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Intestinal Microbiota of Indigenous Peoples of the North: a Systematic Review

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ABSTRACT

BACKGROUND: The microbiota of the indigenous population of the North may play a pivotal role in the development of the polar (northern) type of metabolism supporting increased energy demands and maintaining body homeostasis in extreme cold climates. However, this area remains relatively understudied. Sequencing of bacterial 16S rRNA allows for establishing the full taxonomic composition of microbial communities, thereby facilitating novel insights into the interplay between microbiota, environmental conditions, and the formation of health in different populations.

AIM: The aim of this review is to evaluate the factors and principles of microbiota development in extreme climatic conditions and its potential impact on health in the indigenous peoples of the North.

MATERIALS AND METHODS: A systematic review was conducted based on the 2020 PRISMA guidelines. Original studies were searched for across the PubMed, eLibrary, and Google Scholar databases using Russian keywords “микробиота кишечника” (“intestinal microbiota”), “Север” (“North”), and English “gut microbiome,” “16S rRNA,” and “Arctic.”

RESULTS: Having filtered the results of the primary selection of articles in accordance with the search criteria, five publications were identified that presented the results of intestinal microbiota 16S rRNA studies in Canadian Inuit, Alaska Natives, and Yakuts of the Sakha Republic (Yakutia). The intestinal microbiota of native residents of the North differs is characterized by inter- and intra-population variability in the diversity and taxonomic composition. Despite similar climatic conditions and dietary patterns, microbiota composition of different Northern populations reflects differences in traditional activities, dietary habits, and surrounding animals.

CONCLUSION: Results of available studies are insufficient to form a comprehensive understanding of the northern microbiome and its role in maintaining the health of the indigenous peoples of the North. Nevertheless, the composition of the intestinal microbiota of the northern populations is shown to be diverse and favorable for the metabolic health; further studies are required to identify the mechanisms of the metabolic health formation in cold climate conditions.

Keywords: gut microbiome; 16S rRNA; North; adaptation; cold; Inuit; Yakut; Sakha.

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Кишечная микробиота коренных народов Севера (систематический обзор)

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АННОТАЦИЯ

Обоснование. Микробиота коренного населения Севера может иметь важное значение в формировании полярного (северного) типа метаболизма, направленного на обеспечение повышенных энергетических потребностей и сохранение гомеостаза организма в экстремальных условиях холодного климата, однако эта область остаётся малоизученной. Секвенирование 16S рРНК бактерий позволяет установить полный таксономический состав микробного сообщества, что открывает перспективы для изучения связи микробиоты с условиями окружающей среды и формированием здоровья в разных популяциях.

Цель. На основе обзора литературных данных оценить факторы и принципы формирования микробиоты в экстремальных климатических условиях и её возможную роль в формировании здоровья у коренных народов Севера.

Материалы и методы. Систематический обзор проведён на основе рекомендаций PRISMA (2020 г.). Поиск источников оригинальных исследований осуществляли в базах данных PubMed, eLibrary и Google Scholar по ключевым словам: «микробиота кишечника», «Север», «gut microbiome», «16S rRNA», «Arctic».

Результаты. После фильтрации результатов первичного отбора статей в соответствии с критериями поиска было выявлено 5 публикаций, в которых представлены результаты исследования 16S рРНК кишечной микробиоты канадских инуитов, коренных жителей Аляски, якутов Республики Саха (Якутия). Кишечная микробиота представителей народов, проживающих в условиях Севера, отличается по разнообразию и таксономическому составу как от других групп населения, так и между собой. Несмотря на имеющееся сходство климатических условий и типа питания, различия в традиционных занятиях, рационе и видах окружающих животных находят отражение в составе микробиоты разных популяций Севера.

Заключение. Проведённые к настоящему времени исследования недостаточны для формирования цельного представления о северном микробиоме и его роли в сохранении здоровья коренных народов Севера. Тем не менее показано, что состав кишечной микробиоты популяций Севера разнообразен и имеет черты, благоприятные для метаболического здоровья, что требует дальнейшего изучения для выявления механизмов формирования метаболического здоровья в условиях холодного климата.

Ключевые слова: кишечный микробиом; 16S рРНК; Север; адаптация; холод; инуиты; якуты; саха.

