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Global Journal of Interdisciplinary Social Sciences

Research Article

The human microbiome, social phenomena and the hologenome concept of evolution

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ABSTRACT

The recently developed hologenome concept of evolution posits that all plants and animals, Including humans are holobionts, consisting of a host and diverse symbiotic microorganisms, Termed the microbiome, acting in numerous ways as a single unit. This article offers an initial consideration of how this concept can add a different perspective to the understanding of three social issues. (a) Mother`s microbiome influences offspring`s health and social standing. (b) Cooperation, going hand in hand with competition, occurs at all levels, from cells to organisms to societies. (c) The microbiome, that can store and express acquired information between generations, is a possible mechanism for understanding collective memory.

Keywords: hologenome, holobiont, microbiome, evolution, social darwinism, collective memory, unconscious memory, motherhood

INTRODUCTION

Three recent articles have discussed the relevance of biological theory to sociology (Nichols 2020). One article traces the history of evolutionary thinking in sociology, its rise, demise and recent resurrection (Schutt and Turner 2019). However, even with this revival, sociologists have been reluctant to accept more recent approaches, that are bringing biology and evolutionary analyses back into the core of the discipline. Another article argues that sociologists should become familiar with what they refer to as the new evolutionary sociology, which includes group selection (a proposed mechanism of evolution in which natural *selection* acts at the level of the *group*), epigenetics (a branch of genetics studying changes in the DNA that do not alter the back bone sequences), gene-environment interactions, and social neuroscience (Turner, Schutt and Keshavan 2020). Further, they suggest that this new evolutionary sociology can expand sociological explanations of human behavior, interaction, and social organizations. The third article (Shalin 2020) discusses recent developments in social neuroscience, cultural biology and behavioral epigenetics that support early ideas proposed independently by George Herbert Mead (1863-1931) and Norbert Elias (1897-1990). Shalin argues that both authors accepted Darwin's view that consciousness is a product of natural evolution and strongly favored an interdisciplinary approach including psychology, physiology, biology, physics, and philosophy (Mead 1932, 1934, 1938; Elias 1987a, b, 1991). These topics were deemed marginal at the time to many sociologists (Jackson and Rees 2007).

All of the above publications and several others (e.g., Udry 1995; Meloni 2018; Dubois et al. 2019) present compelling arguments for consideration of biological theories, especially evolutionary biology, within the discipline of sociology. In this regard, during the last fifteen years an additional and essential biological entity has emerged, the microbiome, which has to be considered within the framework of evolutionary theory. The hologenome concept of evolution placing the microbiome as an essential part of its host`s fitness

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Received: July 07 2021; **Accepted:** July 22, 2021; **Published:** July 23, 2021

Citation: Rosenberg E. (2021) The human microbiome, social phenomena and the hologenome concept of evolution. Global J Interdiscipl Soc Sci. 10: 04. doi: 10.35248/ 2319-8834.20.10.010

is an attempt at expanding evolutionary theory to include symbiotic microorganisms (Zilber-Rosenberg and Rosenberg 2008; Theis et al. 2016; Rosenberg and Zilber-Rosenberg 2018; Rough garden et al. 2018; Suárez and Triviño 2019). Concurrently, this concept demonstrates the existence of cooperation, side by side with competition, in biological evolution (Rosenberg and Zilber-Rosenberg 2014). In the present article we will discuss the ways in which the gut microbiome composition can impact social behavior, since gut microorganisms influence brain function and social behavior through neural, endocrine and immune pathways (Cryan and Dinan 2012; Parashar and Udayabanu 2016; Smith and Wissel 2019).

This article is an initial attempt at trying to touch on the subject of how microbiomes and the hologenome concept can be incorporated into some aspects of social thought. The first part will outline the hologenome concept of evolution, which seeks the best way to understand the interactions between the microorganisms living within and on the human body (the microbiome) and humans (the hosts) and to explain the evolutionary advantages of this complex system. The next three parts will include illustrations demonstrating how this concept can add a novel dimension to the understanding of three social phenomena: motherhoods and social standing, biological cooperation versus Social Darwinism, and collective memory.

The hologenome concept of evolution

One cannot explain words without making incursions into the sciences themselves, as is evident from dictionaries; and, conversely, one cannot present a science without at the same time defining its terms.

—Gottfried Wilhelm Leibniz

Understanding the hologenome concept of evolution requires familiarity with certain terms:

Symbiosis, symbionts: Anton de Bary first coined the term symbiosis in 1879, as "the living together of different species" (Oulhen, Schulz and Carrier 2016). This broad definition is still generally accepted. The symbiotic system is constructed from a large partner termed the **host** and smaller partners called **symbionts**. Symbiosis takes different forms: Commensalism is a relationship benefiting one party, while the other is unaffected; mutualism is a relationship benefiting both parties; and parasitism is a relationship benefiting one party to the other's detriment.

Holobiont: Margulis (1991) introduced the term holobiont to describe a host and its primary (mostly intra-cellular) symbiont. The meaning was subsequently expanded to include the host plus all of its symbiotic microorganisms (intra-cellular and extra-cellular), including Bacteria, Archaea, eukaryotic microorganisms and viruses (Rohwer et al. 2002).

Microbiome (sometimes termed also microbiota): Following Lederberg and McCray (2001), a microbiome refers to all the symbiotic microorganisms, which share the "body space" of a host.

Hologenome: All the genes in the microbiome plus the genes of the host constitute the hologenome (Rosenberg et al. 2007).

Species: A group of interbreeding or potentially interbreeding organisms (Mayr 1942). Because this criterion cannot be applied to bacteria, the 97% identity of 16S rRNA genes is routinely used to define a bacterial species. 16S ribosomal RNA (or 16S rRNA) is the RNA component of the small subunit of a prokaryotic ribosome (part of the protein synthesis machinery). The genes coding for this component are referred to as 16S rRNA genes and are used in reconstructing phylogenies, due to their slow rates of evolution.

