid (+)	People with type 2 diabetes lack *A.h.* in the gut. Due to the ability of *A.h.* to utilise glucose and form butyrate, is an important microorganism for the metabolic balance of the gut. Trophic interactions between bifidobacteria and *A.h.* lead to the formation of acetate, butyrate, propionate, and formate [87]. *As used*, D- and L-lactate in the presence of acetate and probably affects host bile acid metabolism [110]. *A.s.* improves insulin sensitivity [48]
Anaerostipes butyraticus	Anaerobic, spore-forming, nonmotile, long rods that occur in filaments, mesophilic, Gram (+)	GIT of human and animal. Plant, soil and aquatic samples	Butyric acid (+), acetic acid (+), propionic acid (+)	*Ab* depends on host health – one study reported reduced abundance in the faeces of patients with multiple system atrophy [28]

Table 5 (continued)

Name	Morphology and growth conditions	Global distribution of 16s sequence	Selected activity	Beneficial/non-beneficial impact for human and animal health (literature)
Blautia coccoides, *B. glucerasea*, *B. producta*, *B. pseudococcoides*	Anaerobic, most strains being spore-less (*B.c.*), no-spore-forming (*B.g.*, *B.p.*), spore-forming (*B.p.*), no-motile or motile (*B.p.)*, spherical/ oval, appear in pairs or strands (*B.c.*), mesophilic, Gram (+)	GIT of human and animal. Plant, soil and aquatic samples	Catalase (-), lactic acid (+), acetic acid (+) (*B.c.*, *B.g.*, *B.p.*), additionally formic acid (+) (*B.g.*), succinic acid (+) and ethanol (+) (*B.p.*)	*B.c.* degrades glycosylceramides to ceramides and then metabolises the ceramides to fatty acids and sphin-goid bases, which are absorbed by the intestine and produced a benefi-cial effect [52]. *B.g.* produces a specific extracellular glucosylceramide enzyme that hydrolyses glucosylceramide into functional substances with a spe-cific preventive effect against colon cancer [52]. *B.pr* inhibits the growth of vancomycin resistant enterococci by secreting a lantibiotic. Because the lanthipeptide does not affect other commensal bacteria, *B.pr.* may be a potential probiotic to prevent the transmission of conditional antibi-otic-resistant pathogens. *B.pr* inhibits the proliferation of *C. perfringens* [52]
Butyricicoccus pullicaecorum	Anaerobic, without spore formation, no motile, coccus shaped, usu-ally arranged in pairs (occasionally in short chains), mesophilic/ thermo-philic, Gram (+)	GIT of human and chicken. Plant, soil and aquatic samples	Butyric acid (+)	*B.p.* decreases intestinal myeloperoxi-dase (MPO), tumour necrosis factor α (TNFα) and interleukin (IL)−12 levels [105]. *B.p.* reduces feed conversion and protects from potentially harmful intestinal microorganisms and necrotic enteritis in broilers [27, 29]
Faecalibacterium butyricigenerans, *F. duncaniae*, *F. gallinarum*, *F. hattorii*, *F. longum*, *F. prausnitzii*	Anaerobic or extremely oxygen sensi-tive (Fp), no spore-forming, no motile, rod-shaped (*F.b.*, *F.p.*), straight rods (Fd, Fg, Fh) or long rods (*F.l.*), mesophilic, Gram (-)	GIT of human (Fb, Fg, Fl) as well as GIT of human and animals; plant, soil, and aquatic samples (*F.d.*, *F.h.*, *F. p.*)	Catalase (-), butyric acid (+) (Fg), addi-tionally formic acid (+), lactic acid (+) (Fd, Fh, Fp) and acetic acid (+) (*F.b.*, *F.l.*)	*F.b.* produces SCFAs and has the func-tion of treating ulcerative colitis [116] as well as *F.d.*, *F.g. and F.h.* are described as the main producers of SCFAs [82, 116]. *The f.p. has* an important role in providing energy to colonocytes and maintaining intestinal health. A decrease in the count of *Fp* is fre-quently observed in various diseases with associated intestinal inflammatory processes, such as inflammatory bowel disease, type 2 diabetes, colorectal cancer, and Crohn's disease [59, 62, 76]. *F.p.* modulates inflammatory signals by releasing immune-suppress-ing molecules [53]