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北方原住民的肠道微生物群（系统综述）

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摘要

背景。北方原住民的肠道微生物群可能在形成极地（北方）代谢类型中具有重要作用。这种代谢类型旨在满足高能量需求并在寒冷气候的极端条件下维持机体稳态。然而，该领域的研究仍然十分有限。通过16S rRNA细菌测序可以揭示微生物群的完整分类组成，为研究微生物群与环境条件的关系以及不同群体健康状况的形成机制提供了前景。

研究目的。基于文献数据综述，评估在极端气候条件下形成肠道微生物群的因素与原则，并分析其在北方原住民健康维持中的潜在作用。

材料与方法。本系统综述遵循PRISMA（2020年）指南。研究人员通过关键词“肠道微生物群”、“北方”、“gut microbiome”、“16S rRNA”、“Arctic”，在PubMed、eLibrary和Google Scholar数据库中搜索相关原始研究文献。

结果。通过筛选符合搜索标准的文章，共发现5篇文献。这些文献涵盖了加拿大因纽特人、阿拉斯加原住民以及萨哈共和国（雅库特）雅库特人肠道微生物群的16S rRNA研究结果。结果表明，居住在北方地区的原住民的肠道微生物群在多样性和分类组成上不仅与其他人群不同，也因各自的传统活动、饮食结构和动物资源的差异而彼此不同。尽管气候条件和饮食类型存在一定相似性，这些差异仍显著。

结论。目前的研究不足以全面了解北方原住民的肠道微生物群及其在健康维持中的作用。然而，现有文献表明，北方原住民的肠道微生物群具有多样性，并具备有利于代谢健康的特征。这一发现表明，需要进一步研究，以揭示寒冷气候条件下代谢健康形成的潜在机制。

关键词：肠道微生物群；16S rRNA；北方；适应；寒冷；因纽特人；雅库特人；萨哈。

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BACKGROUND

The relationship between gut microbiota, environmental conditions, and human health has been actively studied in recent years thanks to the development of modern methods for 16S rRNA sequencing of bacteria. Studies showed that diet, living conditions, and ethnicity had the greatest influence on the diversity and composition of gut bacteria [1–4]. These relationships are based on metabolic pathways formed by complex functional interactions between the microbial community, regulatory systems of the host organism, and the environment.

The main substrates for metabolism by microorganisms in the large intestine include complex polysaccharides and proteins that are stable and poorly absorbed in the small intestine. Anaerobic fermentation of simple carbohydrates formed during the hydrolysis of polysaccharides produces short-chain fatty acids (SCFAs), such as acetate, propionate, and butyrate, with the first of them being the most abundant product of gut microbiota. SCFAs are crucial for maintaining intestinal barrier function and can be used as an energy source [5]. The most studied positive effect is that of butyrate, which has anti-inflammatory, antioxidant, and antitumor properties. Acetate is less studied; however, it is known to be used as a metabolite for other tissues in the body and have a positive effect on the protective functions of the intestine [6]. Gut microbiota can also produce harmful products. For example, phenol, hydrogen sulfide, isobutyric acid, and isovaleric acid can be formed from amino acids during anaerobic fermentation of proteins. Metabolites of branched-chain fatty acid fermentation also produce substances that can negatively affect the health of the host and cause ulcers, colitis, or cancer [7].

In the era witnessing worldwide globalization, the microbiota of populations maintaining traditional diets and lifestyles is a compelling topic for research [8]. For example, studies of populations in Burkina Faso, Tanzania, Mexico, and Venezuela showed a more diverse microbiota compared with industrialized Western populations [9–12]. Severe cold climates have fostered a distinct polar (northern) metabolism among indigenous peoples of the North. Based on the dietary predominance of proteins and lipids, this metabolism type directly addresses elevated energy requirements and thermogenic needs [13, 14]. Despite global transformations, traditional diet and lifestyle continue to occupy a substantial niche in the lives of indigenous peoples of the North. Formed in these conditions, the microbiota has distinct characteristics that differentiate it from that of other populations and exert influence on host health.

The study aimed to assess the factors and principles of microbiota formation in extreme climatic conditions and its possible role in health of indigenous peoples of the North based on a literature review.

MATERIALS AND METHODS

We conducted a systematic review of the literature using ScR methodology (scoping review) based on the PRISMA recommendations [15]. We searched for sources using keywords in the *eLIBRARY.RU*, *PubMed*, and *Google Scholar* databases. Keywords for sources included *микробиота* (*microbiota*) and *Север* (*North*) for Russian-language sources; *gut microbiome*, *Arctic* or *gut microbiome*, *Inuit* for the *PubMed* database in English; *микробиота кишечника* (*gut microbiota*), *Север* (*North*) for *Google Scholar* in Russian; and *gut microbiome*, *16S rRNA*, *indigenous people*, *Arctic* in English. We independently reviewed the titles and abstracts of the publications for compliance with the inclusion criteria; any disagreements were resolved through negotiations. We also performed a manual search for additional sources in the reference lists of the articles we found.

