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Organizing Microbial Diversity and Interspecies Relations through Diagrams: Trees, Maps, and the Visual Semiotics of the Living

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Abstract

This paper aims to understand how and why tree diagrams are of central importance to microbiome scientists in their practices of meaning making. The interfaces that scientists use are, in fact, topological structures that organize the genetic data generated by sequencing technology. They establish relationships among microbes and also between microbes and the conditions of the ecological niche they help construct. The tree structure is a powerful *topos* of knowledge organization in Western culture. However, biomolecular research has revealed the existence of horizontal gene exchange among microbes and other merging forms; these cast doubt on the tree as a valid representational metaphor for the tangle of the microbial world and help to overcome neo-Darwinism. This essay analyzes the software and interfaces used by microbiome scientists as tools for organizing knowledge that shape how we see human-microbe relationships, while escaping a representational function. While trees have long been considered representative forms of visualization of an evolutionary paradigm, we emphasize the non-illustrative and heuristic power of these interfaces, which, although steeped in centuries of reflection and debate on evolutionary theories, respond more to a diagrammatic logic: tools for discovering the new from genetic "black matter" and for exploring new forms of relationships between microbes and humans.

Keywords Tree of life · Diagrams · Data visualization · Visual semiotics · Microbiome · Metagenomics

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Introduction

We are entering Micropia, the world's only museum devoted entirely to microbes, a part of Amsterdam's Artis Zoo. A large, full-wall map introduces us to the exhibition: it is a massive Tree of Life, depicting all types of living or extinct organisms findable on Earth (Fig. 1). The tree develops from the top, departing from a supposed unnamed common ancestor of all living species. On the right-hand side at the bottom, one of the last ramifications is circled: this is the class of mammals, where a standing human figure can be detected. A delicate color contrast distinguishes the still-living organisms perceptible to the human eye (in yellow) from the vast majority of invisible ones (in white). Some organisms mapped on the right side of the graph can be seen live outside this space, throughout the Artis Zoo and the nearby botanical garden. Meanwhile, the specimens of some invisible species mentioned in the tree are hosted inside this enclosed space. Microbes live here, or rather are kept alive, co-habiting with machines, screens, laboratory instruments, and scientists, who perform as museum operators. The large petri dishes in which the micro-organisms swim, feed, and reproduce are connected to screens that transmit live what is visible – and alive – under the microscope. Visitors can interrupt the live feed and acquire information about the microbial species they are observing. Suddenly, the tree of life appears on the screen: individual microbes are zoomed out and positioned on the same map we saw as a wallpaper at the beginning of the exhibition. However, now it works not only as a general view of the relationships among all
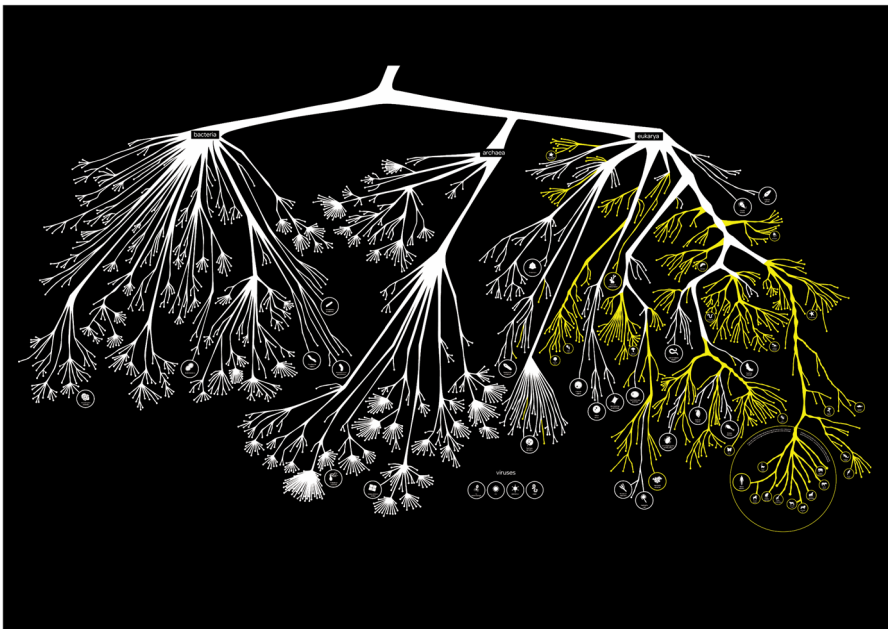

Fig. 1 The tree of life appearing as a wall map at the entrance to the Micropia museum, Amsterdam. Credits: ARTIS-Micropia

living beings, but also as a tool for locating a particular microbe in the long history of evolution. Two forms of visualization coexist in this specific movement of zooming in and out: first, a microscopic view, which, beginning with Van Leeuwenhoek's discovery of small "animalcules" in 1683, has developed into today's sophisticated techniques of digital scan and magnification; secondly, a general overview, which locates each species within a complex map of phylogenetic relationships. In many microbiology laboratories today, there is a constant coming and going between these two forms of visualization, which are related to two types of practices commonly referred to as *dry* and *wet* (Raffaetà, 2022): on the one hand, metagenomics, i.e. the study of a microbial community through the application of advanced DNA sequencing techniques, helps with identification of the species within a taxonomic reference scheme that can have the shape and structure of a tree; on the other hand, the more traditional in vitro cultivation helps with the detailed study of microbial form and behavior in controlled circumstances.