Genetic variation: Modification in genes that can bring about changes in characteristics**.**

Superorganism: The term has incorrectly been used in some scientific publications and the popular press to describe holobionts (Gordon et al. 2013). However, a superorganism is a colony of eusocial insects, such as ants (Holldobler and Wilson 2008). The "super" in superorganism denotes a higher level of organization, an association composed of multiple organisms of the same species, whereas holobionts are constructed from different species.

Probiotics: Live microorganisms which, when administered in adequate amounts, are expected to confer a health benefit to the host.

The hologenome concept of evolution posits that the holobiont (host + symbionts) with its hologenome (host genes + microbiome genes) is a level of selection in evolution (Zilber-Rosenberg and Rosenberg 2008; Roughgarden et al. 2018). The hologenome concept is based on four general principles, each of which is supported by experimental data and demonstrates the many aspects in which the holobiont acts as a single unit:

All natural plants and animals, including humans, are holobionts.

1. Competition and cooperation exist within the holobiont. Cooperation between the host and the microbiome contributes to the fitness of

the holobiont, including adaptation, behavior, development, metabolism and evolution.

2. A significant fraction of the microbiome genome (the sum of the genomes of all symbiotic microorganisms) together with the host genome, i.e., the hologenome, is transmitted from one generation to the next.
3. Genetic variation in the hologenome can be brought about by changes in either the host or the microbiome genomes. Since the microbiome genome can adjust to environmental dynamics more rapidly and by more processes than the host genome, it can play a fundamental role in the adaptation and evolution of the holobiont.

All natural organisms are holobionts. Numerous studies have demonstrated that all natural animals and plants contain abundant and diverse symbiotic microorganisms. The human body, for example, contains about the same number of bacterial cells as human cells (Sender, Fuchs and Milo 2016). Because the microbial community is composed of several thousand different species of bacteria, the genetic information encoded in the microbiome (22 million non-redundant genes) is ≈1000 times greater than the information in the human genome (19,000 genes) (Tierney et al. 2019).

The microbiome contributes to the fitness of holobionts. In spite of the existing competition within the holobiont accepted by scientists for many years, between the hosts and its microorganisms and between the microorganisms themselves, and the component of disease causation, there exists also an important element of cooperation. A large number of studies have demonstrated the existence of beneficial interactions between microbiomes and their hosts, leading to a better-adapted holobiont. With regards to humans, the most recognized benefits include protection against bacterial and viral pathogens (Donia et al. 2014; Drekonja et al. 2015; Brown, Sequeira and Clarke 2017), stimulation of immune system (Toscano et al. 2017), angiogenesis (creating new blood vessels) (Khandagale and Reinhardt 2018), vitamin synthesis (Biesalski 2016), fiber breakdown (Baxter et al. 2019) and participation in energy metabolism (Khan et al. 2016).

Of particular relevance to this article is the fact that bacteria in the mammalian gut modulate brain development and behavior, including social behavior (Heijtz et al. 2011; Sherwin et al. 2019, Buffington et al. 2021). Microbial gut–brain signaling is bidirectional. The circuitry of neurons, hormones, and neurotransmitters allows messages to be transmitted between the brain and the gut via the blood system or the vagus nerve (a central nerve with many branches, connecting body parts, including the gut, to the brain). For example, partially cutting the vagus nerve impairs vagal signaling to the gut and abolishes gut microbial effect on behavior in mice (Sgritta et al. 2019). Also the rate at which food is being moved along the alimentary tract and how much mucus is lining the gut, both partially controlled by the brain, have a direct impact on the environmental conditions the gut microbes experience. On the other hand, the neurotransmitter (a compound that stimulates nerve cells) serotonin can function in the opposite direction. Serotonin is synthesized in the gut by specific human cells and by certain bacteria that are part of the healthy microbiome (Foster & Neufeld 2013; O`Mahony et al. 2015). Serotonin stimulates the vagus nerve in the gut and/or is absorbed from the gut into the blood system, from where it reaches the brain by crossing the blood-brain-barrier. A key function of serotonin in the brain is to moderate anxiety and stress, and promote peacefulness and coping (Carhart-Harris and Nutt 2017). Gut microbes affect also the level of the neurotransmitter GABA (gamma amino butyric acid) an inhibitory neurotransmitter (Frost et al. 2014), and thus influence behavior. In spite of the information described here, much is still to be learned about the mechanisms that effect the interaction between microbiome and brain (Jameson et al. 2020).

Symbiotic microorganisms are transmitted between generations and propagate the unique properties of the holobiont. The human genome is transferred from one generation to the next via the eggs and sperm (gametes) with accuracy. However, the microbiome is not carried over with the gametes. In spite of that, it has been shown that microbial symbionts can be transmitted with reasonable fidelity from parent to offspring (Asnicar et al. 2017; Maqsud et al, 2019; Fehr et al. 2020). This is achieved in different organisms by a variety of methods, including cytoplasmic inheritance (transmission of genes that occur in the cell, but outside of the nucleus), coprophagy (consumption of feces), direct contact during and after birth, and via the environment (Rosenberg and Zilber-Rosenberg 2014). In humans, most of the colonization of the newborn gut occurs when the baby transits the birth canal via inoculation by maternal vaginal and fecal microbes (Mueller et al. 2014; Makino 2018). In addition, human breast milk has been shown to be a continuous source of bacteria to the infant gut (Sakwinska et al. 2016; Fehr et al. 2020). Analyses of the DNA of several bacterial strains isolated from mother's milk demonstrated that they were identical to those found in the offspring

(Milani et al. 2015; Asnicar et al. 2017), providing evidence for vertical transmission (from parent to offspring). Very long-term (evolutionary time scale) transmission of microbiomes was studied by comparing gene sequences of bacteria associated with great apes, including humans (Ochman et al. 2010; Sanders et al. 2014; Moeller et al. 2016). The authors concluded that over evolutionary timescales, the composition of the gut microbiome among great ape species is phylogenetically conserved and has diverged in a manner consistent with vertical inheritance from parent to offspring along many generations. Gut bacteria therefore are not simply acquired from the environment, but have co-evolved for millions of years with hominids to participate in their fitness within their surroundings.