The inclusion criteria were the following: 1) language: Russian, English; 2) study population: indigenous peoples of the North and the Arctic (the Inuit, the Yakuts, other indigenous peoples of the North); 3) age of participants over 18 years; 4) original studies of gut microbiota; 5) study method: 16S rRNA sequencing of bacteria. Exclusion criteria: studies of the gut microbiome of animals or children, review articles. The last search was conducted on April 22, 2024.

The initial screening using the above search queries yielded 13 publications from the *eLIBRARY.RU* database, 29 publications from the *PubMed* database using the Humans filter, 1,170 results for the Russian-language query, and 14,700 results for the English-language query from the *Google Scholar* database. After evaluating titles and abstracts, we excluded duplicates and publications that did not meet the inclusion criteria. After filtering, five sources remained. The stages of article selection are presented in Fig. 1.

The taxonomy of microorganisms in the article is given in accordance with the latest version of the taxonomic database of the National Center for Biotechnology Information (NCBI) (https://www.ncbi.nlm.nih.gov/Taxonomy/Browser/wwwtax.cgi). Earlier versions of taxon names are given in brackets.

RESULTS

Studies to investigate the gut microbiota of indigenous peoples of the North are scarce; 16S rRNA data of Canadian Inuit, Alaska Natives, and the Yakuts were published (Table 1).

Girard et al. compared the gut microbiome of a small Canadian Arctic Inuit population and Caucasian individuals from Montreal, within Canada’s temperate climate zone [16]. The majority of Inuit adhered to a traditional Inuit diet and consumed arctic char, reindeer meat, marine mammals, or raw game every day, whereas the Caucasian individuals from Montreal adhered to a Western diet. In terms of taxon diversity and representation, the gut microbiota profile of Nunavut and Montreal residents was similar and close to other Western populations, while differing significantly from residents of Burkina Faso, Tanzania, and Venezuela with traditional lifestyles.

To identify Nunavut Inuit microbiota biomarkers, we used linear discriminant analysis, which showed the following

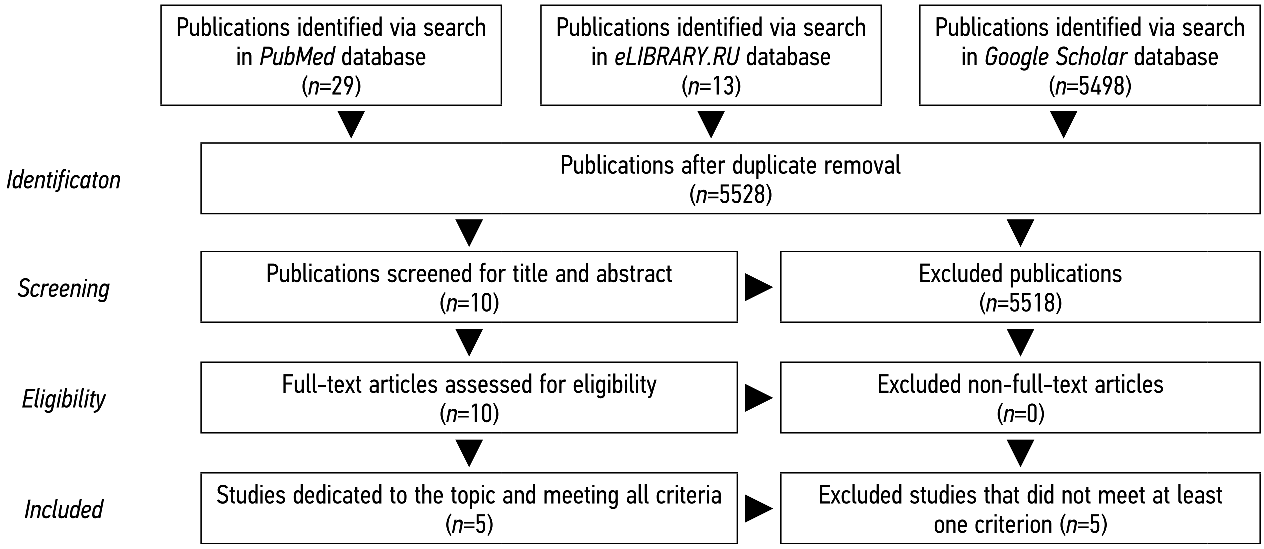

Fig. 1. Flow-chart for selection of articles.

