The Metabolic Microbe: the historical split between medical and ecological Microbiology from a feminist approach

Author: Tamar Schneider, Ph.D.

https://orcid.org/0000-0001-8045-4691

(tamisch0106@gmail.com, tamarsc@openu.ac.il)

Affiliation: The Open University of Israel

Final draft forthcoming in Synthese

Abstract

This paper examines the historical split of microbiology into the fields of medicine and ecology from a feminist perspective, using Helen Longino's contextual empiricism and her onto-epistemic view of interactions. Examining microbial interactions is interesting for two reasons, one is ontological as microbial metabolic interactions constitute the bio-geo-chemical cycles that are the driving force of life on Earth. The second reason is epistemic, involving our conceptual challenges in understanding microbial traits and classification, as their activities and ability to evolve are, for the most part, driven by their interactions. I follow the work and methodology of Sergei Vinogradskii (1856-1953) and Robert Koch (1843-1910), as two main founders each of a different microbiology field. Koch focused on medicine, developing pure mass cultures and the Koch postulates. Vinogradskii focused on soil microbiology and ecosystem ecology, developing the elective culture technique, and is known for the Winogradsky Column. I use contextual empiricism to discuss their methodological differences in classification and cultivation and reflect on their position regarding microbial individuality and interactions. For instance, Vinogradskii's research focused on metabolic interactions and microbial life cycles, considering individual microbes as part of their environment and never in isolation. This view emphasizes the individual, the interactions, and the environment as equally focal in causal explanations. Thus, in his view, the individual should be studied as part of its milieu and never in isolation. Based on Longino's ontology of interactions, I elaborate on this view of the microbial individual in a given state of interdependence with changing levels of autonomy. This onto-epistemic

understanding of the microbial phenomena is empirically consistent with today's microbiome studies and discussions on host-holobiont definitions in microbiology, ecology, and medicine.

Keywords: microbiology; life cycle; autonomy; interdependence; interactions; individual

1. Introduction

The history of microbiology deals with three main issues concerning questions ofs classification and microbial activity: 1) the debate on microbial identification, morphisms, and lineages; 2) the study of pathogenic microbes and vaccine development; and 3) the study of microbial environmental activity such as fermentation and biogeochemical metabolism (O'Malley 2014). The first issue deals with the identification and classification of these microscopic organisms. The second and third concern their activity of interactions with their surroundings and the implications of such activity. These issues concern the concept of microbial individuality, whether relating to the unicellular microbe or a single species. Understanding microbial individuality is crucial in theory and methodology because of the microscopic scale and characteristics such as asexual reproduction, genetic exchange, and the tendency of microbes to live in symbiotic relationships.

In this work, I look at the onto-epistemic conceptualization of microbial individuality as reflected in the historical development of scientific practices in microbiology. I use Helen Longino's contextual empiricism and her onto-epistemic view of interactions in this historical split analysis. Longino's contextual empiricism is rooted within the feminist philosophy of science. She argues that science is social knowledge and that social interactions shape the epistemic practices of knowledge production. Furthermore, the ontology of interactions is foundational to her view not only of the processes of knowledge production but also of the conceptualization of the subject matter itself (Longino 1990). My analysis of the historical split in microbiology is based on Longino's philosophy of interactions. Thinking about the object or subject of study I follow the conceptualization of the microbial individual in early microbiology.

The epistemic and ontological aspects of microbial interactions make their study compelling for two reasons: first, microbial interactions and metabolic activity are significant events facilitating crucial chemical and environmental processes maintaining life on this planet including their roles in disease and decay. The second reason is that, as of today, there is still a lack of sufficient classification and species conceptualization of microbes similar to that of macro-organisms (Rinke et al. 2013; Hugenholtz et al 2016; Rainey et al. 2020; Schneider 2022).[1] Despite advances in molecular techniques for microbial identification, interactions such as horizontal gene transfer and mobile genetic elements can override genetic classification. Furthermore, microbial phenotypes can be heterogeneous depending on their interactions and dynamics in their respective ecological communities and niches (Rainey et al 2020; Quistad et al. 2020).

In the early 19th century the study of microbes was done by scholars from different fields such as chemistry, botany, zoology, and medicine, and later developed into distinct fields within microbiology, medicine, and other applied fields such as agriculture, the food industry, and soil microbiology (Ackert 2013; O'Malley 2014). Drawing on the historical work of Lloyd Ackert (2006, 2013), Mathias Grote (2018), and others, I discuss these differences focusing on two founders of microbiology Sergei Vinogradskii (1856 - 1953) and Robert Koch (1843 – 1910). Each is considered to be part of the founding of microbiology, Koch in medicine developing the pure culture and Vinogradskii in soil microbiology and ecosystem ecology developing the elective culture technique (Penn and Dworkin 1976; Carter 1988; Wainwright 1997; Grote 2018; Ackert 2013; O'Malley 2014).

Based on Longinian Critical Contextual Empiricism and feminist epistemic practices (Longino 1987, 1990, 1994, 2008, 2020, 2021), I examine the historical origins of conceptualizing the microbial individual as an object of study in microbiology: as the pathological microbe in

[1] Classification and the species concept for macro-organisms also present many conceptual challenges and puzzles, some dealing with similar questions that arise in microbiology. However, because of size and time scale, the heavy dependency on technology in microbiology highlights problems concerning issues that are less straightforward in the macro–world. For example, the practice of classification in microbiology is often based on the monoculture technique of growing a colony from a single cell.

medicine and the metabolic microbe in ecology. Each conceptualization describes the phenomenon in question (i.e., the object of study) emphasizing different aspects of microbial individuality. I show how these two objects of study in microbiology are framed within two ontological aspects of microbial individuality: autonomy, and interdependence. Autonomy and interdependence are two aspects of onto-epistemic causal explanations in general, however, each aspect is considered differently depending on the methodology and conceptualization of the object of study. I discuss the perspectives of the autonomy and interdependence frameworks in connection with their methodology, practices, and the types of questions related to the examined phenomena, such as pathogenicity, fermentation, and chemosynthesis. Discussing these scientific methodologies I show that the aspect of autonomy is associated with a structural interpretation of classification and the practice of pure culture, and the aspect of interdependence is associated with a functional interpretation of classification and the method of elective culture (which led to the development of the Winogradsky Column).[2]