Microorganisms play a fundamental role in genetic variation and evolution of animals and plants. Genetic variation in holobionts can be brought about by changes in either the host or the microbiome genomes. Since the microbiome`s genome can adjust to environmental dynamics more rapidly and by more processes than the host genome, it can play a primary role in adaptation and evolution of holobionts. Consideration of the holobiont as a level of selection in evolution brings forth previously under-appreciated mechanisms of genetic variation and evolution, such as (i) acquisition of novel bacteria from the environment and (ii) horizontal gene transfer (HGT) of DNA.

Microbes were on this planet for 2.1 billion years before there were any animals or plants. During this time, they evolved enormous biochemical diversity. The first eukaryote cell was probably formed by the acquisition of bacteria to eventually form the intracellular organelles, the mitochondria, organelles that generates energy (Dyall, Brown and Johnson 2001) and chloroplasts, the plant organelles that convert light energy into stored energy (McFadden and Van Dooren 2004). It also has been hypothesized that the cell nucleus was formed by the uptake of an Archaea by Bacteria. (Martin 2005). Archaea is a taxonomic domain of single-celled organisms lacking nuclei, formerly called archaebacteria, but now known to differ fundamentally from Bacteria. Uptake of microbes into multicellular organisms continued to provide genetic variation for holobionts throughout evolution.

Animals and plants come into random contact with billions of microorganisms during their lifetime, via air, water and interaction with different surfaces. Occasionally some of these microbes find a niche and under appropriate conditions become established in the host. Unlike mutation, which causes small changes in existing genomes, acquisition of a microbe introduces hundreds of new genes into the holobiont. Rather than reinvent the wheel, animals and plants can acquire pre-evolved genetic information in the form of microbes. An example of a major evolutionary event that was driven by the acquisition of bacteria is the ability of many animals, including humans, to use plant fiber, such as cellulose, as nutrients. These bacteria convert the complex polysaccharides to fatty acids that are a major source of carbon, energy and signal molecules for their host animal (Baxter et al. 2019). There are many other examples of evolutionary events that were driven by the acquisition of microbes from the environment, including acquisition of chemosynthetic bacteria by deep-sea animals, which allows for life in the absence of light (Breusing et al. 2020), acquisition of algae by corals, which created photosynthetic animals and enabled the emergence of coral reefs (Liao, Xiao and Li 2019), and acquisition of nitrogen-fixing bacteria by legumes, which permits plant growth under limiting nitrogen conditions (Afkhami et al. 2018).

Horizontal gene transfer (HGT) is the transmission of genes between organisms by means other than parental to offspring inheritance. HGT is a well-known evolutionary mechanism in prokaryotes (Kloub et al. 2020) and is more frequent than mutation in the bacterium *Escherichia coli* (*E. coli*) colonizing the mammalian gut (Frazao et al. 2019). HGT between different types of bacteria can lead to genetic variation and evolution of animal and plant holobionts. An interesting example of evolution of humans by HGT between bacteria is the ability of Japanese people to break down agar (an abundant ingredient in their diet since antiquity), since they have a bacterium in their gut, that contains genes that code for the enzymes that degrade agar. Westerners lack this bacterium in their gut and therefore cannot breakdown agar. The way it occurred will be described later under the subject of collective memory.

HGT can also take place from microorganisms to animals (Cordaux and Gilbert 2017). Recently, the availability of large numbers of fully sequenced genomes has led to the conclusion that HGT in animals was, and probably still is, more frequent than observed previously (Sieber, Bromley and Hotopp 2017). For example, it was estimated that the human genome contains 1,467 regions that were attributed to past events of HGT, involving 642 known genes (Huang et al. 2017). In another study, Crisp et al. (2015) reported that 145 human genes, not present in other primates, were attributed to HGT. A major event in evolution, the formation of placental mammals, including humans, was the acquisition by HGT, from a virus, of the gene

coding for the protein syncytin (Dupressoir, Lavialle and Heidmann 2012). Today this gene enables growth and maturation of the fetus. It should be born in mind that in humans and other more complex animals, HGT can generally be observed only over evolutionary time scales.

In general, acquisition of microbes and microbial genes is a powerful mechanism for driving genetic diversity and evolution of complexity, e.g., evolution has produced some remarkably complex organisms, such as *Homo sapiens*. In essence, holobionts are collectives and evolution proceeds both via cooperation (between microbes and between microbes and their hosts) and competition (between microbes and between microbes and their hosts), going hand in hand. Let us now examine how new aspects of some social issues can be highlighted by the hologenome concept of evolution.

Mothers, the microbiome and social standing and interactions

Women belong in all places where decisions are being made.

Ruth Bader Ginsburg

Motherhood involves central roles in both biological and social worlds. In this section, we will discuss three biological stages of motherhood in which the microbiome intertwines with both these aspects of motherhood: pregnancy (development of the fetus and the placenta), birth and the postnatal stage. At each stage, the microbiome can affect social aspects of an individual, and vice versa, social situations exist, which affect the microbiome and the life-long outcome of the offspring.