taxa: representatives of the *Bacillota* (formerly *Firmicutes*) phylum, i.e. the *Lachnospiraceae* family, which ferment polysaccharides to form SCFAs, and the *Peptococcus* genus, which metabolizes peptone and amino acids to form fatty acids, synthesizing hydrogen sulfide, acetic, lactic, citric, isovaleric, and other acids; representatives of the *Bacteroidota* (formerly *Bacteroidetes*) phylum, i.e. the *Bacteroidales* order; poorly studied representatives of the *Pseudomonadota* (formerly *Proteobacteria*) phylum such as the *Betaproteobacteria* class and the *Bilophila* genus, which produce hydrogen sulfide from taurine; the *Cyanobacteriota* phylum. *Lachnospiraceae*, *Betaproteobacteria*, and *Bilophila* representatives were also identified as biomarkers for the Inuit diet. The authors identified differences between the two populations at the strain level. Representatives of the *Prevotella* genus (*Bacteroidota* phylum) were found in both Montreal and Nunavut samples; however, seven operational taxonomic units (OTUs) were associated with the Western diet, while only one was associated with the Inuit one. Differences in OTUs were also detected within the *Akkermansia* genus of the *Verrucomicrobiota* (formerly *Verrucomicrobia*) phylum, which was found in both populations.

A further study investigated changes in the gut microbiota of the Inuit from the same region of Canada over time during one year [17]. The taxonomic profile of the Inuit microbiota in this case differed from previous results. However, some taxa were consistent with those previously identified. In this study, the following were identified as markers of the Inuit microbiota: representatives of the *Bacillota* (formerly *Firmicutes*) phylum such as the *Erysipelotrichales* order, which is associated with lipid metabolism; the *Megasphaera* genera, which produce SCFAs; *Eubacterium*, *Lactobacillus*, *Peptococcus* with a wide range of metabolic functions; representatives of the *Bacteroidota* (formerly *Bacteroidetes*) phylum such as *the Bacteroidales* order and the Prevotella genus, which also produce SCFAs; representatives of the *Actinomycetota* (formerly *Actinobacteria*) phylum such as the *Bifidobacteriaceae* family, which produce lactate and support the intestinal barrier, the Coriobacteriales order, which converts bile salts and steroids in the intestine and activates dietary polyphenols; representatives of the Fusobacteriota (formerly Fusobacteria) phylum such as the Fusobacteriales order, which produce butyric acid, and others.

There were no obvious seasonal changes in the microbiomes of participants from Nunavut or Montreal. Intraindividual microbial diversity varied more in Nunavut residents than in Montreal residents, consistent with a more diverse and highly individualized diet in Nunavut. More diverse

Table 1. Studies of gut microbiota in populations of indigenous peoples of the North

Northern population, *n*	Comparison population, *n*	Source
Inuit of Canada, *n*=19	Europeans of Montreal, *n*=26	[16]
Inuit of Canada, *n*=15	Europeans of Montreal, *n*=9	[17]
Inuit of Canada, *n*=275	Non-industrial, *n*=73 Industrial, *n*=104	[18]
Alaska natives, *n*=32	Rural people of Africa, *n*=21	[20]
Yakuts, Russian Federation, *n*=11 (healthy)	Residents of Moscow, *n*=101	[22]

microbiomes tended to have a stable profile over time. The study found that traditional foods (raw fish, raw game meat, and fermented meat) influenced the microbiome profile in the Inuit. Based on the two studies, the authors noted that modifications towards a Western diet in the Inuit contributed to decreased microbiome diversity and seasonal variability [17].

The gut microbiota of the Inuit youth from Nunavik, another northern province of Canada, was investigated by Abed et al. [18]. The study participants also consumed traditional foods such as marine and land mammals, fish, shellfish, and wild birds and plants. These data were assessed in comparison with industrial and non-industrial populations selected from MetagenomicData R [19]. The Nunavik Inuit were found to have a homogeneous microbiome, as evidenced by low interindividual diversity but high intraindividual diversity.

The genomic microbiome content in the Nunavik Inuit was shown to be distinct from other previously studied populations, including that of the Nunavut Inuit. Although the Nunavik diet is rich in animal products, the predominant species in their microbiome were saccharolytic and produced SCFAs, mainly butyrate. Other metabolic products of the Inuit microbiome included acetate and propionate. Two species of bacteria, *Ruminococcus bromii* and *Bifidobacterium adolescentis*, used starch as an energy source and broke it down into acetate and lactate. The main metabolic pathways in the Inuit metagenomes included the biosynthesis of amino acids such as the synthesis of L-isoleucine from threonine, L-valine, precursors of phenylalanine, tryptophan, tyrosine, and folates. The authors suggested that protein fermentation (in the diet) may also significantly influence the gut microbiome profile of the Nunavik Inuit. Overall, taxonomic and functional features suggested that the Inuit gut microbiome was able to adapt to various factors and maintain host health. Although defining a healthy or robust microbiome is difficult, some characteristics of the Nunavik gut microbiome (such as high intraindividual diversity, dominance of SCFA-producing bacteria [primarily butyrate], and a potential capacity for resilience against environmental stress such as antibiotics) contribute to the maintenance of host homeostasis and improve health outcomes within the Arctic environment.