Table 5 (continued)

Name	Morphology and growth conditions	Global distribution of 16s sequence	Selected activity	Beneficial/non-beneficial impact for human and animal health (literature)
Fournierella massiliensis	Anaerobic, no-spore-forming, no-motile, rod-shaped, mesophilic, Gram (-)	GIT of human and animal. Plant, soil and aquatic samples	Catalase (-), oxydase (-), butyric acid (+), isobutyric acid (+), acetic acid (+), propionic acid (+)	[100]
Fusicatenibacter saccharivorans	Anaerobic, without spores, without germs, rod or spindle-shaped, arranged in pairs and short chains, Gram (+)	GIT of human and animal. Plant, soil and aquatic samples	Lactic acid (+), formic acid (+), succinic acid (+), acetic acid (+)	[95, 96]
Gemmiger formicilis, *G. gallinarum*	Anaerobic, no-spore-forming, no-motile, rod-shaped, mesophilic, Gram (+)	GIT of human and animal. Plant, soil and aquatic samples	Catalase (+), oxydase (-), butyric acid (+) (*G.f.*), additionally *lactic* acid (+) (*G.g.*)	The activity of *Gf* results in the release of specific volatile odour compounds (exhaled metabolites in the breath) indicating the state of health and assess recent or long-term exposure to various contaminants [11]. *G.g.* produces SCFA [114] and has a protective role via the reduction of inflammatory cytokines [101]
Gorbachella massiliensis	Anaerobic, no-spore-forming, no-motile, rod-shaped, mesophilic, Gram (-), halophilic	GIT of human	Catalase (-), oxydase (-), butyric acid (+)	*SCFA G.M.* produces of SCFAs [25, 26]
Gordonibacter pamelaeae	Anaerobic, without spore formation, motile with subpolar flagellum, coccobacillus or ovoid shaped, in pairs or in short chains, mesophilic, Gram (+)	GIT of human and animal. Plant, soil and aquatic samples	Catalase (+), urolithins (+)	*G.p.* have been implicated as a cause of ulcerative colitis, liver and anal abscesses [112] and systemic bacteraemia [109]. Urolithins are relevant for the development of novel probiotics, functional foods, and food complements, especially for people with metabotype 0 who are unable to produce bioactive urolithins [85, 86]
Helicobacter pullorum	Microaerophile, nospore-forming, motile, slightly curved rod with a single polar flagellum that is non-sheathe, mesophilic or thermophilic, Gram (-)	GIT of human and animal. Plant, soil and aquatic samples	Catalase (+)	*Hp* is associated with hepatobiliary and gastrointestinal diseases in chickens and humans [15]. *H.p.* is able to tolerate high bile stress, variation in expression of certain bile stress response proteins, and oxidative. Its DNA was detected in livers from patients with primary sclerosing cholangitis, cirrhosis, and hepatocellular carcinoma. Few data are currently available on the incidence of antibiotic resistance of *H.p.* [45]

Table 5 (continued)

Name	Morphology and growth conditions	Global distribution of 16s sequence	Selected activity	Beneficial/non-beneficial impact for human and animal health (literature)
Intestinimonas timonensis	Anaerobic, no-spore-forming, no-motile, rod-shaped, mesophilic, Gram (-)	GIT of human	Catalase (-), oxydase (-), acetic acid (+), butyric acid (+), propionic acid (+)	Genome analysis indicates the ability to utilise starch, sulphur and l-serine and to produce l-cysteine and riboflavin (vit B2) [2, 26]
Lactobacillus crispatus, *L. gallinarum*, *L. helveticus*	Aerotolerant anaerobe or microaerophil; no-spore-forming, no-motile, rod-shaped, mesophilic or thermophilic (*L.h.*), Gram (+)	Vaginal discharge (*L.c.*), GIT of human and animals. Plant, soil and aquatic samples	Catalase (-), lactic acid (+), additionally hydrogen peroxide (+) (*L.c.*), indole-3-lactic acid (+) (*L.g.*) and butyric acid (+) (*L.h.*)	*L.c.* effectively treats bacterial vaginosis if used alone or alongside antibiotic treatment if an infection had already arisen [9, 92, 94]. *L.c.* is a major component of the chicken GIT microbiota [9]. *Lg* modulates the gut microbiota and produces anticancer metabolites to protect against colorectal tumorigenesis (Sugimura et al. 2021). Their presence reduces the count of *E. coli* O157 excreted in faeces. Indole-3-lactic acid has anti-inflammatory properties. *Lg* is most persistent in the ileum and ceca due to its sensitivity to bile [33, 92]. *Lg* effectively adheres to chicken LMH epithelial cell lines in vitro and can strongly colonise the gastrointestinal tract of broiler chickens in vivo [55, 92]. *L.g.* can reduce colonization of the cecum by C. jejuni [5]. *L.h.* has higher proteolytic activity than most other lactobacilli [22, 35, 97], reduces blood pressure without adverse effects, improves sleep in patients aged 60–81 years, reduces the length of upper respiratory tract illnesses, has a positive effect on calcium metabolism in women between the ages of 50–78, decreases parathyroid hormone, associated with bone loss and with *Bifidobacterium longum*, taken in combination, reduces symptoms of anxiety and depression [21, 61]