The tree of life is thus, in this atypical museum dedicated to microbes, an orientation device on par with the timeline we find in the neighboring Rijksmuseum. The latter, with a graphical scheme typical in the world of art history, introduces each section via time segments along a line, contextualizing each artist in the historical period in which they lived; the tree of life, on the other hand, situates each microbe in a particular moment of the evolution of life, while confirming its present survival as a species. The tree of life is thus a time diagram that does not show a linear succession of time segments, but instead possible parallel levels of coexistence. In the didactic form of the museum's map, the tree of life presents itself as a scheme that organizes the phylogenetic relationships among all living forms; it works well, in its completeness, compactness, and inclusiveness, as a reference map for orienting oneself in the study of the living.

The tree is everywhere in microbial narratives, both in scholarly journals and popular science. It is used not only as an educational device to facilitate people's access to knowledge about microbes, but also as an analytical and organizational tool among the community of bioinformaticians. The tree structure, having roots in Darwin's evolutionary theory, has found new life with the molecular and informatic turn in biology today. The disciplinary field of evolutionary biology has gone through an epochal change in the last 50 years, mainly due to the criteria through which evolutionary relationships have been reconstructed (Kitchin, 2014; Leonelli, 2016; Sapp, 2009; Stevens, 2013; Strasser, 2012). While, from Darwin's *Origin of Species* (1859) until halfway through the twentieth century, the criterion for distinction of a species was based on observation of morphological differences, more recent discoveries in genetics have instead led biologists to compare genotypical features of organisms through the computation of similarities and differences in their DNA, RNA, and protein molecules. The caption projected under Micropia's tree of life reminds us: "we are one big family with the same building blocks: DNA". However, discoveries about genetic transmission between bacteria such as Horizontal Gene Transfer (Lederberg & Lederberg, 1957) and endosymbiosis (Margulis, 1970) have threatened the tree of life's utility as a descriptive tool.

This paper aims to understand the visual mapping systems that microbiome scientists use to organize and sort microbial genetic data. In particular, this essay aims

to find reasons why trees are still valid as a framework for organizing knowledge about microbial diversity, despite their limitations. We will see that the tree persists as a reference structure for practical reasons, but also because of its connection to an imagery rooted in centuries-old visual culture and still familiar to today's observer. We should remember that scientific visual practices are imbued with cultural values and ways of seeing and classifying the natural world; at the same time, they shape how we see the relationship between humans and these invisible non-humans. In the case of the tree of life used in bioinformatics, scientists organize knowledge and provide a model for interpretation of the world through the design of interactive software for analysis and visualization of biological data. The tree is irreplaceable as a heuristic device, as it helps to project a virtual level onto a descriptive dimension. Other visualization methods, such as Principal Component Analysis, will introduce alternative schemes of microbial visualization that, while still based on evolutionary information and phylogenetic kinship, open up research to a more holistic and eco-systemic approach.

We will use the semiotic notion of diagram (Peirce, 1960; Stjernfelt, 2017) to ascertain how this kind of visual configuration – halfway between figuration and abstraction – does not illustrate or translate a content that is already available, but instead allows the emergence of the unknown and the virtual. In other words, we will examine diagrams as inscriptions through which scientists discuss and construct percepts, concepts, and objects (Latour, 1984, 1987). The tree will also be examined in relation and opposition to alternative ways of representing relationships among the living to suggest different ontologies emerging from using the images (Lynteris, 2017).

The empirical material for this paper is mainly composed of visualization tools for microbial databases. In particular, we will analyze two tree-based visualization programs (iToL and GraphlAn) due to their efficiency in managing big biological data and design sophistication in visualizing diversity and organizing knowledge.[1] The corpus of analysis will then comprise tree-like visualizations in software, scientific papers, and more general press. However, we will first analyze a sub-corpus of less recent images: we will reconstruct the genealogy of cutting-edge technologies of visualization, dipping their roots in a predigital and proto-digital visual culture of trees, corals, geological imagery, and pioneering computer programs. The visual analysis of the interfaces is conducted through semiotic methodology and image theory. The relationship between the form and function of the visualizations is observed through the lenses of design theory and practice. At the same time, the study of the images is nurtured by some ethnographic observations on the practices around using these tools in metagenomic labs, in-depth interviews with microbiome scientists, and a careful reading of scientific papers where these images are utilized

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[1] iTol (interactive Tree of Life) was launched in 2007 by Ivica Letunic, a bioinformatic developer, and Peer Bork, director of EMBL Heidelberg since 2020. It has since been implemented in different versions, with the latest version (v6) released in 2023. GraphlAn is an open-source software tool designed by Nicola Segata with contributions from Francesco Asnicar during his research period at the Huttenhower Lab in Harvard in 2015. They are not the only visualization tools used for metagenomics, but are among the most accessible and easy to read.

as arguments in scientific discoveries (Bastide, 1990; Dondero & Fontanille, 2014). This plurality of approaches is due to the different backgrounds of the two authors of this essay and their positioning: the first author is trained in semiotics, visual, and design studies. She has the main authorship for this article, the structure and approach of which reflects her expertise. The second author has experience in ethnographic fieldwork in metagenomics labs and has supported the first author in identifying the relevant research question and developing the argument. Moreover, the first author has also benefitted from working – as the sole non-anthropologist – on a project on the anthropological analysis of different case studies related to microbiome science.