In 2020, a study was conducted to compare the gut microbiota of Alaska Natives with rural Africans in relation to the high risk of colorectal cancer in rural Africans [20]. Healthy Alaska Natives had lower intraindividual diversity (alpha diversity) of their microbiota compared with rural South Africans. Increased levels of *Actinomycetota* (formerly *Actinobacteria*) and *Verrucomicrobiota* (formerly *Verrucomicrobia*) were seen. The content of saccharolytic bacteria families such as *Oscillospiraceae* (formerly *Ruminococcaceae*) and *Prevotellaceae* was reduced, while the content of *Lachnospiraceae* (due to the *Blautia* and *Lachnoclostridium* genera) was increased. The *Escherichia*, *Shigella,* and *Bifidobacterium* genera were also common in the gut of Alaskans. Choline and formate were major intestinal metabolites in Alaska Natives, while Africans had more diverse metabolic pathways. Alaska Natives were shown to have high levels of 7-α-dehydroxylating bacteria, which are involved in bile acid metabolism and production of secondary bile acids, thus maintaining gut health and reducing the risk of metabolic disease [21].

As for indigenous peoples of the North of Russia, a study was conducted to investigate the gut microbiota of a small population of the Yakuts [22]. The Yakuts live in a vast territory of northeastern Russia in an extreme, sharply continental climate and, unlike the indigenous peoples of North America, are primarily pastoralists, raising cattle and horses. Hunting and fishing also play a significant role in their traditional way of life. The Yakut diet is based on various dairy products, meat of domestic and wild animals, and lake fish. A pilot study to evaluate the feces of 11 healthy representatives of the Yakuts showed that their gut microbiota differed from that of Moscow residents in terms of diversity and structure of taxonomic composition. Intraindividual diversity was statistically significantly higher in the Yakuts than in urban residents. An increased level of 11 genera and a decreased level of 9 genera of microorganisms were seen in the microbiota of the Yakuts. In the Yakut samples, *Bacillota* (formerly *Firmicutes*) was the predominant phylum (79%), and the ratio of *Bacillota* (*Firmicutes*) to *Bacteroidota* (*Bacteroidetes*) was 9.4 to 1.0. At the phylum level, a significant increase in the proportion of the *Actinomycetota* (formerly *Actinobacteria*) was found. Among representatives of *Bacillota* (formerly *Firmicutes*), an increased level of the *Erysipelotrichales* order was found, including the *Coprobacillaceae* family (in the Yakuts, *Catenibacterium* were found). They were associated with immunogenicity, but their role remains unclear. There were also producers of active cellulases such as bacteria of the *Oscillospiraceae* family (formerly *Ruminococcaceae*) and degraders of plant materials such as representatives of the *Lachnospiraceae* family (*Blautia* genus), which also actively ferment fats. The optimal balance of these bacteria regulate carbohydrate metabolism and reduce the risk of metabolic disease. Anaerobic conditions in the intestine are also maintained by facultative aerobic bacteria of the *Bifidobacterium* genus and the *Coriobacteriaceae* family, which belong to the *Actinomycetota* (formerly *Actinobacteria*) phylum; they absorb oxygen from the blood.

The microbiota of the Yakuts had some specific features. In particular, *Ligilactobacillus ruminis* (formerly *Lactobacillus ruminis*), an atypical representative of the *Lactobacillaceae* family with unique immunomodulatory and probiotic activity, was identified, which was not found in Moscow residents. *L. ruminis* suppressed pathogenic flora by producing lactic acid and reducing the pH values [23]. *L. ruminis* suppressed pathogenic flora by producing lactic acid and reducing the pH values. *L. ruminis* strains were shown to modulate immune response by decreasing levels of some proinflammatory cytokines and increasing levels of IL8 and NF-kB. *L. ruminis* was shown to significantly improve gut microbiota diversity in mice [24]. They produce lactase, thus alleviating lactose intolerance that can be genetically identified in the Yakuts [25].

Non-pathogenic *Treponema succirifaciens* was found in the Yakut microbiome. It is common in traditional rural populations and related to transmission from animals [26]. These bacteria have an enzyme called pyruvate formate lyase to oxidize pyruvate to acetyl-CoA and formate. This involves interactions with other commensal bacterial species that decompose plant fibers. *T. succirifaciens* is very sensitive to antibiotics and, therefore, cannot be found in the urban population. This suggests the beneficial influence of the traditional pastoral lifestyle on the microbiota of the modern indigenous peoples of Yakutia.

Microbiota diversity and profile in the indigenous peoples of the North are presented in Table 2.