The first biological stage of motherhood involves the formation and development of the fetus during pregnancy. The fetus is connected by the umbilical cord to the placenta, the organ that is implanted in the mother's uterus during pregnancy. Macronutrients (glucose, amino acids and fatty acids), micronutrients, (vitamins and minerals), oxygen, and hormones can cross directly through the placental membrane by diffusion to fetal blood circulation and are consumed by the fetus. The health and growth of the fetus are dependent on these materials and on this complex interaction, and the microbiome of the mother is an active partner in this too. In sum, diet, air quality, the emotional state of the mother, her microbiome and other factors during pregnancy affect the health of the fetus and subsequently influence growth and development in childhood and adolescence (McManley and Woods, 2008; Polanska et al. 2021) and also health and quality of life during adulthood (Nakagawa et al. 2020). One important example is the effect of the microbiome on energy metabolism. During the second and third trimester of pregnancy, the microbiome of the human and mouse female gut and vagina undergo dynamic and microbial compositional changes (Codagnone et al. 2019a; Mesa et al. 2020). These changes have been shown to affect the metabolism and development of the fetus. For example, the importance of the mother`s microbiome in the energy metabolism of both her and her fetus has been demonstrated. Previously, it has been shown that obesity is correlated with a certain microbiome (Turnbaugh et al. 2006; Ridaura et al. 2013). Research has also revealed that the numbers of these "obese bacteria" in the mother`s gut increase during the third trimester of pregnancy (Koren et al. 2012). Such a microbiome induces metabolic changes that promote energy storage in fat tissue of the mother that in turn encourages growth of the fetus in utero and subsequent milk production after birth. A second example, one more crucial to the subject of this paper, is the increasing recognition that an important link exists between the mother's microbiome and neurodevelopment of the fetus (O`Mahony et al. 2017; Codagnone et al. 2019a, b). An important phenomenon in pregnancy that has been demonstrated is that stress of the mother affects the fetus (Walsh et al. 2019) and has long-term consequences (O`Mahony et al. 2017; Van den Bergh et al. 2017). Interestingly, stress has also been shown to influence the composition of the gut microbiome via the neuro-immuno-endocrine systems, termed the brain-gut axis (Jang et al. 2020). These changes may in themselves affect the development of the fetus, especially that of the brain, during pregnancy and after birth (Codagnone et al. 2019a, b). Moreover, the latter may have cognitive, behavioral and psychiatric implications, which in turn may reflect eventually also on social behavior.

The second stage, the natural birthing process, involves bacterial colonization of the newborn gut, skin, mouth, respiratory system and the urogenital system, initially via inoculation with maternal vaginal and fecal microbes when the baby transits the birth canal. The sterility of the fetus (Gil et al. 2020) is broken when the amniotic sac bursts. During labor, the new-born swallows bacteria-rich fluids from the surroundings and rubs against the walls of the birth canal. By the time the birthing process is completed, a diverse population of microbes has made its way into the infant's gut, onto its skin and other body parts open to the surrounding (Rasmussen et al. 2020). Thus, although classical genetics contends that fathers and mothers contribute equally to the genome of their

offspring, we now know that the vast majority of unique genes in humans are in the microbiome, and that mothers are responsible for the majority of the initial microbiome of her offspring. It follows that mothers play the primary role in providing genes and genetic variation to offspring (Rosenberg and Zilber-Rosenberg 2019). The consequence of this conclusion may be far reaching.

Studies have suggested that delivery mode shapes the microbiome's establishment and, subsequently, its role in child health (Dominguez-Bello et al. 2010; Shao et al. 2019). Many modern human babies are not exposed to vaginal microbes at birth and are born via Cesarean section (C - section). The global average of C-section deliveries increased from 6.7% in 1990 to 19.1% in 2014 (Boatin et al. 2018), and in 2019 stood on an average of 28.1% in the 37 OECD countries (OECD, 2019). Whereas vaginally delivered infants harbor bacterial communities resembling those of the maternal vagina and gut, C-section–delivered infants have a less diverse microbiome, which is enriched in microbiome resembling their mother's skin, mouth, and bacteria from surrounding surfaces (Rutayisire et al. 2016). Epidemiological studies have reported associations between C-section delivery and an increased risk, after birth or later in life, of obesity, asthma, allergies, type 1 diabetes, immune deficiencies and a higher rate of pathogen infection (Cardwell et al. 2008; Dominguez-Bello et al. 2016; Johnson and Own by 2016; Tun et al. 2018; Shao et al. 2019). Some pilot studies where the C-section babies were exposed to mother`s vaginal fluid (Dominguez-Bello et al. 2016) or mother and baby were supplemented with appropriate probiotics (Korpela et al. 2018a) demonstrated the possibilities of correcting the differences. Such corrections may be crucial not only for prevention of health problems, but also because of their social and economic consequences.

During the third stage, after birth, the mother is still the main source of the infant's gut microbiome, which includes maternal breast milk and direct contact via kissing and hugging. Human breast milk contains ca. 10^5 bacteria per ml, composed of hundreds of species of beneficial bacteria (Malinowska-Pa□czyk et al. 2019). Mode of delivery, lactation stage, gestational age and mothers' diet all influence the composition of bacteria present in breast milk (LeMay-Nedjelski et al. 2021). In addition, human milk contains abundant oligosaccharides (short-chain carbohydrates) that selectively support the growth and function of these protective bacterial strains while inhibiting the proliferation of undesirable bacterial strains (Walsh et al. 2020). Furthermore, given the bidirectional communication of the gut-brain axis, as described above, optimizing gut microbiome composition ensures proper metabolism and availability of vitamins and amino acids essential for neurologic development (Lu et al. 2018). The crucial and rapid development of the infant microbiome has an impact on the maturation of the gut-brain axis and thus has the potential to affect infant cognition, mood, and social behavior, with lifelong implications (Yang et al. 2016; Forssberg 2019). Experiments with mice, often used as model systems, have demonstrated the importance of the early input of gut bacteria that affect the brain, and behavior (Heijtz et al 2011; Fülling, Dinan and Cryan, 2019). Germ-free (GF) mice (born and grown under sterile conditions) are more active and spend more time scurrying around their enclosures than conventional mice. They are also less anxious and more likely to take risks, such as spending long periods in bright light or open spaces, compared to the normally bred mice. GF mice also display reduced preference for social novelty. Moreover, inoculating gut bacteria from normally bred mice into GF newborn mice causes them to behave in the "normal" way. However, if GF adult mice are inoculated with the same gut bacteria, their behavior does not change, suggesting that bacteria affect the early development of the brain that subsequently influences adult behavior (Foster and Neufeld 2013; Wang et al. 2018).