I begin by discussing the interactionist perspective in microbiology drawing on the analysis of onto-epistemic interactions by Longino (2020, 2021) underlining the conceptualization of pathogenicity as belonging to the individuals, and the characterization of microbial biochemical processes within the context of interactions. I continue with the historical narratives in microbiology, starting with the debate on microbial morphology and its impact on Koch's and Vinogradskii's understanding of classification and their different methodologies. Then, I link the

[2] The elective culture method was designed to study bacterial metabolic processes, life cycles, and their environmental impact. The Winogradsky Column, a device named after Sergei Vinogradskii, demonstrates the functional dependency between microbial communities with different metabolic processes. The column is a mixture of mud and water containing various nutrients such as cellulose, eggshells (which contain calcium carbonate), and a source of sulfur. Left for several weeks in the light, the mud and nutrients in the cylindrical device start to sink, creating different patches with different levels of nutrients and oxygen. The microbial communities growing in the different patches have different metabolic functions, from anaerobic cellulose-degrading bacteria at the bottom to aerobic photosynthetic cyanobacteria at the top. This arrangement demonstrates a biochemical cycle. See also: https://tumblr.amnh.org/post/142650634919/make-your-own-microbial-medley-a-famous

interaction perspective with the view of the microbial life cycle and suggest this view better accommodates the growing knowledge of microbe-macrobe-environment relationships, providing an alternative conceptualization for microbiome studies and host-holobiont understanding of individuality.

2. Longino's ontological category of interactions and the conceptualization of microbial activity

In her analysis of scientific research on aggression, Longino identifies behavior as the object of study. She distinguishes between two forms of ontological categorization of behavior. One is an individualist categorization, studying behavior as a disposition understood as a property belonging to an interacting individual. The other categorization is interactionist, studying behavior as resulting from mutual exchange between interacting individuals within a certain social domain (e.g., workplace, family unit, or institutions) (Longino 2020, 2021). I use this distinction to think about the conceptualization of microbial activity and its possible two onto-epistemic ways of investigation, one is the study of microbial individuals by their morphological (i.e., structural, genetic) classification and the other is the focus on microbial interactions (activity or function).

The interactionist framework suggests a further examination of the processes of interaction and the dynamics of interaction patterns. This framework aims to shift "the focus from individuals and collections of individuals to an exchange between or among individuals, from stable objects to events or processes." (Longino 2021, 60). The ontological shift from stable individuals to processes does not marginalize individuals in favor of interactions but rather shifts the perspective from the individual's autonomy to that of interdependence. Also, the perspective on interaction discussed here is an onto-epistemic conceptualization of interactions as the object of study. This differs from frameworks or models in biology that focus on complex systems and modeling interaction networks. However, conceptualizing interactions as the object of study can also be applied in such cases.

The epistemic tendency to simplify complex natural phenomena is supported by focusing on individual entities and their classifications as the focal causal entity. Longino discusses the conceptualization of behavior in the study of aggression, and I discuss the conceptualization of microbial activity in microbiology. I show that microbial activity is conceptualized within the medical framework as either pathogenic, beneficial, or commensal, and in ecology, the microbe is studied through its metabolic activity. The germ theory of disease, based on Koch's apparatus of pure culture, has conceptualized microbial activity in the form of a trait belonging to an individual species, such as pathogenicity. Koch's postulates, connect the existence of a specifically identified microbe to disease through the isolation of this microbe from an organism with a disease and the successful infection of a healthy individual (Ross and Woodward 2016). Alternatively, Vinogradskii classified his bacteria by their physiological activity (specifically nutrition and respiration) and used the elective culture technique. This practice involves close observation of the change and exchange between organic and inorganic matter in the environment affecting the internal changes within the microbial cells to identify microbial metabolic activity. I elaborate more on these methodologies and their historical background in the next section.

The notion of interactions in this paper is understood as the process of mutual exchange, taken from an interactionist approach to social interactions as co-regulating mutually affecting individuals constituting a self-sustaining organization with a changing effect on the individuals' autonomy (De Jaegher et al. 2010, 442). This conceptualization also adopted by Longino is relevant here because of its emphasis on the interactions as the subject matter, and their influence (augmented or reduced) on the autonomy of the interacting individuals. It is important to note that the interactionist approach does not dismiss autonomy in favor of interdependence or co-dependence. Instead, it sees autonomy as the outcome of interactions and the context in which they occur. The definition here points to the process of interactions and their action of "co-regulating" and mutually affecting the individuals and their autonomy.

Longino’s ontology of interactions is a non-reductionist view that rejects the simplicity of identifying or classifying individuals' traits as sufficient to explain their interactions. Whether humans, groups, cells, or other entities, individuals are dynamic and influenced by their reactions and interactions with their milieu. By sharing a niche, they also impact and change it through their actions and interactions, creating interdependencies based on their shared ability to respond to their environment. A non-reductionist approach to studying microbial interactions involves considering individuals in their context and their interdependent relationships of becoming together (Schneider, 2021). Thus, the interactionist view regards the individual's autonomy as dynamic and relational, depending on the type of interactions within the social and environmental context, assuming autonomy lies on a spectrum (Longino 2020, 2021). The opposite reductionist approach looks for the individual’s disposition to react regardless of the context, reactions, and intentions. Using this analysis, I elaborate on this perspective in microbiology underlining the practices of bacteria cultivation and elective culture.[3]

My interpretation of Longino’s view on interactions regards interdependency through individuals’ mutual response-abilities to their niche (Haraway 2016; De La Bellacasa, 2017).[4] These actions not only change the environment and the individuals within it, but they are also responsible for an ongoing circular or spiral change of individuals becoming together (Haraway 2016). Therefore, this emphasis on interactions involves the entanglement and inseparability of individuals from their environment. In microbiology, this entanglement occurs both through the relationships of interdependence via environmental exchange (e.g., metabolic interactions) and through shared response-ability to their environmental niche modifications (Núñez Casal, 2021). The concept of interdependent relationships introduces an understanding of dynamic individuals, similar to Donna Haraway's idea of individuals becoming together (Haraway 2016). Thus, Longino’s interpretation of interactions as mutual exchanges and the necessity for a non-reductive study of interactions assumes that individuals are not static beings, but are constantly evolving (changing) through their interactions with others. These background beliefs concerning individuality presuppose that individuals are not simply standalone entities, but as entities in the process of becoming, situated within their context of interactions and intra-action (Barad 2007;

[3] I do not assume microbial intentionality but follow microbial ecological studies documenting heterogeneous metabolic pathways that depend on biotic and abiotic interactions.