DISCUSSION

Microbiota under cold stress conditions

The ecological niche of residence and biotic interactions with the environment have an obvious modulating effect on the gut microbiota profile. Under cold exposure, metabolic pathways are remodulated to maintain thermogenesis, where gut microbiota plays an important role. The review showed that the gut microbiota of the populations of the North has not been well studied. However, in recent years, animal studies allowed understanding the principles of interactions between the microbiota and the host organism during cold stress [27–29]. Chevalier et al. [27] showed that cold exposure in mice to develop cold tolerance led to changes in the microbiota taxonomic profile, increasing *Firmicutes* (formerly *Firmicutes*) vs *Bacteroidota* (formerly *Bacteroidetes*) ratio and almost completely depleting the *Akkermansia* genus, a representative of the *Verrucomicrobiota* (formerly *Verrucomicrobia*) phylum [27]. Increased levels of the *Bacillota* (formerly *Firmicutes*) phylum due to the *Bacteroidota* (formerly *Bacteroidetes*) with cold exposure were also shown in other studies in rodents [28, 29]. The involvement of microbiota in cold adaptation was also confirmed by experiments on transplantation of microbiota from cold-adapted mice (called “cold microbiota”), which promoted cold tolerance in control mice [27, 29].

The cold microbiota enhances the production and consumption of thermal energy through several mechanisms. Firstly, with prolonged cold exposure and transplantation of cold microbiota, the absorption surface of the epithelial layer of the small intestine increased due to physiological gut elongation and villi thickening and elongation [27, 29]. Expanded gut volume and absorptive interface facilitated increased retention of undigested organic compounds. Following microbial fermentation, these compounds generate metabolites required for synthesis of energy storage molecules (fat) as an energy reservoir. Secondly, there is a competition for the consumption of energy substrates between microorganisms and host tissues. During adaptation to cold, the host eliminates bacteria that actively consume energy resources such as SCFAs, which can provide 5–10% of a person’s energy needs [30]. Elimination of *G. Akkermansia* as an active energy consumer can serve as an example. This enhances mobilization of energy resources to ensure thermogenesis during the development of cold tolerance in mice. Thirdly, when the metagenomic reads of the microbiota from cold-exposed mice were mapped to a gut microbial gene catalogue, the gut microbiota was shown to assist the host in resisting extreme temperatures through regulating the host’s insulin pathway [29]. During adaptation of mice to cold, the microbiota promoted a shift of the brown adipose tissue phenotype to the white adipose tissue with increased generation of thermal energy [31–34]. Other aspects that regulate host energetics and thermogenesis during cold acclimation include the interaction between the microbiota, gut, and brain, which is mediated through the biosynthesis of neurotransmitters [28]. SCFAs can also be signaling molecules by acting on receptors responsible for appetite regulation, thermoregulation, and energy homeostasis [35]. Adaptation of humans to prolonged cold exposure in the North is likely to be also associated with biochemical and physiological responses associated with taxonomic changes in the microbiota profile. They may determine the specific phenotype of indigenous peoples of the North.

Effects of the diet and lifestyle on the microbiota in the North

Besides climatic conditions, the human gut microbiota is also influenced by several key factors such as nutrition and lifestyle. This can be clearly seen in ethnic groups that live in comparably similar natural and climatic conditions in the North. In the Yakuts, the taxonomic profile of the microbiota in the large intestine has been formed by the traditional way of life of livestock breeders, who use herbivores such as cattle (cows) and horses as their main source of food. The modern diet of the Yakuts contains a lot of simple carbohydrates. *Bacillota* (formerly *Firmicutes*), the predominant phylum in the Yakut microbiome, had the most diverse profile of microorganisms with the gram-positive cell wall and an ability to ferment both cellulose and complex non-starch polysaccharides. Substrate specificity and differences in fermentation products depend on the genus and species of microorganisms. Bacteria of the *Ruminococcaceae* family, which were common in the test population of the Yakuts, are known to break down plant cellulose and anaerobically ferment glucose mainly to acetate but also to propionate and butyrate. The *Lachnospiraceae*, another common family, which includes the *Blautia* and *Dorea* genera, also metabolizes glucose and other carbohydrates but does not produce butyrate. *Catenibacterium*, a member of the *Coprobacillaceae* family, showed an association with a high consumption of fermented milk products, carbohydrates, and fiber in Tibetan highlanders [36]. Levels of this bacteria were shown to

Table 2. Microbiome of indigenous peoples of the North in comparison with other populations