In addition to breast-feeding, microbial colonization occurs by close physical contact of the offspring with parent or family, community members, and the physical environment (Sarkar et al. 2020). Also at this stage, the main caregiver to date is usually the mother. Kissing, hugging and touching result in the transfer of microbes (Brown, Sequeira and Clarke 2017; Browne et al. 2017). It was calculated that an average 10-second kiss transfers approximately 80 million bacteria (Kort et al. 2014). And mothers kiss more, and the kiss with other physical and emotional signs are important for child`s development (Maselko et al. 2011; Hossain & Barik, 2020).

Though, as discussed, mothers have been shown to be more dominant in transferring the microbiome to the offspring, the fathers of western countries today have also a certain input (Jo et al. 2021), especially by transferring novel, not common, strains (Korpela et al. 2018b). The changing role of fathers, is a process starting in the 1960-1970`s (Dette-Hagenmeyer et al. 2014; LaRossa 2007). In the past, fathers played a more distant role in the raising of children (LaRossa 2007), and thus had probably a lesser role in determining their microbiome. Today fathers participate more in caring for offspring (Bureau of Labor Statistics 2014; Schoppe□Sullivan & Fagan 2020) and so have a greater chance of affecting

their physical, mental and social development. Knowing the role of the microbiome in human physiology and development, it will be interesting to study how the changing role of fathers will affect the microbiome and with it the maturation and wellbeing of the offspring. Will the influence of the father`s microbiome play a role in the general social changes occurring today, as for example in general social standing and interactions, or specifically women`s equity?

What do microbiomes, which are obtained still today primarily from mothers, have to do with social standing or social equity? Ishaq et al. (2019) have discussed how alterations in the microbiome, which greatly impact our health, can arise from social inequalities, such as access to perinatal care, healthy foods, and quality housing. For example, nutritional or psychological stress during pregnancy, as discussed above, can alter both maternal and offspring immune function that results in an altered bacterial community and metabolic profile (Jašarevi et al. 2015; Gomez de Aguero et al. 2016), that in turn may affect the nervous system, as discussed above. Thus, access to healthcare, healthy foods (Chen et al. 2011), a friendly environment, that aid in maintaining and acquiring beneficial microorganisms, are, as we suggest, part of the fundamentals necessary for creating and resolving social standing and equity and vice versa, social equity is needed in order to achieve a healthy microbiome.

Biological Cooperation Vs Social Darwinism

Competition has been shown to be useful up to a certain point and no further, but cooperation, which is the thing we must strive for today, begins where competition leaves off.

 Franklin D. Roosevelt

Social Darwinism is a sociological theory first popularized in late nineteenth-century Europe and the United States. It merges Charles Darwin's theory of evolution by natural selection and Herbert Spencer's sociological theories and can be used to justify imperialism, racism, laissez-faire capitalism, and other economic policies. Social Darwinists argued that individuals and groups, just like plants and animals, compete with one another for success. This assertion was and still is used to justify social stratification by claiming that individuals or groups of individuals at the top of social, economic, or political hierarchies belong there, as they had competed against others and had proven to be better adapted. Moreover, any social or political intervention that weakens this existing hierarchy would undermine natural order (Degler 1991).

Social Darwinism was the product of late nineteenth-century economic and political expansion. As the European and American upper class sought to extend their economic and political power, they employed scientific explanations to justify the increasing gap between rich and poor and social stratification. The Social Darwinists' reliance on "natural laws" allowed social, political, and scientific leaders to dismiss more equal distribution of wealth and power by claiming that it violated natural hierarchy. Public interest and respect for the sciences contributed to the success of Social Darwinism, since policies that had the stamp of scientific legitimacy were accepted to be above political interest or influence (Bannister 1979). Recently, Rudman and Saud (2020) have discussed how Social Darwinism in the USA during the Trump era is responsible for justifying police brutality and support for budgets that slash the social safety net and endow the wealthy with tax cuts.

Since Social Darwinism was invoked to justify phenomena, such as inequality, racism, and colonialism, it is not surprising that biological and evolutionary approaches were resented in the social sciences and humanities (Blancke and Denis 2018). Although competition amongst animals of the same species for food, territory and mating rights is commonly observed, and accepted, several social scientists (e.g., Etkin 1964; Montagu 1976; Sayers 1982; Kaye 1997; Sanderson 2001) and anthropologists, e.g., Franz Boas (Lewis 2001) and Margaret Mead (Hogan 2010), opposed Social Darwinism, and argued that the theory of human aggression as "innate" is simplistic and incomplete. They take issue with the practice of linearly extrapolating from the evidence of animal behavior to human behavior, and argue that humans are capable of complex behaviors, and those are determined by the interaction between culture, learning experience and genetic constitution and include competition and cooperation. Moreover, as we discuss below, a clear argument for cooperation emerges from our current understanding of the importance of cooperation in biological fitness and evolution, which exists side by side with competition.

According to the hologenome concept of evolution, symbiosis, once thought to be reserved for a few rare species, is now known to be an essential part of the fitness and evolution of all animals and plants (Rosenberg and Zilber-Rosenberg 2014, 2018). Daniel Christian Wohl (2017) wrote, “A holistic understanding of modern evolutionary biology suggests that life evolves by a process of diversification, and subsequent integration of diversity, through collaboration”. This is seen in a fundamental way by the interaction between microbiomes and their hosts. The power of this concept

is persuasively illustrated by the case of the intracellular organelle, the mitochondrion, which can be considered very successful in biological terms. Mitochondria were initially formed, as described above, by a cell acquiring a bacterium, which subsequently evolved into a mitochondrion (Fan et al. 2020). Mitochondria reside inside the cells of every eukaryotic organism (from yeast to multicellular animals and plants), in which they provide the machinery of oxidative energy production. A second example is the intracellular plant organelle the chloroplast, that was formed by cyanobacteria taking a similar route into eukaryotic cells and evolved there into plant chloroplasts (Matsumoto and Awai 2020; Stadnichuk and Kusnetsov 2021). The chloroplasts are the primary harvesters of solar energy, which drive the production of oxygen and fix carbon into glucose, both of which nourish the rest of the biosphere. These cases reveal how far collaboration between hosts and symbiotic microbes can go. Thus, competition in the biological world can often be viewed as natural selection between cooperative systems. For example, animals as different as lions, dogs, piranha, killer whales and ants have all evolved the ability to hunt in groups (Lang and Farine 2017). However, also competition exists within individuals - between them and their microorganisms and between the microorganisms amongst themselves - for food, space etc., but in parallel, there exists also cooperation that enables better adaptation of the holobiont to its surrounding. Still, biologists for many years doubted the existence of cooperation in biology.