[4] The term "response-ability" expands on the concept of responsibility by emphasizing the capacity to respond depending on the conditions and abilities available to them.

Haraway 2016).[5] In the following section, I will illustrate how Vinogradskii's research corresponds to this notion of interactions and dynamic individuals.

Centering on interaction as the phenomena in question involves questions about the frequency of the interactions, their temporal or spatial distribution, and the dynamics, and conditions that facilitate or inhibit certain interactions (Longino 2021). Furthermore, studying interactions means the shift from studying organisms and species as reliably stable or constant (e.g., pathogenic/non-pathogenic) to investigating them as contingent events or processes (such as the ecological classification by biochemical interactions of nitrogen-fixing bacteria). Therefore, the environmental context is an essential factor influencing the type of interactions that will be facilitated or inhibited. Thus, in the process of mutuality of interactions, it is crucial to comprehend the biotic and abiotic context. In social behavior, the context is culture and social institutions, and in microbiology, the context is the microbiomes in their geographical and environmental ecosystems. Context and interdependence are a given state for living organisms that breathe, grow, develop, and reproduce, resulting in changing levels of autonomy depending on the dynamics of the interactions. Therefore, from an interactionist perspective, individuals are interdependent, exhibinitng different levels of autonomy.

The psycho-social understanding of autonomy in psychology relies on the presupposition that autonomy is a process (not a state) that can change depending on the dynamics of interactions. The individual is never an isolated entity and cannot be understood outside of social connections and interactions. The individual's autonomy is measured by the way their interactions reduce or increase coercion. In this sense, autonomy is always relational and the context of relationships is a given (De Jaegher et al. 2010). In biology, the conceptualization of an individual usually entails its autonomy, and the autonomous individual is considered a given. The intuition connecting degrees of cohesion with interactions, autonomy, and dependence is the same. However, in biology, less autonomy also reflects on definitions of individuality - with less

[5] While Barad and Haraway make historical, cultural, and social claims regarding onto-epistemic perceptions of relationships and interactions in science, Longino focuses on background beliefs about interactions and relationships and their role in shaping the research questions and the object of study. I thank the anonymous reviewer for this clarification.

autonomy the biological entity is thought to be less of a distinct individual (Godfrey-Smith 2013; Clarke 2013). This means that an entity with cohesive interactions with other entities can lose its onto-epistemic individuality. Using an interactionist perspective from a feminist approach, I wish to challenge this perception of individuality in biology and microbiology, introducing the view of individuals as events of becoming together.

Viewing the autonomous aspect of the individual as relational and dependent on the dynamics of interactions is less intuitive in biology. How is it possible to be both an individual and an entity with low autonomy? Is it possible to experience levels of autonomy while remaining under the category of individuality? How should levels of autonomy be defined in relation to interdependence? The interactionist perspective analyzes levels of autonomy as construed within conditions of interdependence (of entanglement and becoming together through interactions and intra-actions) defined by different types and dynamics of interactions. In this sense, interactions are multidimensional and can be good or bad, leading to growth or decay. This onto-epistemic approach to individuality consists of the relationships of response-ability as part of sharing the ecological niche (Haraway 2016, 125). In the rest of this paper, I discuss the different individualist and interactionist conceptualizations of microbial activity following Koch’s and Vinogradskii's methodologies and practices.

3. Koch’s and Vinogradskii’s background, motivation, and methodologies

In their 1976 paper, Penn and Dworkin describe two visions of microbiology: essentialist and interactionist, attributing the former to Koch and the latter to Vinogradskii. Koch’s attitude toward pure cultures is considered an essentialist view “of microbial cells as independent entities possessing an intrinsic anatomic and physiological scenario.” In contrast, Vinogradskii's approach considers the microbial cell as ”always located in cell populations, and their physical and chemical properties derive, accordingly, from various interactive processes within the population.” (Penn & Dworkin 1976, 279-280). In this section, I discuss Vinogradskii’s practice of locating microbial properties as derived from their environmental interactions, showing its epistemic difference from Koch's practices, **which reflected an essentialist view of microbial specificity** in the germ theory of disease.

In 2013, the microbiologist Tanja Woyke coined the term Microbial Dark Matter to express the classification enigma microbiologists face when attempting to identify microbial species from environmental sampling. Despite new and advanced molecular technologies, which reveal such a wide variety of microbial life, specific identification seems almost impossible (Rinke et al. 2013; Hugenholtz et al 2016). These classification challenges date back to the early days of microbiology. Microbial classification deals with spatial and temporal challenges posed by microbes' minuscule size and short life cycles. Depending on technology, observations of microbes during the mid-19th and early 20th centuries allowed only a limited understanding of their morphology and physiology. Better accessibility to the microbial genome and molecular activity offer only a wider glimpse into this immense complexity and heterogeneous microbial life, raising old-forgotten, and falsified perspectives from the dusty 19th-century microbiology (Doolittle 2013). With the discoveries of rapid dynamic morphological and phenotypic changes (e.g., horizontal genetic transfer, mobile genetic elements, and phenotypic heterogeneity), these minuscule organisms still challenge our understanding of processes, such as reproduction, development, and growth at a microscopic level.

The famous debate over spontaneous generation vs. lineage heritability was settled in the late 19th century. This debate was also part of a general inquiry into microbial (mostly bacteria and yeast) classification, growth, and reproduction. As part of this microbial investigation, the question of microbial morphology and classification was also debated (Lankester 1886; Penn and Dworkin 1976; Wainwright 1997; Doolittle 2013; Ackert 2013; Grote 2018). One way of understanding the many different microbial shapes and growth rates within a culture flask was by attempting to find a mutual trait/property that can establish linear and developmental continuity between the different morphological shapes (Lankester 1886; Wainwright 1997). However, in solving this puzzle of two or more forms of cells existing in the same cultured flask, two camps formed with different presuppositions regarding microbial genealogy and classification. One held a monomorphic perspective, arguing that different cell forms belonged to different species. The other held a pleomorphism belief, which viewed the different morphological forms as different stages of developmental or environmental adaptations of the same species (Ackert 2013; Doolittle 2013; Grote 2018).