Population	Microbiome diversity	Features	The most significant biomarkers (top 5) and their taxonomic affiliation: domain; type; class; order; family; genus	Source
Inuit of Nunavut, Canada	No differences from Montreal Caucasian participants	Similar microbial profiles in the Inuit of Nunavut and residents of Montreal. Some poorly studied taxa found in the Inuit. Differences in species variety	*– Bacteria; Bacillota; Clostridia; Lachnospirales; Lachnospiraceae;* *– Bacteria; Bacteroidota; Bacteroidia; Bacteroidales; Muribaculaceae;* *– Bacteria; Pseudomonadota; Betaproteobacteria;* *– Bacteria; Pseudomonadota; Betaproteobacteria; Burkholderiales;* *– Bacteria; Pseudomonadota; Betaproteobacteria; Burkholderiales; Sutterellaceae; Sutterella;*	[16]
Inuit of Nunavut, Canada	No differences from Montreal Caucasian participants	Traditional Inuit foods affecting microbiome profile	*– Bacteria; Bacteroidota; Bacteroidia; Bacteroidales; Muribaculaceae;* *– Bacteria; Actinomycetota; Actinomycetes; Bifidobacteriales; Bifidobacteriaceae;* *– Bacteria; Bacillota; Bacilli;* *– Bacteria; Bacillota; Negativicutes; Veillonellales; Veillonellaceae; Megasphaera;* *– Bacteria; Bacteroidota; Bacteroidia; Bacteroidales; Prevotellaceae; Prevotella*	[17]
Inuit of Nunavik (Quebec), Canada	Intraindividual diversity of the Nunavik gut microbiome was significantly higher than in non-industrial and industrial populations	The Inuit microbiome differed from other industrial and non-industrial populations. SCFA-producing bacteria predominating in microbiome structure	*– Bacteria; Actinomycetota; Coriobacteriia; Coriobacteriales; Coriobacteriaceae; Enorma;* *– Bacteria; Bacteroidota; Bacteroidia; Bacteroidales; Prevotellaceae; Prevotella;* *– Bacteria; Bacillota; Erysipelotrichia; Erysipelotrichales; Erysipelotrichaceae; [Clostridium] innocuum;* *– Bacteria; Bacillota; Clostridia; Eubacteriales; Oscillospiraceae; Flavonifractor;* *– Bacteria; Bacillota; Clostridia; Lachnospirales; Lachnospiraceae; Enterocloster*	[18]
Alaska Natives	Lower diversity in Alaska Natives vs rural Africans	Increased levels of *Actinomycetota* (formerly *Actinobacteria*) and *Verrucomicrobiota* (formerly *Verrucomicrobia*). Low levels of saccharolytic bacteria and higher microbial capacity for converting bile acids	*– Bacteria; Bacillota; Clostridia; Lachnospirales; Lachnospiraceae;* *– Bacteria; Bacillota; Clostridia; Lachnospirales; Lachnospiraceae; Blautia;* *– Bacteria; Bacillota; Clostridia; Lachnospirales; Lachnospiraceae; Lachnoclostridium;* *– Bacteria; Actinomycetota; Actinomycetes; Bifidobacteriales; Bifidobacteriaceae; Bifidobacterium;* *– Bacteria; Pseudomonadota; Gammaproteobacteria; Enterobacterales; Enterobacteriaceae; Escherichia-Shigella*	[20]
Yakuts of the Russian Federation	Intraindividual diversity of the microbiome in healthy Yakuts higher than in Moscow residents	The microbiota of the Yakuts differs from that of the Inuit and residents of central Russia. High *Bacillota* (*Firmicutes*) to *Bacteroidota* (*Bacteroidetes*) ratio. Increased levels of *Actinomycetota* (formerly *Actinobacteria*) phylum	*– Bacteria; Bacillota; Erysipelotrichia; Erysipelotrichales; Coprobacillaceae; Catenibacterium;* *– Bacteria; Bacillota; Bacilli; Lactobacillales; Lactobacillaceae; Lactobacillus;* *– Bacteria; Actinomycetota; Coriobacteriia; Coriobacteriales; Coriobacteriaceae;* *– Bacteria; Bacillota; Clostridia; Eubacteriales; Oscillospiraceae; Ruminococcus;* *– Bacteria; Bacillota; Clostridia; Lachnospirales; Lachnospiraceae*	[22]

increase in people with obesity or those who consume animal fats. Other authors found a positive correlation between *Catenibacterium* and *Ligilactobacillus ruminis* (formerly *Lactobacillus ruminis*) and consumption of omega-6 fatty acids with food [37].

We can assume that the traditional Yakut diet, which is rich in carbohydrates and animal fats, is balanced by a microbiota shift towards increased *Bacillota* (formerly *Firmicutes*) levels. Indirectly supported by murine cold-exposure studies showing Bacillota proliferation, this shift can optimize energy balance in cold environments via enhanced caloric extraction. An increased ratio of *Bacillota* (*Firmicutes*) to *Bacteroidota* (*Bacteroidetes*) is considered to be associated with an increased risk of obesity. This association was explained by the lack of competition for energy sources produced by the microbiota between the microorganisms and the host [38]. However, the association of this parameter with obesity is considered debatable [39]. The concepts of the main enterotypes proposed by Wu et al. should probably also be updated [40].