As the journal's editor has pointed out, just like the tree of life, this article is also a 'boundary object': between the standards and categories of biology and the standards and categories of humanities. As such, we have added small summaries at the opening of each section to increase legibility for a varied readership.

The Shape of the History of Life: The Tree

In this section, we analyze Darwin's first drawings of the tree of life as machines for thinking rather than as reliable descriptions of the mechanisms of life's evolution. We observe these groundbreaking schematic representations of evolution across geological time as foundational aesthetics of contemporary interfaces that visualize microbial diversity.

Although the use of the tree of life as a structure to organize biology dates back to Augustin Augier (1801), and its first use in evolutionary terms can be found in Lamarck's "tree of dots" (Lamarck, 1809, quoted in Quammen, 2019, 19), Darwin can be considered the father of tree-thinking about evolution. Many drawings of arborescent structures have been found in his notebooks. However, for reasons connected to the greater spread of the print medium compared to the unicity of the hand-drawn drawing, his best-known tree is the lithograph contained in *The Origin of Species* (1859) – the only image present in the book.[2] This image does not refer to any named species but represents the general scheme of evolution. It is based on the observation of morphological differences between living beings, but rather than describing concrete features, it extracts from them the general operating form of the evolution machine and the rules of diversity and adaptation: the bifurcated oblique lines of descent connect one species to another from bottom to top, while the vertically rising lines show species that have not changed over time. The horizontal axis of the graph presents some generic discrete categories that could refer to different species; the vertical axis is a timeline, scaled by the layered depth of paleontological time and traversed by evolution. As Darwin explains, each layer corresponds to a thousand generations. The ascending lines show the progress of evolution through dead spots and solid lines. According to Greimas and Courtès (1979), who approach the "arborescent graph" as a semiotic structure, trees are usually made up of two

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[2] Darwin's printed diagram can be found either in his book or, in form of digital image, here: https://en.m.wikipedia.org/wiki/File:Origin_of_Species.svg. Last access April 26, 2024.

components: lines designating relations and labels designating structural terms. The absence of labels in Darwin's tree demonstrates that the main contribution of the diagram is a visual definition of the type of relations between beings: at a plastic (eidetic) level, the opposition between /obliqueness/ and /verticality/ and that between discontinuity/ and /continuity/ stand for an opposition in semantic terms between "variation" and "permanence".[3] These are the fundamental laws of life.

Although this tree was highly influential in informing the vision of the history of life until the late twentieth century, Darwin himself was not very convinced that the tree was the correct metaphor to represent evolution. In his Notebook B, written in 1837, he sketched a scheme that, as he said, "should be called the coral of life, base of branches dead" (Darwin, 1837, 25) rather than the tree of life.[4] The use of the tree structure in his sketches is more a part of a thinking process than an illustration of a theory: the 1837 sketch is the snapshot of an intuition, an "active thinking sketch" (Atzmon, 2015, 143), which precedes the publication of the theory of evolution by 20 years. The statement "I think" at the top of the page frames the content of the drawing as a title. In this way, the sketch is explicitly defined by its author himself as a visible process of elaboration of the idea. The captions around the drawing also reinforce this fruitful exchange between image and words (Voss, 2010).

Another drawing, less well-known than the "I think" sketch and dating back to 1850, uses a grid of concentric circles as a formal skeleton crossed by lines of evolutionary continuity.[5] The radial structure, recalling tree-rings, represents the passage of time according to a recognized logic of "self-inscription", a way, according to Offenhuber (2024), in which phenomena embody information such as the passing of time. This indexical modality is enriched with the semantics of geological stratification, according to the visual culture to which Darwin himself was exposed at that time.[6] Compared to his contemporaries' geological schemes, Darwin's sketch

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[3] I still find it very efficient when reading images to use the methodology of visual semiotics analysis, as theorized and practiced by Greimas (1984) and Floch (1985). My main reference in distinguishing a chromatic, eidetic, and topological dimension in the plastic plane of the visual text is Thürlemann (1981). Structural semiotic analysis makes us read diagrams in terms of oppositions: where Tim Ingold (2007) saw Darwin's tree as an underlying discontinuist paradigm under "a reconstituted continuity of discrete individuals in genealogical sequence" (114), we see the discontinuity of the dotted line as a form for expressing change and variation in a phyletic line, opposed to the invariability of the continuous line, equal to itself generation after generation.