Pleomorphism is the general understanding that the morphological diversity within an individual species results from environmental conditions and a complex life cycle (similar to that of a butterfly). Believing that one species can go through many morphological or physiological variations, the pleomorphic understanding of classification demanded grouping together what monomorphism would describe as distinct genera. Monomorphism, the accepted view today, holds that the bacterial world can be classified into different genera and species by their relatively stable heritable characteristics. Therefore, the practice of pure culture developed by Koch and others in the monomorphism camp was central to the debate concerning microbial classification and activity, as it stabilized microbial plasticity and heritability.

Classification of microbes (mainly fungi) demanded a fine-grain observation of properties and their heritability, which could only be provided by various cultivation techniques. The first observations of microbes such as fungi and algae by 19th-century botanists and microbiologists such as Anton De Bray, Oscar Brefeld, and Ferdinand Cohn established the early understanding of microbial reproduction and life cycles (Carter 1988; Grote 2018). For these first observations, botanists used various cultivation practices in the lab similar to those used for plants (Ackert 2013; Doolittle 2013; O'Malley 2014). Later, these observation practices developed into culturing techniques used for bacterial identification and led to the first observations of bacterial spores and germination in the late 1870s by Cohn, Pasteur, and Koch (Carter 1988; Drews 2000; Dworkin 2012; Grote 2018).

Observations of microbial variations cultivated in the lab faced dismissal from the monomorphism camp, which attributed such multiple morphologies to impure or contaminated culture media (Carter 1988; Wainwright 1997; Grote 2018). Koch's isolation techniques, starting from a single cell, centered observing the continuity of similar morphology during the colony's growth for several generations without change. If, during cultivation, there were some morphological changes in the microbial cells, it was an indication of contamination. The lack of morphological changes indicated purity and an undisturbed process of heredity (Grote 2018). This technique also provided a clear approach to bacterial processes of reproduction and heredity, which settled the monomorphic/pleomorphic debate, also placing the study of bacteriology within an evolutionary context (Sakula 1982; Carter 1988; Grote 2018). Therefore, it is easy to see how such evolutionary presuppositions could benefit from the apparatus of pure culture, constraining all developmental processes of bacteria, narrowing them to clonal growth in isolation while marginalizing morphological transformations and environmental changes as confounding variables (Ackert 2013).[6]

Both Koch and Vinogradskii belonged to the microbial monomorphism camp and followed Cohn's taxonomy (Penn and Dworkin 1976; Drews 2000; Ackert 2013; Grote 2018). For Koch and others in the monomorphism camp, the practice of classification by pure culture and its verification of monomorphism fit well with a bacterial etiology that emphasized inherent microbial properties. This, however, was not intuitive for Vinogradskii's physiological approach. Although they shared the monomorphic perspective and the practice of culturing in the lab for the identification of species, they differed in their attitude toward culturing techniques as the means of understanding microbial activity and causality. This difference in attitude also arose from their backgrounds, scientific training, and cognitive goals. Koch aimed to prove the germ theory of disease, while Vinogradskii aimed to prove the germ theory of fermentation. Koch and Vinogradskii studied bacterial effects on their surroundings with different motivations, each developing a distinct apparatus. Thus, the cultivated bacterial medium played a different role in their investigations.

Koch studied medicine and was a practicing physician also serving as a public health official and Vinogradskii studied botany and came from a family of farmers. It is clear to see that each occupation and training background had a great influence on how they perceived the aim of their study and their epistemic motivation. Koch emphasized the specific aspect of bacterial interactions with a host leading to a pathological condition. He was interested in proving the germ theory of disease (Dworkin 2012). Vinogradskii came to study bacteriology from his training in botany, experimenting with the life cycles of fungi and learning about their nutritional and respiration from a thermodynamic perspective of matter and energy flow. He was interested

---

[6] Vinogradskii's investigation did not aim to exploring these organisms' complex adaptation processes within the framework of natural selection (Ackert 2013, pp 30 - 31). Even if he was aware of such issues, he did not invest in asking questions limited to heritable versus acquired traits, striving instead to understand the metabolic and respiratory factors in the processes of their life cycle.

in Pasteur's germ theory of fermentation and in providing scientific proof of the bacterial role in these biochemical processes (Dworkin 2012; Ackert 2013).

Koch's use of a solid medium was a helpful tool in creating morphological stability and enabling the observation of microbial growth by cloning (Dworkin 2012; Grote 2018). His striving to discover the etiology of disease in the form of a single bacterial species is known for his contribution to developing ager-ager solid medium (Sakula 1982; Carter 1988; Grote 2018).[7] This method of pure cultures enabled the observation and measurement of microbial generations in uniformity or purity by growing a single cell into a colony to its full capacity on a petri dish. To ensure the causal connection between bacteria and the disease, the pure culture apparatus simulated their generational development, demonstrating heredity from parent to offspring and guaranteeing the same germline (Koch 1876). The end goal for Koch was to separate a single bacteria species taken from a sick host's tissues and fluids isolating from other microbes.

Purity and uniformity of the culture were so important for Koch, that during his first attempts to find the etiology of Anthrax, he was the first to note the bacterial life cycle and the formation of spores, but considered these findings, as important as they were, to be an obstacle in establishing the protocol of causality (Carter 1988; Drews 2000; Grote 2018). This causal explanation relies on the feasibility of establishing a pure culture of a single species, and on the binary categorization of a single microbial species as either pathogenic or non-pathogenic, regardless of its context (i.e., background condition, interdependence, and mutual interactions. Thus, to establish a causal connection between the cloned bacteria and the developed symptoms of a disease, Koch re-conceptualized pathogenicity as an inherent microbial property (Sakula 1982; Carter 1988; Grote 2018).[8]

---

[7] Koch's methods relay on the successful innovation of his two colleagues: the flat petri dish named after R. J. Petri and the ager medium, the use of which was suggested by Fanny Hesse and subsequently developed by her husband Walter Hesse (Hitchens and Leikind 1939).