One of the frequently raised arguments against cooperation in biology is the case of "cheaters". Cheaters exploit cooperative benefits without contributing their fair share and are therefore, in the short run, competitively superior to their cooperating counterparts (Douglas 2008). Accordingly, cheaters should destroy cooperation. However, a close examination of several symbiotic systems indicates how holobionts limit cheating. Let us consider the well-studied symbiosis between aphids and the bacterium *Buchnera aphidicola* (Baumann 2005). Neither the host aphid nor the symbiont B. aphidicola can survive without the other (absolute mutualism). B. aphidicola overproduces and excretes essential amino acids that are lacking in the phloem sap diet of the insects. The aphid depends on these essential amino acids furnished by the symbiont, and the symbionts are completely dependent on their host to meet their nutritional requirements (Feng et al. 2019). However, traditional ecological and evolutionary theory predicts that mutualistic symbiosis should fall apart because mutant parasites will develop in the aphid. These mutants (cheaters), which benefit from the host, but do not provide amino acids to the aphid, are predicted to grow more rapidly than the beneficial symbionts and thus dominate in the host. However, aphid holobionts with a high concentration of cheaters will not be able to compete against other aphid holobionts and will die off, eliminating the cheaters. The fact is that stable cooperating symbioses between animals and microorganisms originated more than 500 million years ago (Gruber-Vodicka et al. 2011) and are a general phenomenon of biology.

A physicist view on biological cooperation comes from Cohen and Marron (2020) who have suggested that entropy (a term used in physics to describe a thermodynamic quantity, often interpreted as the degree of disorder or randomness in a system) drives cooperation and the evolution of complexity. At first glance, one would assume entropy brings about randomness, not cooperation and complexity. However, entropic destruction can be overcome by interactive cooperation. For example, single stranded DNA undergoes rapid entropic destruction, but the cooperative interaction with another DNA strand to form double stranded DNA stabilizes the molecule. The same argument can be made for the interactions in organisms and societies.

The microbiome and social behavior. Regarding the subject of cooperation in animals (including humans) leads to the question: what evolutionary forces bring about group living and social cooperative behavior? The accepted theories concentrate mainly on the basic evolutionary survival advantages of mutual aid against predation, finding food, and caring for offspring. An additional evolutionary benefit that was suggested by some biologists is linking animal cooperation and sociality to transmission of mutualistic microorganisms (Troyer 1984; Lambardo 2008; Montiel-Castro et al. 2013; Archie & Tung, 2015). Troyer was the first to consider a connection between symbiotic microbes and social behavior. She claimed that herbivores could not survive without their symbiotic fermentative microbes. To retain the best-evolved microbes the individuals had to concurrently evolve social behaviors that would enable transfer of the microbes by forcing close contact between members of the group, in addition to their accurate transfer from one generation to the next. As discussed above in the paragraph on fitness, animals are dependent on microbial symbionts for several reasons, the important ones being digestion of complex plant materials, synthesis of important nutrients, protection against pathogens and development of the immune system. The associations between transmission of mutualistic symbionts and group living of their hosts

is an ancient phenomenon not only in herbivores, and the origin of these symbioses coincided with the evolution of host sociality (Montiel-Castro et al. 2013). De Waal, (2000), Lombardo (2008) and Montiel-Castro et al. (2013) suggested the possibility that kissing in primates, especially humans, accepted as a means of communicating affection, reassurance, and reconciliation, initially arose as a way for parents to transmit required symbionts to their offspring, as do koalas by coprophagy (Osawa et al. 1993). Archie and Tung (2015), summarize the interaction between microbiome and social behavior by demonstrating that not only does the microbiome have an important effect on social behavior, but the effect goes both ways, social behavior has also a marked effect on the microbiome. This means that changing social interactions can bring about taxonomic and genetic changes in the microbiome, which in turn can affect human behavior. Sarkar et al. (2020) propose the "social microbiome" as the microbial meta-community of animal and human social networks. A social network represents a set of islands or patches (group of hosts) linked by social connections that enable the transmission of microbes.

Whilst the transmission of parasites and pathogens within animal social networks has been extensively researched (Schmid-Hempel 2017) and experienced throughout 2020/21 with the pandemic of COVID 19, the social transmission of commensal and beneficial microbes has only recently garnered increasing attention (e.g. Browne et al. 2017). One report demonstrated that similar gut microbes were found among married couples who ranked their relationships especially close, while the mean gut microbial similarity between married couples reporting lower levels of closeness was not significantly different from that of individuals living separately (Dill-McFarland et al. 2018). Regarding kissing, Kort et al. (2014) demonstrated experimentally that intimate kissing affected the salivary microbiome in intimate partners. Social forces are likely to influence the "social microbiome" (Archie & Tung 2015) at multiple levels, including at the individual level, within social groups, between groups, within populations and species, and finally between species, as has been shown for pet dogs and humans (Song 2013).