[4] The sketch in Charles Darwin's notebook can be seen in Cambridge University online archive: https://cudl.lib.cam.ac.uk/view/MS-DAR-00121/38. Last access April 26, 2024.

The coral would have been a much better metaphor, for the reasons explained by Bredekamp and Joschke (2008) and Podani (2019). Coral suggests the idea of chance, as it shows the chaotic and anarchic development of the living from lifeless petrified branches. In contrast, the tree is a structure representing progress ordered from the living trunk to the twigs at the extremities.

[5] This drawing is visible in Cambridge University Library's online archive. https://cudl.lib.cam.ac.uk/view/MS-DAR-00205-00005/372. Last access April 26, 2024.

[6] As Pietsch (2012), Torrens & Barahona (2013), Quammen (2019), and Dahan-Gaida (2023) point out, Darwin was certainly influenced by forms of visualization that circulated in his times: the diagram contained in *The Origin of Species* has some relation with the famous first "paleontological graph" by Edward Hitchcock in *Elementary Geology* (1840) and with the "spindle diagram" in *Recherches sur les Poissons Fossiles* by Louis Agassiz (1833). The circular graph is reminiscent of the geological map included in *Principles of Zoology* (1848), also by Agassiz, representing the evolution of animals on the basis of the different geological strata of the Earth's crust, as described by Lyell (1830–1833). Both

emancipated the representation of time from the concrete geological strata in which the fossils were found, thus acquiring an abstract dimension, just like the grids in a cartesian plan. Combining the visual structure of the bifurcating tree with those of geological stratification and circular tree-ring temporalization, Darwin brought together different imaginaries in a synthetic image, which appears now, in our anachronic gaze,[7] to be the ancestor of the "phylogenetic mandalas" (Hasegawa, 2017) that dominate biological visual culture today. In its rough sketch form, this graphic also "participates in the thought elaboration process, providing active support to the intellectual process designated by words" (Dahan-Gaida, 2023, 432, my translation). Darwin's drawings, then, far from being descriptions, illustrations, or even metaphors, can already be considered heuristic devices, machines for thinking, or, in other words, diagrams. The botanical trees of Ernst Haeckel (1866), the greatest popularizer of Darwinian theory at the end of the nineteenth century, literally translated the arboreal metaphor into an image that was figuratively denser than Darwin's model[8]: this has contributed to reducing the original Darwinian scheme's polysemy and consolidating the tree structure as the main form of visualization of biological diversity and variety.

The Tree and the Digital Turn

In this section, we recount the fortunate encounter of two visual and epistemic cultures – that of evolutionary biology and that of informatics – due to the discovery of DNA as genetic code and the consequent digitalization of molecular biology.

With the advent of the so-called "molecular revolution",[9] scientists began to look at proteins and other macromolecules to identify the organisms' biological

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Footnote 6 (continued)

Agassiz and Hitchcock introduced leaf area size to represent the relative abundance of species belonging to the same taxonomic group, but they did so (in the opinion of Pietsch 2012; Sepkoski and Tamborini 2018) quite crudely and roughly, not respecting the numerical proportions. The width of the area as a form of expression of taxonomic abundance has become a convention strongly used in contemporary forms of visualization, as we will examine later.

[7] Our approach to reading images is rooted in visual studies: what we want to reconstruct is not a diachronic line from Darwin's diagrams to contemporary interfaces, but a non-linear genealogy that uses contemporary interfaces to re-read historical diagrams. On the concept of anachrony, see Nagel & Wood (2010) and Mengoni (2013).

[8] In the view of the Lithuanian-French semiologist Algirdas Greimas (1984), images can have different degrees of "figurative density" according to the level of detail through which they are recognizable as figures of the world: Darwin's tree diagram is less figuratively dense (and thus more abstract) than the representation of an oak or a maple. The figure of the tree has stabilized for a certain time the directionality of evolution from bottom to top. Whenever the directionality has turned from top to bottom (as in Micropia's tree), gravity asks to be included in the interpretation. In Waddington's famous diagram (1957), for example, evolution is represented as driven by external forces, depicted as valleys and cringes "canalizing" the cell towards bifurcated paths (Humphrey, 2022; Sharov & Kull 2023). Although the metaphor used for Waddington's "epigenetic landscape" is no longer the tree but instead mountainous scenery, the bifurcation of the path makes us think of a tree structure with a background that is neither neutral nor empty as in the Darwinian model, but rich in contextual forces.