[8] This approach involves observing, measuring, and collecting data on bacterial growth in isolation based on the assumption of generalizability across host conditions. However, because of the requirement for purity and monomorphological restrictions, successfully isolating cultivating the putative microbe was already challenging in Koch's time (Sakula 1982; Carter

Vinogradskii was exceptional in his approach to the study of microbes because he rejected the view of pleomorphism of any sort, but also strongly criticized the striving for pure culture universality. For him, such striving for uniformity that ignores the biological dynamics of the organism's physiology, development, and decay was artificial (Penn and Dworkin 1976; Wainwright 1997; Ackert 2013; Grote 2018). Therefore, he argued that observations should be conducted as close to natural conditions as possible (Ackert 2013; Grote 2018). His unique position on monomorphism also informed his classification techniques, which considered microbial physiology (not morphology) as classification criteria.[9] He was interested in the understanding microbial metabolic and respiratory activity, which involved consuming matter from the environment and converting it to energy. This means that the questions leading his attempts to cultivate microbes centered around the chemical changes in their environment and the role of such changes in the microbial life cycle i.e., development and growth. Thus, his cultivation processes were not concerned with morphological continuity but rather aimed at investigating the metabolic activity of converting inorganic matter (e.g., Sulfur in *Beggiatoa*, iron in Leptothrix, and eventually nitrogen fixation) to cellular energy (Ackert 2013, p. 69).

In his *Beggiatoa* experiments, Vinogradskii discovered the microbial ability to absorb minerals from the environment, and then oxidize them in a metabolic process while releasing by-products

1988; Ross and Woodward 2016). Although he successfully identifyed organisms causing diseases such as anthrax, and tetanus, Koch acknowledged that other putative agents did not meet all the postulates (Evans 1976; Fredericks and Relman 1996).

[9] Vinogradskii was influenced by his graduate teacher, the Russian botanist Andrei Famintsyn (1835 - 1918). Famintsyn was interested in plant life cycle from a thermodynamic perspective, investigating plant physiology and photosynthesis (Ackert 2013, p.25 - 40). Famintsyn's approach to plant physiology, viewing it from the perspective of the exchange of matter and transformation of energy, emphasized these processes of interactions over the individual morphological growth of the plant, as quoted by Ackert on p. 25: “Famintsyn explained that “[t]he necessary condition for the life of every living organism—both plants and animals—is the acquisition of food from without and its conversion into organized formations—cells and tissues; the life and growth of the organism are sustained by the exchange of matter with the surrounding environment.” (Famintsyn 1883, 141).”

into the surrounding environment. His physiological classification framework led his investigation to look for mutual interactions involving the exchange between the bacteria and the environment. Looking for such exchange, he created a cultivation technique to follow the movements and correlations between environmental changes, on the one hand, and bacterial physiological changes, on the other. For example, his *Beggiatoa* project investigated the appearance and disappearance of the sulfur granules within the bacterial filaments. Unlike others, he rejected the assumption that these granules were merely morphological and was interested in their physiological role in the bacterial nutrition and respiration processes. Thus, differently from his peers, he asked about the role of these sulfur granules in the bacterial life cycle (Ackert 2013, 56). Looking for the answer, he discovered the bacterial ability to use hydrogen sulfide as an energy source by oxidizing it. Later, he generalized this ability as a physiological classification criterion for organisms with the ability to oxidizse inorganic chemicals to generate energy (i.e., chemolithotrophy).[10]

Vinogradskii's investigation of the microbial ability to absorb minerals from the environment and then release by-products into the surroundings also led him to look for signs of changes occuring in the macro-environment, such as changes in the medium's colors and texture (Ackert 2013, 81). Based on the *Beggiatoa* studies, when studying nitrification, Vinogradskii hypothesized the microbial metabolic process of oxidation and set out to prove it. Nitrification, he suggested, was the biological oxidation of ammonia similar to the biological oxidation of sulfur by the *Beggiatoa*. In this experiment, Vinogradskii needed to observe the molecular exchange and transformation between the bacteria and the inorganic ammonia without having the observable granules in the cells. Thus, he created an elective culture mix of water with a direct sample from the soil and inorganic ammonia (see footnote 2, for a better understanding of this practice). Then, he observed the ammonia salt changing color and texture after a few days from solid white to gray with a gelatinous consistency, and using a sample under the microscope, he saw the bacterial cells around this gray matter (Ackert 2013, 80). The next task was of isolating the specific bacteria responsible for the process of ammonia oxidation. However, to show the

[10] Chemolithotrophy became a subgroup in a larger classification of autotrophs organisms that can convert inorganic compounds into organic matter. Autotrophs also include photosynthesis and chemosynthesis organisms and microbes.

metabolic activity, it was not enough to isolate this bacterium on a petri dish. To prove the actual process of exchange of matter, the bacteria needed to grow while digesting the minerals, showing the environmental changes and the conversion from inorganic to organic matter.

Both Grote and Ackert discuss Vinogradskii's unique position of connecting monomorphism with a complex life cycle, leading to his physiological classification (Penn and Dworkin 1976; Ackert 2013; Grote 2018). I wish to highlight the difference between morphological and physiological classification/investigation, pointing to the onto-epistemic aspects of individuality. While the pure culture in a solid medium equated growth in isolation with morphological identification, the elective culture was designed to investigate the process of microbial nutrition and respiration. Thus, for Vinogradskii, the ability to cultivate and grow the bacteria in the changing medium was proof of the successful process of mutual exchange of matter between the bacteria and its environment. In other words, the issue of classification and species distinction can be discussed within two ontological frames: thinking of species within the frame of the autonomous individual, in which a species definition should be based on its morphology that remains stable in time and space (held by Koch and the pure culture technique); or, thinking of species within the frame of interactions among entities going through cycles of change in time and space by physiological processes of metabolism and respiration (manifesting in Vinogradskii's elective cultures).

4. The ontology of microbial interactions: autonomy and interdependence

Ackert in his book identifies two syntheses done by Vinogradskii. The first synthesis is between the notion of thermodynamics in plants with Pasteur's germ theory of fermentation. In his first project, Vinogradskii investigated the life cycle of the microbial fungus *Mycoderma*, incorporating the ideas of thermodynamics and the exchange of matter and energy in botany synthesized with the Pasteurian germ theory of fermentation (Ackert 2013, pp.3 - 36). Right from the start, Vinogradskii conceptualized the fungus's activity from the perspective of its metabolic interactions as part of its life cycle. The different stages of the fungal life cycle result from its nutritional and respiratory interactions with the environment. These interactions release metabolic by-products that alter the environment, leading to fermentation processes. Hence, the decision to explore the microbial life cycle framed the research topic as the interplay between the microbes and their environment. This approach also led Vinogradskii to study microbial activity by examining their metabolic and environmental interactions (biochemical interactions) using elective culture techniques.