Human groups with more cooperative patterns have been shown to be more successful and displace less cooperative groups (Apicella and Silk 2019). Furthermore, the scope, scale, and variability of human cooperation greatly exceed that of other animals. In evolutionary terms, this already can be seen in the cooperative lifestyle of hunter-gathers, whose relics live today in small, mobile, residential bands comprising several nuclear families, such as in Hadza hunter-gathers, an indigenous ethnic group in north-central Tanzania (Apicella and Silk 2019). At the present time, it is clear that many of the challenges that pressured our human hunter-gatherer ancestors into cooperation are gone (Perc et al. 2017). However, we are still cooperating, and on ever larger scales, to the point that we may deserve being called "Super Cooperators" (Nowak and High field 2011). The key point emerging from the microbiome human and animal co-socialization is that, though in biology competition and cooperation go hand in hand, cooperation may have an upper hand.

Collective Memory: The term "collective memory" is widely used in disciplines such as history and sociology. Collective memory refers to a shared pool of experiences, memories, knowledge and information of a social group that is significantly associated with the group's identity and that can be recalled at a later time (van Dijck 2004). Collective memory can be transmitted orally, stored in writings, films, museums and other memorial sites, in our DNA, and also in the human microbiome (Dinan et al. 2015; Rotem and Rosenberg 2017).

Maurice Halbwachs (1925, 1992) was the first sociologist to use the term collective memory, which provided the foundation for the study of shared memories of a group. Halbwachs suggested that all individual memory was constructed within social structures and institutions and argued that individual personal memory can only be comprehended within a group context; these groups can be any size, from families to organizations and nation-states. Collective or social memory is the specific trait that a person derives from belonging to a distinct society and culture. In fact, it develops as a result of socialization and customs (Assmann 2003). Olick and Robbins (1998) reviewed historical aspects of sociological theories concerning social memory.

Carl Jung (1876 -1961) used the term "collective unconscious" to describe the broad concept of inherited traits, intuitions and collective wisdom of the past (Jung 1953). The collective unconscious, unlike the personal unconscious, is a type of genetic memory that can be shared by people with a common ancestor and/or history. According to Jung, the collective unconscious consists of implicit beliefs and thoughts held by our ancestors (Lu 2012). Although we are unaware of the collective unconscious, it can influence how we behave. What Jung termed the collective unconscious or genetic memory, has been suggested, already by Jung himself and his followers, to be referred to as DNA-based memory (Samuels 1986; Colangeli 2020). It has been suggested that DNA modification by methylation, a

biological process by which small methyl groups are added to the DNA molecule without changing the sequence of the DNA back bone (epigenetics), may serve as a contributing biological mechanism in memory formation and storage (Day and Sweatt 2010; Kim and Costello 2017, Colangeli 2020).

Both cultural or collective and DNA-based memories can be gained or lost. Acquisition of collective memory requires a shared experience and the deposition of the experience in a manner that can be recalled later (Gintis 2011). An example of a recent cultural memory is the Holocaust, which has been documented in personal accounts, historical writings, paintings, films and museums. As is often the case, different groups share divergent versions of the event, as is evident from the foci of various National Holocaust Museums (Rotem 2013).

An entirely different example of collective memory is the use of agar in the Japanese cuisine. This memory is both culturally-based and DNA-based within the human microbiome. Agar is a complex long-chained carbohydrate found in red seaweed. Throughout history into modern times, agar has been used as a food ingredient mainly in Japan, but also in other countries in East Asia. Foods containing agar include wagashi, a dessert made of small cubes of agar jelly, mizu y□kan, another popular Japanese food and almond tofu. The techniques for preparing these foods have been passed down from generation to generation and constitute part of the Japanese cultural collective memory. Tax records from the eighth century list seaweed as payment to the Japanese government, showing that it had an important role in early Japanese culture (Nisizawa et al. 1987).

Interestingly and in parallel, as described above regarding the phenomenon of HGT, the Japanese also have acquired and retained in their microbiome DNA the ability to digest agar, which the Westerners lack. How did the Japanese acquire the genes to digest agar? The source of the genes was traced to a marine bacterium that was present on fresh dietary seaweed. When a Japanese person consumed the seaweed, genes from the marine bacterium were horizontally transferred (HGT) to a resident gut bacterium. This gut bacterium that contained the agar degrading genes spread throughout the Japanese population by vertical and horizontal (via the environment) transmission and became part of the hologenome of the Japanese (Hehemann et al. 2010). It should be stressed that until recently, it was accepted that only the process of altered chromosomal DNA of the host, such as mutation or methylation, affected biological memory.

However, beyond host DNA mutation and epigenetics, when considering the microbiome and the hologenome concept, the data demonstrate that biological memory can also be changed by experience (Rosenberg and Zilber-Rosenberg 2021). When a person eats a particular raw food, the specific bacteria, which can multiply on that food, will amplify in the gut and may be transferred to future generations. Thus, the phenomenon contains the two following principles concerning the effect of the surrounding on individuals, known as Lamarckian inheritance. This theory, which had been dismissed for many years, has made a comeback in the last twenty years (Yablonka & Lamb 2005; Rosenberg, Sharon and Zilber-Rosenberg 2009):

1. Use and disuse - individuals lose characteristics they do not use and develop characteristics that are useful.
2. Inheritance of acquired characteristics - individuals transmits acquired characteristics (in microbiome genes) to offspring.

Each person possesses his or her own personalized fingerprint of gut bacteria (Faith et al. 2013). This includes a core microbiome of ca. 100 species (Risely 2020), which are common to all or most humans (part of the collective memory of the human species) and hundreds of microbial species that are common to a particular geographical and generational group that can be summed up as a cultural group (Yatsunenko et al. 2012). In addition, the personal microbiome includes thousands of microbial species that are present in a combination unique to each individual (Shapira 2016; Johnson et al. 2019). Some strains of symbiotic bacteria are so well conserved within cultural groups that they can be used as a window into human migration (Moodley 2016; Waskito and Yamaoka 2019). In particular, the ulcer causing stomach bacterium *Helicobacter pylori* has been used as a marker of ancestry and migration (Falush et al. 2003; Dominguez-Bello and Blaser 2011). For example, an American whose great-great- grandmother came from Japan may still be inhabited by the Japanese strain of *H. pylori*.