[9] See Marshall and Schopf (1996) and Olby (1990) for a critical review of the term.

specificity. Zuckerkandl and Pauling (1965), constructing a molecular phylogeny through protein sequence data, are considered the first scientists to have designed evolutionary trees based on quantitative and discrete criteria. Although they were not yet using computational machines, this was around the time that computers were rising to prominence in both science and society, as noted by Higgs and Attwood (2004). Immediately afterwards, Margareth Dayhoff, considered one of the founders of bioinformatics (Sapp, 2009, 130), began using computers to infer phylogenies from molecular sequences (Dayhoff & Eck, 1966). In the 1970s, George Fox, supported by Carl Woese (Fox et al., 1977), developed a program running on IBM punch cards that mathematized the relationships between genetic codes. He called the mathematical value that emerged from the relationships the "similarity coefficient". This number would be the basis of all trees created from that moment on. The direct measurement of genealogical relationships based on levels of homology between genes (Higgs & Attwood, 2004; Suárez-Díaz & Anaya-Muñoz, 2008) is a mathematical concept; as such, it is immediately translatable into a two-dimensional space. Fox and Woese then derived from those measurements a horizontal dendrogram (Fox et al., 1977, 4541, Fig. 1) that visually shows the distance relationship between bacteria and methanogens.[10] This diagram, visual evidence of a new discovery, helps to understand the significance of Woese's revolutionary discovery of a third domain of life alongside Bacteria and Eucarya, that of Archaea (Woese et al., 1977; 1978). To make the concept more immediately understandable, in a subsequent publication (Woese et al., 1990, 4578, Fig. 1) the tree would turn 90° and regain its traditional directionality from bottom to top.

What transpires from this brief history is that the rise of the molecular approach and genetics in the 1960s had produced a "digital" revolution within biology even before the use of machine computational methods. The identification of a species through a recognizable sequence of discrete units (the nucleobases) was the necessary ground for a possible logical-mathematical translation of the world of the living. Indeed, computers allowed comparisons through fast computation of amounts of data, the quantity of which was growing in the meantime due to the development of the techniques of RNA and DNA sequencing. This was how informatics and biology converged into bioinformatics, a discipline managing and analyzing biological data through suitable computational systems and tools. This discipline has caused biology and computer science to become more and more interdependent and entangled (Stevens, 2013, 11), to the point that some have even speculated about the complete interchangeability of materials and functions in the biological and computer domains, based on the fundamental equivalence of genetic codes and computer codes (Thacker, 2004). The figure of the tree of life has been critical to the success of the marriage between the two disciplines. First, the arborescent organization is a space structuring system that responds well to the needs of information technology. In mathematics, it is part of graph theory and therefore its "geometric

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[10] Methanogens are microorganisms living in hypoxic conditions. Their metabolism produces methane. Woese had the insight that they did not belong to the kingdom of bacteria and tested this hypothesis through genetic reading.

structure provides a mathematically tractable framework for quantifying the biological concept of a phylogenetic tree" (Morrison, 2014, 631). Algorithmic processes, indeed, automatically translate mathematical relationships, based on similarity and difference, into a bifurcating structure. Secondly, the tree of life is a well-known and established infrastructure of scientific knowledge that is "as central to biology as the periodic table is to chemistry" (Eiserhardt et al., 2018).

As such, it can be considered a "boundary object" (Star & Griesemer, 1989) at the visual encounter between two different epistemic cultures and communities of practices – in particular those of biology and informatics. This happens because biology has moved from the field of analogical observation through instruments such as optical microscopy to the domain of data mining (Hug et al., 2016), anticipating a general process of "cultural transcoding" (Manovich, 2001, 63), i.e. a "logical-mathematical translation of the world into discrete units (*that*) constitutes the process of universal construction of knowledge" (Biggio, 2022, 36). As a cultural construction, however, the tree carries within itself a sedimentation of historical and epistemic connotations. It is symbolically linked to a well-defined way of understanding the evolutionary relationships of living beings. The tree has then been associated with a neo-Darwinist gene-reductionist approach, emerging from the modern synthesis (see Kull, 2015) at a moment in which thinking about evolution has in turn evolved over time, paving the way for approaches such as that of the Extended Evolutionary Synthesis, which pays more attention to the organism's responsiveness to its environment and epigenetic factors and less to the mere digital accounting of the species' DNA.

The Shape of the Tangle of Life: the Web

In this section, we review the theories that have debunked the idea of the tree diagram as a reliable representation of the way evolutionary events unfolded. However, we also show that the tree and the structure proposed as an alternative – the web— are not mutually exclusive configurations. Rather, they interpenetrate each other.

Although the synergy between evolutionary biology and informatics celebrates the tree as the perfect instrument for representing the new vision of life based on molecular analysis, the ground on which the Darwinian tree was rooted has been shaken several times from then until now. It was Lynn Margulis (1970) who brought her theory of *endosymbiosis* to the fore of the biological debate: the organelles present in eukaryotic cells (chloroplasts and mitochondria) could originally have been bacteria phagocytosed by other primitive organisms.[11] These chimerical creatures,

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[11] According to Sapp (2009, 116), Ernest Haeckel had already anticipated the theory of endosymbiosis in the late nineteenth century, through his observations of blue-green algae. Julian Huxley, in the 1920s, had also understood that bacteria exchanged genetic material. However, the scholar who brought more solid evidence to the complex theory of "symbiogenesis" was the controversial Russian biologist Constantin Merezhkowsky, who, at the beginning of the century, had already hypothesized that the eukaryotes cell was the result not of a gradual evolution but instead of the incorporation of a cell into another cell that then reproduced in this double form. For his "atypical" biography, read the compelling account by David Quammen (2019).