The second synthesis is between monomorphism and microbial physiology. After his work on the fungi *mycoderma*, Vinogradskii continued to study the bacteria *Beggiatoa*'s ability to oxidize hydrogen sulfide. To disqualify the claims of pleomorphism, he showed that the various appearances of sulfur granules in the bacterial cells were part of its life cycle in sulfur springs (Ackert 2013 p.56-58). Here, Vinogradskii synthesized the notion of microbial taxonomy and classification developed by Cohn and Koch, and based on microbial monomorphism, with his already conceptualized notion of the bacteria physiology and life cycle. Both conceptual syntheses of the thermodynamics and monomorphic life cycle view the individual organism (or species) through its life cycle of biotic and abiotic interactions.

To prove the germ theory of disease, Koch centered on the homogeneity and specificity of a single species and its unidirectional causality. He conceptualized the pathogenic trait as belonging to the bacterial organism and, therefore, was looking for a single species with a specific trait responsible for the disease. Vinogradskii, alternatively, resisting the intuition forwarded by the stable morphology and the pure culture technique, developed the elective culture as a way of studying the biochemical interactions between the bacteria and their biotic and abiotic environment. This allowed him to examine the physiology of the organisms and their metabolic interactions. Furthermore, because of his view regarding microbial interactions and the life cycle, he criticized the inferences about microbial life based mainly on laboratory studies as insufficient for understanding their interactions. A good demonstrating of these differences in conceptualizing microbial interactions from a reductive or non-reductive perspective is discussed in Grote's paper on the background assumptions needed for the practice of pure culture, on page 9:

> The pure culture technique implied, first, that microbes could be generally grown apart from their original environments (i.e., that one would catch what was present in a sample), and second, that growing a parasitic microbe on a plate, for example, would not significantly change its characteristics (Hueppe 1889, p. 108).

Pure cultivation practices necessitate the assumption that bacterial cells can grow and develop independently of their biotic and abiotic environment. Particularly, regarding pathogenic microbes, the assumption is that they grow and develop independently of their host. considering Vinogradskii's practices involving the cultivation of microbes in isolation, he shared at least some notions regarding the first assumption. However, he rejected the second assumption - that growing a pathogenic or parasitic organism in isolation gives sufficient information about its behavior, growth, and development, especially when investigating the microbial life cycle.

With his unique training in botany, Vinogradskii did not believe organisms could be studied without their environmental and organismal context (i.e. their interactions of mutual exchange of matter and energy flow, such as metabolism and cross-feeding). Ackert explains Vinogradskii's critical view of soil microbiology that relies solely on practices of laboratory observations using pure cultures:

> For Vinogradskii, soil microbiology lacked a comprehensive method that combined laboratory experiments with the wildness of nature. Microbiologists, for example, had studied microbes in determined and extremely varied conditions of artificial cultures; however, they had followed microbial activity in their natural environment "only mentally." 51 Soil biochemistry, on the other hand, was too limited in scope because it studied only the ultimate chemical effects that occurred in the soil without ever considering the agents indicated by microbiological investigations (the micro fl ora). Consequently, even the combination of these two approaches (he thought of them as categories of facts) could produce no substantial results because they did not rely on direct experiments. They could offer, thus, only weak hypothetical conclusions. (Ackert 2013, p. 118)

What was lacking in pure culture practice according to Vinogradskii, was a profound understanding of the interactions between the organisms and their environment. He was interested in the identification of different species by their physiological processes, which demanded an understanding of their interactions with the biotic and abiotic environment. Thus, Vinogradskii's insistence on biochemical activity as the subject of investigation led him to perceive microbial individuals as entities that are also entangled, becoming together, or interdependently part of their biotic and abiotic environment. Furthermore, after his nitrogen-fixing studies, he generalized such interdependent relationships as necessary for the growth and thriving of plants everywhere (Ackert 2013, 82). The reason for his generalization was his understanding of the microbial (or biological) response-ability for the chemical processes in the soil and water.

The epistemic framework of thinking with interactions in its broader scope includes the understanding of interacting individuals, their mutual effects, and the environmental context. This emphasis was also held by Vinogradskii regarding the significance of observation in the natural environment, or as close as possible to the natural environment using direct methods (Ackert 2013; Dworkin 2012; Grote 2018). The epistemology of interactions necessitates contextualizing the individual. Isolating knowledge from its natural context is insufficient, though it can be part of the investigation. This approach presents an interactionist ecological perspective. It views individuals as being interdependent while also experiencing changing levels of autonomy. The interdependent life cycle of organisms is rooted in the basic activities of a living being: breathing and metabolizing. Therefore, the individual organism is not distinguished from such ecological interactions but is a part of them, mutually developing and becoming together.

The differences between Koch's and Vinogradskii's methodologies point to the differing conceptualizations of the microbial individual as the object of study in medicine and ecology. In medicine, microbial individuality is construed as autonomous, defined bys innate traits. In ecology, microbial individuality is viewed as interdependent due to its environmental interactions, understood as a process of becoming together as part of its life cycle. When considering microbial individuality as a process of interdependence with various levels of autonomy, the scientific examination centers on the biotic and abiotic interactions and the environmental conditions that shape their metabolic and molecular activity. In this view of individuality, interactions of cohesion and levels of dependency do not determine microbial individuality. As an interdependent being, microbial individuality is a given. Therefore, the inquiry focuses on the various heterogeneous interactions and changing levels of autonomy. This differs from the perspective of microbial individuality as autonomous, wherein levels of interdependency are considered the criteria for its individuality.

Today, microbial ecology studies how microorganisms interact and change over time, particularly concerning their metabolic processes. For instance, oceanic microbiology studies show the dynamic nature of microbial pathogenicity. Researchers found that the same microbes are harmful in some environments, while harmless or beneficial in others, depending on their interactions (Beiralas et al. 2023). This perspective acknowledges that microbes are interdependent entities with varying degrees of autonomy. It also aligns with the ongoing complexities of microbial behavior, including their ability to exchange genetic material and coordinate their physical characteristics. Understanding the microbial pathogenic or beneficial role in their community also impacts the debate about holobiont individuality. Pathogenic microbes are typically considered antagonistic and not seen as part of the interactive holobiont. However, if pathogenicity depends on the type of interactions and the environmental context, then pathogenic activity may no longer be a relevant criterion for defining the holobiont's individuality.