As discussed throughout the paper, there is growing evidence to support the initial findings that the microbiome and its metabolic activity affect directly memory, cognitive activity. Experiments with mice, described above in the section on mothers and the microbiome, have demonstrated that gut bacteria affect the brain and behavior, and what is particularly relevant to our present topic, they affect memory (Shen et al. 2017; Mao et al. 2020). Germ-free (GF) mice displayed an absence of working memory compared to mice

with a microbiome (Gareau et al. 2011). The presence of microbes is apparently crucial for the development of hippocampus-dependent memory (Dinan et al. 2015). Furthermore, transplanting young mice with microbiome from aged mice led to impaired spatial learning and memory in the young mice by affecting the hippocampus nervous plasticity (D`Amato et al. 2020). The hippocampus is a brain structure that plays an important role in learning and memory and is affected in different neurological and psychiatric disorders.

However, the microbiome not only affects the human body and mind, it is in itself affected by the surrounding, and can act as a reflection of past experiences. Because learning about situations that are necessary for survival of a species is probably stored as a kind of unconscious genetic memory, some of these fundamental human experiences could be somewhere not only in our human chromosomal DNA, or methylated chromosomal DNA (epigenetic), but also in our microbiome DNA. Consider that one of our ancestors had a very bad experience with fire. Such an experience, resulting in knowledge useful for survival, could possibly be encoded in the hologenome and passed on to future generations. In the fields of human genetics and microbiomes so much is not known that theories about deep DNA memories cannot be ruled-out.

A certain support for this idea of biological stored collective memory comes from experiments, in which mice taught to fear an odor, before even conceiving offspring, transmitted this fear to the next generation (Szyf 2014; Dias and Ressler 2014; Liu 2018). Similarly, paternal exposure to a specific herbicide altered the behavior of zebrafish offspring (Lamb, Chia and Johnson 2020). Such memory phenomena may contribute to the etiology and potential intergenerational transmission of risk of some neuropsychiatric disorders, such as phobias, anxiety and post-traumatic stress disorder (Johnson 2017), that have personal and social ramifications, as discussed in the section on motherhood. They can also contribute to general human fears from snakes, cockroaches or certain noises.

Cultural and DNA-based collective memories can also be lost if they are not used, a hallmark of Lamarckian inheritance. Many languages have completely disappeared because of processes associated with colonization. For example, of the more than 300 different languages that were spoken in North America when the Europeans first arrived, only 91 are still spoken (Braun 2009). When a language becomes extinct, it can take along with it much of the history and culture of the people who spoke it. In the example, we discussed above, if the Japanese population stops eating food that contains agar, the agar-degrading bacteria will be lost together with the collective memory of this particular cuisine. People working on cultural evolution (e.g. Mesoudi and Thornton 2018) discuss the issue of use and disuse, and its effect on loss of cultural memory when not used or gain of novel cultural traits.

In conclusion, the hologenome, namely, chromosomal DNA plus microbiome DNA, can serve as vehicles for collective memory. While the microbiome responds rapidly to the environment, and changes in the microbiome are transmitted to offspring, the chromosomal DNA responds much slower but is more stable. What particular parts of the DNA-based collective memory reside in the human DNA or in the microbiome is an interesting subject for future exploration.

Conclusions

The concept of a holobiont with a hologenome posits that all plants and animals, including humans, function in many ways as one unit, consisting not only of a competing but also of a cooperatively interacting host with its symbiotic microorganisms. Such an inclusive approach can provide a novel understanding of some social phenomena.

Under the subject of biological cooperation and Social Darwinism, we demonstrate the possibilities of extrapolation from biology to human society, via the complex interplay between competition and cooperation in biology and in human society. Basing Social Darwinism only on "innate" human aggression is constructing a social narrative on a narrow facet of animal and human behavior. Modern biology teaches us that evolution, in fact, in many cases, selects for cooperative practice over selfish behavior at all levels, from cells to organisms to societies.

We also suggest a biological mechanism that would be able to store cultural memories for generations. Collective memory is an important asset in human culture and an interesting topic in the disciplines of history and sociology. Some collective memory is transmitted orally, stored in writings and other memorial sites. A biological basis to collective memory should be something that is capable of changing as a consequence of common experiences. Our DNA is meant to be stable, and embody human characteristics that is transferred from one generation to the next and therefore not meant to change in short time scales. Memories, however, are specific stories that happened at a certain time and thus storing them must be achieved probably via different ways than chromosomal DNA

sequences. One possibility is epigenetics as suggested by Kim and Costtello (2017), another possibility is the human microbiome that has a common core of microbial species, but also a loser part that can change with changing events and environments. Consequently, this would enable not only storage of personal memories, but also storage of collective memories, since the microbiome can be transferred to the surrounding and to the next generation.

From the beginning of our lives, we are endowed with a certain microbiome that is based on the woman that gave birth to us, mostly our mother, and only later we become "infected" with other microbes from the father, the siblings, the environment etc. The initial microbiome may have a greater impact on our lives than we imagine, on our physical and mental health and thus also on our social standing. An interesting 3-month intervention trial was carried out in Bangladesh, in which a group of 123 slum-dwelling infants, 12-18 months, with moderate to acute malnutrition was fed a dietary supplement that was previously shown to bring about a healthy infant microbiome. This novel supplement was compared to a standard supplement used for treating malnourished babies. The study demonstrated that by changing slightly the nutritional content, even with a lower caloric content, not only a healthier microbiome was achieved, but also healthier blood proteins and better weight gain compared to the results of the standard supplement (Chen et al. 2021). This short-term intervention study together with the mice studies described above (particularly Buffington et al. 2021), demonstrate what an affect the microbiome can have on the well-being of an infant that may reflect on her or his life and may affect also the life of the surrounding people. In sum, eventually, when we find out what is the healthiest microbiome for each and one of us at each age and health state, it may be possible to contribute to the managing of autism, dementia and other diseases and improving social health as well..

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