given the advantages of life as a couple, would then have reproduced together, generating the eukaryotic cell. Margulis, like her predecessors, had based her discoveries on microscopic observation, but her theories would soon be confirmed and developed by the molecular analysis of Bonen and Doolittle (1975). Margulis' theory undermined the Darwinian tree, setting up the happening of convergence in opposition to the law of divergence: while, according to Darwin, organisms gradually differentiated from each other through small random mutations, the new theory posited that different organisms from different evolutionary models had entered into symbiosis to become another entity. In the drawing by Laszlo Meszoly, the scientific illustrator whom Margulis commissioned to illustrate her book (Fig. 2), two trees – that of Monera and that of Protists – are connected in two ways: through filiation (with a long continuous line connecting one kingdom to the other) and through symbiosis (with dashed lines abruptly crossing the borders of the two kingdoms). New forms of representation emerged: Robert Whittaker, for example, represented the kingdoms of life through the strange shape of a "prickly pear cactus" (Quammen, 2019), the leaves of which were partially overlapping sets (Whittaker, 1969; redrawn in Margulis, 1970, 65). From a visual point of view, sets and englobing structures began to be seen next to trees and bifurcating structures: areas overlapped lines of separation; convergence replaced divergence.

Meanwhile, the discovery of horizontal exchange of genetic material between prokaryotes and their ability to inherit spontaneous mutation (Lederberg & Lederberg, 1957; Sapp, 2009) had highlighted the existence of lateral forces disturbing the Darwinian slow mechanism of differentiation through adaptation and chance (O'Malley 2014). The discovery of mechanisms such as symbiogenesis, lateral gene transfer, and infectious heredity induced a change in the evolutionary model that was no longer linear but reticulate: a "network-like pattern of horizontal crossings and mergings that often precede a pattern of vertical descent with modification" (Gontier, 2015a, 2).