Furthermore, this change in perspective from an autonomous to an interdependent individual cannot solve the holobiont debate regarding individuality when based on an autonomous perspective. Many arguments for or against holobiont individuality rely on the cohesive and obligatory interactions between the host organism and its microbial symbionts (Godfrey-Smith 2013; Clarke 2013). These arguments are based on the idea that higher levels of interdependency lead to reduced individuality of the symbionts, i.e., reduced autonomy means reduced individuality. However, Vinogradskii's unique perspective on the organism's life cycle and physiology pictures the individual organism as an ongoing process of heterogeneous interactions that are part of its cycle of life and decay. This understanding of an interdependent individual does not separate or distinguish the individual organism from its close and intimate milieu. Thus, the individual microbe and its microbial community are 'becoming together' just as the individual host and its microbial communities are 'becoming together'.

5. Conclusions

In this paper, I have discussed the historical split of microbial ecology from medical microbiology from a feminist approach, elaborating on the different ontological aspects of microbial individuality. Starting with the debate on microbial morphology, I explored the cognitive goals and background beliefs that shaped the object of study in microbiology and the epistemic attitude towards microbial individuality and its levels of autonomy. When discussing the ontological perspectives on individuality, I presented Koch's conceptualization of pathogenic bacteria, and Vinogradskii development of the direct method of observing the organism in its environment and conceptualizing the metabolic microbe. Lastly, I showed how Vinogradskii's insistence on connecting monomorphism with the notion of the microbial life cycle portrayed an ontology of interdependent microbial individuals with levels of autonomy.

This analysis employs feminist philosophy of science and feminist epistemology to highlight the social and political dimensions of scientific inquiry. This perspective enables a critical examination of how background assumptions and values—both epistemic and non-epistemic—shape scientific practices. A feminist philosophical approach, while focused on exposing narrow, biased, or potentially harmful epistemic perspectives, also aims to bring forth the narratives of individuals from minority or oppressed groups. While this analysis centers on narratives of the privileged (i.e., white middle-class males) scientists such as Koch and Vinogradskii, I believe this illustration of a feminist onto-epistemic lens can encourage further exploration of other silenced narratives and promote interaction-based research methodologies.[11]

I used the ontological category of interaction suggested by Longino to distinguish between Koch and Vinogradskii and their two ways of conceptualization of microbes, from the perspective of autonomy and that of interdependence. Understanding the two different ontological/epistemic attitudes in microbiology and their motivations can help shift the conceptualization of microbial activity from questions centering on species properties to investigating the dynamics of interactions. The interactionist perspective offers ways of understanding pathogenic properties not as inherent traits but as arising from patterns or types of interactions and their environmental conditions.

Today, microbiome studies in ecology continue Vinogradskii's perspective of investigation, studying the dynamics of interactions that facilitate changes in microbial metabolic pathways and activity (Segev et al. 2016). In medicine, on the other hand, the examination of interactions is more complex, involving the host's immune and tissue cells among other environmental conditions (Finlay et al. 2021). With advancements in technological practices of microbial culture-independent classification of microbes, this distinction between medical and ecological

[11] I thank the anonymous reviewer for requesting this clarification.

investigation is narrowing. Furthermore, with the increasing evidence of microbiome-related pathological conditions, the conceptualization of good and bad bacteria is starting to crack. Between the two poles of biochemical processes and genotypic traits, conceptualizing microbial activity through interactions is as relevant as ever, not only in ecology but also in medicine.

References

Ackert, Lloyd (2006) The Role of Microbes in Agriculture: Sergei Vinogradskii's Discovery and Investigation of Chemosynthesis, 1880–1910. Journal of the History of Biology, 39: 373–406 DOI 10.1007/s10739-006-0008-2

Ackert, Lloyd (2013) *Sergei Vinogradskii and the Cycle of Life: From the Thermodynamics of Life to Ecological Microbiology*, 1850–1950. Archimedes (ARIM, volume 34). DOI 10.1007/978-94-007-5198-9

Barad, Karen (2007) *Meeting the Univers Halfway: Quantum Physics and the entanglement of matter and meaning*. Duke University Press, Durham London.

Beiralas, Roni., Ozer, Noy. & Segev, Einat. (2023) Abundant Sulfitobacter marine bacteria protect Emiliania huxleyi algae from pathogenic bacteria. ISME Communication, 3, 100. https://doi.org/10.1038/s43705-023-00311-y

Carter, K Codell (1988) The Koch-Pasteur Dispute on Establishing the Cause of Anthrax. Bulletin of the History of Medicine, 62(1), 42–57. http://www.jstor.org/stable/44449292

Clarke, Ellen (2013). The Multiple Realizability of Biological Individuals. Journal of Philosophy 110 (8):413-435.

De Jaegher, H., Di Paolo, E., and S. Gallagher (2010) Can Social Interaction Constitute Social Cognition? Trends in Cognitive Sciences 14,10: 441–447. DOI: 10.1016/j.tics.20

De La Bellacasa, Maria. P (2017) Matters of Care: Speculative Ethics in More than Human Worlds. University of Minnesota.

Doolittle, W Ford (2013) Microbial neopleomorphism. Biology and Philosophy 28, 351–378. https://doi.org/10.1007/s10539-012-9358-7

Drews, Gerhart (2000) The roots of microbiology and the influence of Ferdinand Cohn on microbiology of the 19th century, FEMS Microbiology Reviews, 24, 3: 225–249, https://doi.org/10.1111/j.1574-6976.2000.tb00540.x

Dworkin, Martin (2012) Sergei Winogradsky: a founder of modern microbiology and the first microbial ecologist. FEMS Microbiology Reviews, 36, 2: 364–379. https://doi.org/10.1111/j.1574-6976.2011.00299.x

Evans AS (1976) Causation and disease: the Henle-Koch postulates revisited. The Yale journal of biology and medicine, 49(2), 175–195. https://www.ncbi.nlm.nih.gov/pmc/articles/PMC2595276/

Famintsyn, A. S. 1883. Obmen Veshchestvo i Prevrashchenie Ehnergii v Rasteniiakh [The exchange of matter and the transformation of energy in plants]. Sankt-Peterburg: Imperatorskoi Akademii Nauk.