Table 5 (continued)

Name	Morphology and growth conditions	Global distribution of 16s sequence	Selected activity	Beneficial/non-beneficial impact for human and animal health (literature)
Ligilactobacillus salivarius		GIT of human and animals, oral cavity of human, porcine and avian. Plant, soil and aquatic samples	Catalase (-), ferment hexoses to lactic acid on EMP pathway, or to lactic acid, acetic acid, ethanol on pentose phosphate pathway, some strains can produce L(+) lactic acid and D(−) isomer	*L.s.* relieves flatulence in individuals suffering from irritable bowel syndrome [69], inhibits pathogens, helps treat inflammatory diseases hereby demonstrating therapeutic benefit in the management of pancreatic necrosis [21, 24]. Symptoms of atopic dermatitis disappear in some children in the presence of *L.s.* [66]
Limosilactobacillus urinaemulieris	Microaerobic, mesophilic/ or thermophilic, Gram (+)	GIT of animals, human urinary tract. Plant, soil and aquatic samples	Lactic acid (+), acetic acid (+), ethanol (+)	[48, 49, [50]
Mediterraneibacter glycyrrhizinilyticus	Anaerobic, no-spore-forming, nomotile, rod-shaped, mesophilic, Gram (+)	GIT of human and animal. Plant, soil and aquatic samples	Catalase (-)	[84, 99]
Megamonas funiformis, *M. hypermegale*, *M. rupellensis*	Anaerobic, nonspore-forming, nonmotile, large rods with or without a central, subterminal or terminal swelling, in young plate cultures, cells consist of fairly homogeneous-sized, mesophilic, Gramme (-) or Gram (-) or variable (*M. hypermegale*, *M. rupellensis*)	GIT of human and animal. Plant, soil and aquatic samples	Catalase (-), oxydase (-), acetic acid (+), propionic acid (+) (*M.f.*, *M.r.*), lactic acid (+) (*M.f.*, *M.h.*), succinic acid (+) (*M.f.*), butyric acid (+) (*M.h.*)	The amount of *M.f.* [83, 102] h. [88] i r. [18] affects the concentration of SCFAs in the intestine, especially *M.h.* which leads to skewed immune function in Behcet's disease patients [88]
Mucispirillum schaedleri	Anaerobic, no-spore-forming, curved to spiral rods with single, unsheathed, bipolar flagella, mesophilic, Gram (-)	GIT of human and animal. Plant, soil and aquatic samples	Catalase (+), oxydase (+), halophile	*M.s.* is causally linked to the development of Crohn's disease-like colitis in immunodeficient mice [79]. *SM* is resistant on oxidative stress and can modify gene expression in host mucosal tissue and participate in inflammation [54]
Neglectibacter timonensis	Anaerobic, no-spore-forming, nomotile, rod-shaped, occur in pairs, mesophilic, Gram (+)	GIT of human and animal. Plant, soil and aquatic samples	Catalase (+)/(-), oxydase (-), halophile	[115]
Oscillibacter massiliensis	Anaerobic, no-spore-forming, nomotile, rod-shaped, mesophilic, Gram (-)	GIT of human and animal. Plant, soil and aquatic samples	Catalase (-), oxydase (-)	[64, 103]
Phascolarctobacterium faecium	Anaerobic, no-spore-forming, nomotile, mesophilic, Gram (-)	GIT of human and animal. Plant, soil and aquatic samples	Acetic acid (+), propionic acid (+)	*Pf* count are changed by adding cruciferous vegetables to the diet. The level of intestinal *P.f.* may be different during human life. The colonisation rate in infants is significantly low for those aged 10–30 years old, 30–60 years old adults, and elders [111]