Unlike the Yakuts, the life of the Inuit is connected with the sea, and their diet is based on marine carnivorous mammals, which can stay underwater for a long time and eat small marine animals, such as fish, mollusks, crustaceans, etc. Metabolic consequences of their underwater swimming include the accumulation of large amounts of glycogen in the muscles, which is used to generate energy by glycolysis during diving [41]. The Inuit diet, which is rich in protein and fat, results in increased levels of the *Bacteroidota* (formerly *Bacteroidetes*) phylum in the gut, making their microbiota closer to that of Western populations. In general, the gut microbiota of the northern populations increasingly resembles that of urbanized communities. This convergence is attributed to dietary transitions and the incorporation of industrially processed foods into the diets of the northern populations.

Microbiota in people in close contact with animals

These microbiome features may be associated with the microbial environment of the Inuit and the Yakuts, in particular their close contact with livestock or game animals.

The microbiota of the Inuit included high levels of anaerobic microorganisms such as *Bacteroidota* (formerly *Bacteroidetes*) and *Pseudomonadota* (formerly *Proteobacteria*) phyla. Seawater is a source of the *Pseudomonadota* (formerly *Proteobacteria*) phylum [42]. The Inuit eat marine carnivores that can stay underwater for long periods and feed on small marine animals. Most distal gut microbiome samples from many marine mammals, including herbivorous sirenians and carnivorous pinnipeds (seals, walruses, and sea lions), were predominantly composed of *Bacteroidota* (formerly *Bacteroidetes*), which can ferment starchy polysaccharides and proteins [43]. Here we can see some similarities in the gut microbiota profiles of humans and game animals.

Similarities in the gut microbiota profile were also found for the Yakuts and the rumen of ruminants (cattle). A significant proportion of the Yakut microbiome was taken by *Bacillota* (formerly *Firmicutes*), in particular bacteria of the *Oscillospiraceae* family (formerly *Ruminococcaceae*). They break down plant cellulose using glycoside hydrolases and are known as the basic component of the rumen microbiome in ruminants [44, 45].

Current evidence indicates that the gut microbiome of modern northern populations varies in diversity and taxonomic profiles. Besides climatic conditions, the taxonomic profile may be influenced by the diet and microbial exposure to domestic and wild animals. Further studies to investigate the microbiome of the populations of the North with different lifestyles and diets may help to identify the mechanisms underlying metabolic health in cold climates.

CONCLUSION

The role of gut microbiota in host health and adaptation to cold climate is undeniable. Based on animal experiments, the concept of cold microbiota was introduced: it has a high content of *Bacillota* (formerly *Firmicutes*) and promotes efficient thermogenesis through the synthesis of SCFAs, decreased consumption of energy substrates by bacteria, and regulation of the host insulin pathway. Cold microbiota is a promising area of research in terms of microbiota participation in maintaining host metabolism in the North.

A review of available studies on the 16S rRNA gut microbiome in populations of the North showed that their taxonomic profiles differed both from other populations and from each other. These studies are not sufficient to fully characterize the northern microbiota, but they can be used to draw some conclusions. Despite shared climatic conditions and dietary patterns, the populations of the North have variations in their traditional livelihoods, diets, and animal exposure, which is reflected in differences in their gut microbiota profiles.

The most adapted microbiome may form through the activation of different metabolic pathways under similar climatic conditions. In the Yakuts and the Inuit, gut microbiomes demonstrated high intraindividual diversity with a predominance of SCFA-producing bacteria. This profile confers metabolic advantages in cold environments through diverse metabolic functions and probiotic effects. Developing activities to preserve and reinforce these distinctive microbiome features in the populations of the North represents a critical priority for future research in this field.

ADDITIONAL INFORMATION

Authors' contribution. T.M. Sivtseva — literature review, collection and analysis of literary sources, writing the text and editing the article; M.A. Stepanova — literature review, collection and analysis of literary sources, preparation and writing of the article; R.N. Zakharova — literature review, collection and analysis of literary sources, preparation and writing of the article; S.I. Semenov — literature review, collection and analysis of literary sources, preparation and writing of the article; V.L. Osakovsky — literature review, collection and analysis of literary sources, writing the text and editing the article. All authors confirm that their authorship meets the international ICMJE criteria (all authors have made a significant contribution to the development of the concept, research and preparation of the article, read and approved the final version before publication).

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