Finlay, B.B.; Amato, K.R.; Azad, M.; Blaser, M.J.; Bosch, T.C.G.; Chu, H.; Dominguez-Bello, M.G.; Ehrlich, S.D.; Elinav, E.; Geva-Zatorsky, N.; et al. (2023) The hygiene hypothesis, the COVID pandemic, and consequences for the human microbiome. *Proceedings of the National Academy of Science*, 118, e2010217118. https://doi.org/10.1073/pnas.2010217118

Godfrey-Smith, P. 2013. "Darwinian Individuals." (In) From Groups to Individuals: Evolution and Emerging Individuality, (ed) F. Bouchard and P. Huneman, 17–36. Cambridge: MIT Press.

Grote, Mathias (2018) Petri dish versus Winogradsky column: a longue durée perspective on purity and diversity in microbiology, 1880s–1980s. History and Philosophy of the Life Sciences 40, 11. https://doi.org/10.1007/s40656-017-0175-9

Haraway, Donna (2016) *Staying with the Trouble: Making Kin in the Cthulucene.* Duke University Press, Durham London.

Hitchens, Arthur Parker, and Leikind, Morris C (1939) The Introduction of Agar-agar into Bacteriology. Journal of Bacteriology, 37,5: 485-493. https://doi.org/10.1128/jb.37.5.485-493.1939

Hugenholtz, Philip, Adam Skarshewski, and Donovan H. Parks. 2016. “Genome-Based Microbial Taxonomy Coming of Age.” Cold Spring Harbor Perspectives in Biology 8(6):a018085. https://doi.org/10.1101/cshperspect.a018085

Hueppe, F. (1889). Die Methoden der Bakterienforschung. Wiesbaden: C.W. Kreidel.

Koch R (1876) The etiology of anthrax, founded on the course of development of the Bacillus anthracis. In: Carter KC (ed) Essays of Robert Koch. Praeger, Westport, pp 1–18

Lankester E Ray (1886) The pleomorphism of the Schizophyta. Nature 33:413–415

Longino Helen E. (1987). Can There Be a Feminist Science? Hypatia, 2(3), 51–64. http://www.jstor.org/stable/3810122

Longino, Helen E (1990) *Science As Social Knowledge*. Princeton: Princeton University Press.

Longino Helen E. (1994). In Search of Feminist Epistemology. The Monist, 77(4), 472–485. http://www.jstor.org/stable/27903405

Longino, Helen E (2008) Values, heuristics, and the politics of knowledge. In: Carrier M, Howard D, Kourany JA (eds) The challenge of the social and the pressure of practice, science and values revisited. University of Pittsburgh Press, Pittsburgh, pp 68–86.

Longino, Helen E (2020) Interaction: a case for ontological pluralism. Interdisciplinary Science Reviews, Volume 45, 2020 - Issue 3: Making Sense of Metaphor: Evelyn Fox Keller and commentators on language and science, pp 432-445 https://doi.org/10.1080/03080188.2020.1794385

Longino, Helen E (2021) Scaling up; scaling down: What’s missing? Synthese 198, 2849–2863. https://doi.org/10.1007/s11229-019-02249-y

Núñez Casal, Andrea (2021) Feminist Para-Ethnographies: A Proposition for a ‘Critical Friendship’ Between Embodied Experiences and Microbiome Science. *London Journal of Critical Thought*, 4, no 1 (2021): 21-35.

O’Malley Maureen A. (2014) *Philosophy of Microbiology*. Cambridge University Press, United Kingdom.

Penn, Mischa and Dworkin, Martin (1976) Robert Koch and two visions of microbiology. Bacteriological Reviews, 40(2), 276–283. https://doi.org/10.1128/br.40.2.276-283.1976

Quistad, Steven D., Guilhem Doulcier, Paul B Rainey. 2020. Experimental manipulation of selfish genetic elements links genes to microbial community function. Philosophical Transactions Royal Society B, 375, 20190681. http://dx.doi.org/10.1098/rstb.2019.0681

Rainey, Paul B., Steven D. Quistad. 2020. Toward a dynamical understanding of microbial communities. Philosophical Transactions of the Royal Society B, 375, 20190248. http://dx.doi.org/10.1098/rstb.2019.0248

Ross Lauren N, Woodward James F (2016) Koch's postulates: An interventionist perspective. Studies in History and Philosophy of Biological and Biomedical Sciences 59:35-46. http://dx.doi.org/10.1016/j.shpsc.2016.06.001

Rinke, C., Schwientek, P., Sczyrba, A. Natalia N. Ivanova, Iain J. Anderson, Jan-Fang Cheng, Aaron Darling, Stephanie Malfatti, Brandon K. Swan, Esther A. Gies, Jeremy A. Dodsworth, Brian P. Hedlund, George Tsiamis, Stefan M. Sievert, Wen-Tso Liu, Jonathan A. Eisen, Steven J. Hallam, Nikos C. Kyrpides, Ramunas Stepanauskas, Edward M. Rubin, Philip Hugenholtz1 & Tanja Woyke. (2013). Insights into the phylogeny and coding potential of microbial dark matter. *Nature* 499, 431–437 https://doi.org/10.1038/nature12352

Sakula Alex (1982) Robert Koch: centenary of the discovery of the tubercle bacillus, 1882. Thorax, 37(4), 246–251. https://doi.org/10.1136/thx.37.4.246

Segev, Einat., Thomas P Wyche, Ki Hyun Kim, Jörn Petersen, Claire Ellebrandt, Hera Vlamakis, Natasha Barteneva, Joseph N Paulson, Liraz Chai Jon Clardy Roberto Kolter (2016) Dynamic metabolic exchange governs a marine algal-bacterial interaction. *eLife* 5:e17473. https://doi.org/10.7554/eLife.17473

Schneider, T. (2022). Different Meaning in Different Sizes: Ecology in Size Scales. Philosophy of Science, 89(5), 1134-1144. doi:10.1017/psa.2022.48

Wainwright, Milton (1997). Extreme Pleomorphism and the Bacterial Life Cycle: A Forgotten Controversy. Perspectives in Biology and Medicine, 40(3), 407-414. doi:10.1353/pbm.1997.0038.

Winogradsky, Serge. 1949. Microbiologie du Sol: Problèmes et Méthodes, Cinquante ans de Recherches, Ouvres Complètes . Paris: Masson et Cie.