Table 5 (continued)

Name	Morphology and growth conditions	Global distribution of 16s sequence	Selected activity	Beneficial/non-beneficial impact for human and animal health (literature)
Phocaeicola coprocola, *P. dorei*, *P. massiliensis*, *P. plebeius*	Anaerobic, no-spore-forming, no-motile, rod-shaped, mesophilic, Gram (-)	GIT of human and animal. Several reported cases of human blood contamination (*P.c.*), one asymptomatic case found in blood (*P.m.*). Common in indigenous Japanese *(P.p.)*. Plant, soil and aquatic samples	Catalase (-)	The 16 S rRNA gene sequence analysis allowed to prepare a description of: *P.c.* [34] *P.d.* [8, 34] d m. [30, 34]. *P.p.* digests porphyran, a polysaccharide derived from Porphyra seaweed (nori), which humans are unable to digest on their own [38]
Ruthenibacterium lactatiformans	Anaerobic, no-spore-forming, no-motile, rod-shaped, occur singly and in pairs, mesophilic, Gram (-)	GIT of human and animal. Plant, soil and aquatic samples	Catalase (-), lactic acid (+), succinic acid (+), acetic acid (+)	*R.l.* reduces inflammation and stimulates CTL (cytotoxic T-lymphocyte associated protein) [89]. The result may point to a noninvasive method of increasing the therapeutic index of immunotherapy with diet or probiotics [32]
Subdoligranulum variabile	Anaerobic, no-spore-forming, no-motile, rod-shaped, mesophilic, Gram (+)	GIT of human and animal. Plant, soil and aquatic samples	Catalase (-), oxydase (-), butyric acid (+), formic acid (+)	*S.v.* forms a consortium of bacterial species commonly present in the intestine and participates in the hydrolysis of dietary fiber [16]. *S.v.* correlates positively with fecal microbiota richness, HDL-cholesterol and adiponectin levels as negative correlates with fat mass, adipocyte diameter and leptin, insulin, CRP and IL-6 levels [104]

multocida, *Riemerella anatipestifer*, *Salmonella enterica* and *Staphylococcus aureus* [5, 31, 57, 74, 104]. The competitive exclusion of unfavorable strains depends on the production of lactic acid, hydrogen peroxide and bacteriocins, as well as the ability of the gut strains to permanently colonize the intestine [76]. Lund et al. [56] indicated that the poultry farm environment therefore plays a key role in the recruitment and development of the gut microbiota on the example of *Gemmiger gallinarum*, *Gorbachella massiliensis*, *Faecalibacterium hattorii*, *F. prausnitzii* and *Subdoligranulum variabile*. *Faecalibacterium gallinarum* and *Subdoligranulum variabile* were found as the most abundant sequences in this work, with an average share of 4.4 to 12.3% among all sequences. They are described in the literature as strictly anaerobic, mesophilic, non-spore-forming, non-motile, rod-shaped, Gram-positive (*S. variabile*, *G. gallinarum*) or Gram-negative (*G. massiliensis*, *F. gallinarum*, *F. hattori*), host-associated and found in the digestive system (cecum, ileum) of birds and mammals, including human. They are associated with health-promoting activity [23]. Their major end-product in M2G medium is n-butyrate. Furthermore, bacteria are mostly cathalase-negative, except for *G. gallinarum*, and can produce formic (*S. variabile*, *F. hattori*) as well as lactic acid (*G. gallinarum*, *F. hattori*) [26, 37, 40, 82, 114]. Diatomite has already been a material for research on the health condition of chicken flocks. This mineral was applied during composting of chicken faeces and its inhibitory effect on *Firmicutes* and *Proteobacteria* communities was confirmed [75].