Ford Doolittle, considered one of the main enemies of the tree metaphor due to the unequivocal meaning of the title of his important article "Unrooting the Tree of Life" (Doolittle, 2000), had drawn his vision of evolution himself. In his previous article (Doolittle, 1999), a natural organism appears; it is not a tree, but still maintains a certain directionality (Fig. 3). As a hand-drawn drawing rather than a stabilized printed diagram, Doolittle's famous sketch looks more like a snapshot of a thinking process than a stable scientific conclusion, somewhat reminiscent of Darwin's coral. For many, then, a network would be a better tool for the representation of the web of life (Dagan & Martin, 2006; Doolittle, 1999; Helmreich, 2003). In the field of biosemiotics, Kalevi Kull (2003) observes a general shift in biological models from the tree to the web, while Ludmila Lacková (2018), quoting Eco (2007), proposes replacing the dictionarial model of the tree with the encyclopedic model of the web, constructed on openness and recombination, just as in Deleuze and Guattari's rhizome. Still, webs and trees are not mutually exclusive visual structures: in their study on the potential use of the tree of life for prokaryotic evolution, Bapteste et al., (2009, 10), though considering the traditional tree of life model to be "very much a problematic framework to study microbial evolution", admit that "trees are special types of networks" and that "a good network approach will always return a
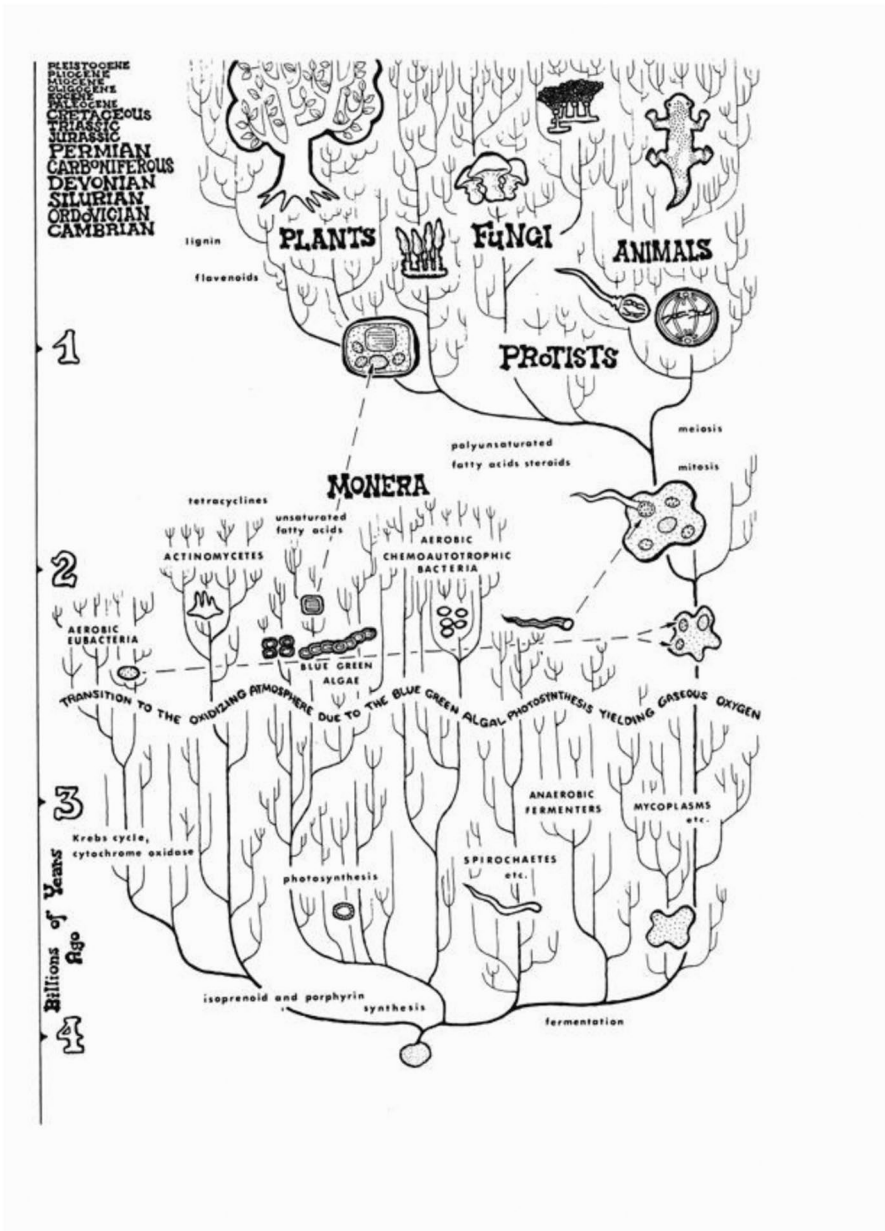
Fig. 2 This tree, enriched by the endosymbiotic passages between different domains, appears on the frontispiece of Lynn Margulis' *Origin of eukaryotic cells* (Margulis, 1970). Used by permission of the estate of Lynn Margulis
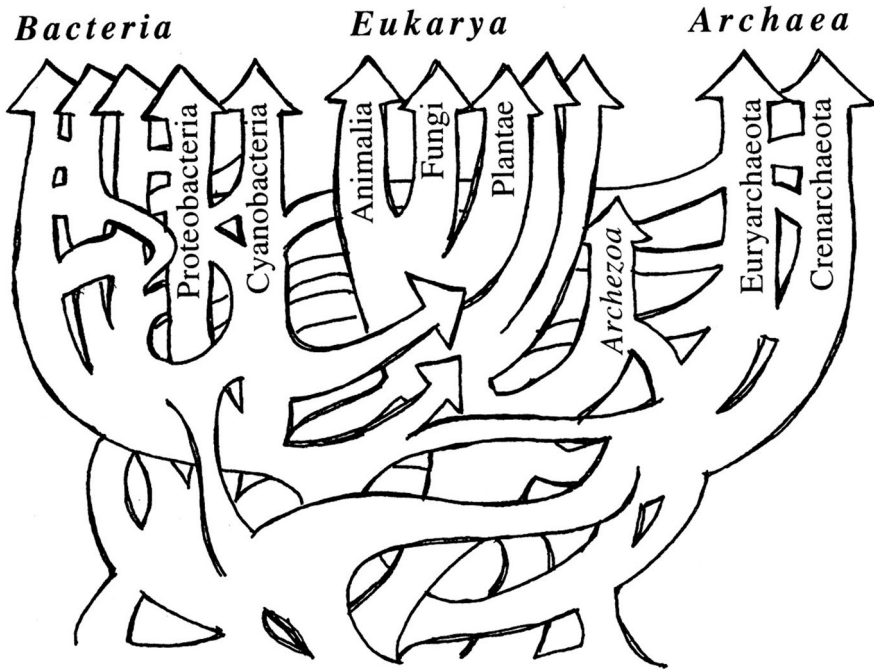
Fig. 3 The entangled tree hand-drawn by Ford Doolittle (1999). © 1999, The American Association for the Advancement of Science

tree if the underlying data have a tree-like structure" (see also Beiko, 2010). This was strongly posited by Deleuze and Guattari, for whom "there exist tree or root structures in rhizomes; conversely, a tree branch or root division may begin to burgeon into a rhizome (…). There are knots of arborescence in rhizomes, and rhizomatic offshoots in roots" (Deleuze & Guattari, 1980, 15–20). Although Doolittle contributed to the understanding of the forces disturbing the vertical growth of the tree of life and denied the existence of a reductionist universal phylogenetic tree based on genetic codes, he did not completely overthrow the tree metaphor. While he sought "other ways of classifying microbes (for instance by gene content or ecological role or indeed by relative position in a multidimensional network)", the tree, as a "relatively stable hierarchical scheme", would serve a very useful organizing function" (Doolittle in Bapteste et al., 2009, 14; quoted in O'Malley & Koonin, 2011).

Thus, on the one hand, the fact that prokaryotes mutate according to the situation, transmit their mutation by heredity in a Lamarckian way, and reproduce nonsexually makes them recalcitrant to the taxonomic classification by species on which the Modern Synthesis is based.[12] On the other hand, neo-Darwinian schemes and models have never stopped being used to organize them.