The increasing research reveals several beneficial effects and therapeutic properties of butyrate-producing bacteria for both humans and animals. A summary of the basal metabolism, probiotic qualities and habitat of selected strains determined in this study is summarised in Table 4. The studies of Pattar et al. [71] indicate that the addition of diatomaceous earth to feed contaminated with aflatoxin B1 and ochratoxin A decreased the toxic effects of mycotoxins. Therefore, there was an improvement in body weight gain, feed conversion ratio, and feed intake, and a reduction in mortality. The addition of this mineral to the broilers diets also had a positive effect on the higher participation of breast muscles and lower fat content of broiler carcasses. Furthermore, the broilers thigh bones were characterized by a higher strength as compared to the control group [42, 108]. In turn, in the research of Isabirye at al. [44] it has been shown the efficacy of diatomite in the treatment of chicken against *Ascaridia galli* and *ectoparasites*. Birds infected *with A. galli* treated with diatomite supplement showed reduce intestinal parasitic load and better controlling mites in chicken.

Conclusions

Diatomite used in a mixture with bentonite (DBM) significantly alters the microbiome, which may have implications in the context of the studied environment and the health-promoting properties of food. Our analysis identified bacterial species not previously found in the intestinal contents of chickens, expanding our knowledge of the complex interactions in this microbial community. We observed that the dietary intervention not only affected the abundance and diversity of bacterial species but also led to the emergence of potentially beneficial or harmful taxa. These findings highlight the intricate and potentially consequential relationship between diet, specifically diatomite supplementation, and gut microbiota composition. The presented results constitute a part of a larger analysis, demonstrating that the use of diatomite-bentonite mixture to the broiler chicken diet in an amount of 1% resulted in a favourable increase in body weight gain, with a tendency to higher overall final body weight of the birds (Micek et al. unpublished).

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Authors' contributions
E.W. and M.A. wrote the main manuscript text, S.M. and K.S. prepared Figs. 1, 2, 3, 4 and 5. Other authors: P.M., K.G., M.L., M.T., D.W., J.K., A.W-P., G.K. participated in the study (laboratory analyses). All authors reviewed the manuscript.

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Data availability
Sequence data that support the findings of this study have been deposited in the National Library of Medicine NCBI with the promary accession code PRJNA1104621.

Declarations

Consent for publication
Not applicable.

Ethics approval and consent to participate
The study was conducted according to the guidelines of the Declaration of Helsinki. All the animals were treated according to the principles stated in Directive 2010/63/EU, regarding the protection of animals used for experimental and other scientific purposes, enforced in Poland by Legislative Decree 266/2015. According to EU/PL law, approval from an animal ethics committee was not required, and the birds were not subjected to any invasive procedures. All broiler chicken rearing procedures were conducted as laid out in the Ross 308 broiler management following Directive [21]/43/EC.

Competing interests
The authors declare no competing interests.

Author details
[1]Department of Infectious Diseases and Public Health, University of Agriculture in Krakow, Al. Mickiewicza 21, Krakow 31-120, Poland. [2]Department of Nutrition, Animal Biotechnology, and Fisheries, University of Agriculture in Krakow, Al. Mickiewicza 24/28, Krakow 30-059, Poland. [3]SPARK-TECH, Sp. z o.o., Rynek Główny 28, Krakow 31-010, Poland. [4]Department of Agricultural

and Environmental Chemistry, University of Agriculture in Krakow, Al. Mickiewicza 21, Krakow 31-120, Poland. [5]Department of Zoology and Animal Welfare, University of Agriculture in Krakow, Al. Mickiewicza 24/28, Krakow 30-059, Poland. [6]Department of Genetics, Animal Breeding and Ethology, University of Agriculture in Krakow, Al. Mickiewicza 24/28, Krakow 30-059, Poland. [7]Doctoral School of Exact and Natural Sciences, Jagiellonian University, Lojasiewicza 11, Krakow 30-348, Poland. [8]Jagiellonian Centre for Experimental Therapeutics, Jagiellonian University, Bobrzynskiego 14, Krakow 30-348, Poland. [9]Specialized Mining Company "Górtech" Sp. z o.o, ul. Wielicka 50, Krakow 30-552, Poland.

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