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[12] As reported by O' Malley (2014, 96), in his reconstruction of the modern synthesis, Julian Huxley said: 'noncellular.

[i.e. viruses] and non-sexual organisms such as bacteria have their own evolutionary rules' (1942, 126).

Trees as Heuristic Diagrams

In this section, we describe and analyze two tree-based interfaces that bioinformaticians use to organize their knowledge about the community of microbes present in any sample. We highlight the design qualities and the semiotic functioning of these interfaces.

Despite all these debates over using a tree to visualize relations among living species, tree structures are still considered efficient schemes for organizing big data arising from the sequencing of microbial communities. Microbiome science, indeed, studies the community of microbes living in an environment (human body, soil, ocean) through the metagenomic analysis of samples of organic material. This specialist field of knowledge, which has lately begun to enter popular culture (Bapteste et al., 2021; Lorimer et al., 2019; Paxson & Helmreich, 2014), primarily uses computational techniques to understand the kind and quantity of microbes that are present in an examined sample. Bioinformaticians always read data, both after sequencing DNA from their samples and when using databases produced by other colleagues, through visualization interfaces, which structure and organize information that would otherwise be an infinite string of As, Cs, Gs, and Ts (the nucleotides making up DNA). Bioinformaticians prepare the prompts to associate sequences with taxonomic entries and to write the parameters of these forms of visual organization when they create the software for data management. While the tree structure is not the only way to map microbial communities in metagenomics, it is "the only visual encoding found in literature (…) which is able to combine hierarchical relations and relative abundance" (Peeters et al., 2021, 6).[13] In fact, arboreal structures are peculiar in that they include, in a compact visualization, both a synoptic snapshot of the composition of a microbial community (*abundance* and *variety*) and a diachronic image of the entire history of microbial evolution with a very precise reconstruction of the timeframe in which genetic modification has occurred.

Software such as iToL or GraPhlAn visually organize, in a compact structure, the different microbial species and strains found in a sample or database. Radial trees can be used on different scales, "ranging from species-level clades to the whole prokaryotic tree-of-life" (Asnicar et al., 2020, 7) as seen in Fig. 4. In terms of design, they are circular visualizations that place the root "at the very center of the diagram, with splitting ranks moving toward the circle's periphery, aligned to a series of concentric rings" (Lima, 2014, 123). The internal, concentric rings are usually made invisible in visualization tools. The length of the branch corresponds to the evolutionary time span; that is, it is proportional to the number of generations that share the same genetic information and therefore belong to the same species (Letunic & Bork, 2016, 245). As in Darwin's archetypical model, the longer the branch, the more resistant over time the species. Radial trees are thus extremely

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[13] Peeters et al. (2021) have analyzed a series of scientific papers on the microbiome and created a list of the visual forms through which microbiologists evaluate the abundance and diversity of microbes in samples, connecting the visualizations with their functions. They enlist many visual forms other than trees from stacked bar charts to heatmaps, bubble plots, scatter plots, and interaction networks.

Fig. 4 A screenshot from the iTOL interface, showing all of the tree of life with Borat as a specimen of the *Homo sapiens* species. https://itol.embl.de/

synthetic images that condense both the long evolutionary times and the co-presence of microbial species in the here-and-now of the analysis process: while the position in the bidimensional space (at what we would call the topological level of expression) represents the evolutionary age of the different species and the chronological relations between them, the outermost half-lines represent the lineages living in the here-and-now of the sample just analyzed. The criticism that the tree represents a maximum of species diversity that does not adequately represent mass extinction events (Vrba & Gould, 1986, cited by Gontier, 2015b, 125) does not hold up in light of its practical use: the tree must actually represent the microbes in the sample and relate them to each other, not offer theoretical hypotheses about evolution and extinction.

An important aspect of circular trees is that they allow us to surround the data obtained through sample analysis with metadata. This is useful for reconstructing the context and finding connections between microbes and the conditions in which they live, such as the age of the host, body site, geographical origin, presence of contaminants in the environment, etc.[14] The external metadata crown becomes a visual locus for grounding microbes in environmental and contextual data (Fig. 5).

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[14] Annotation features are central in iTol, the primary goal of which, from the beginning, "was to offer various ways of annotating phylogenetic trees with external data" (Letunic & Bork 2016, 243). They are also central for GraphlAn (Asnicar et al., 2015). Based on another tool – PhyloPhlAn – which is an analytical instrument for reconstructing phylogenies, GraphlAn has a compact and circular appearance; its main scope is to associate microbes with qualitative and quantitative metadata, such as the physiological properties of the microbes or the state of health of the host. What was called "annotation of additional data" in iTOL becomes the main argumentation frame in GraPhlAn and includes qualitative elements. Metadata are visualized in a set of external rings and mainly represent the features of the context of data collection. For this reason – to allow the readability of the contextual information – GraPhlAn is only circular and does not have a rectangular or unrooted form.
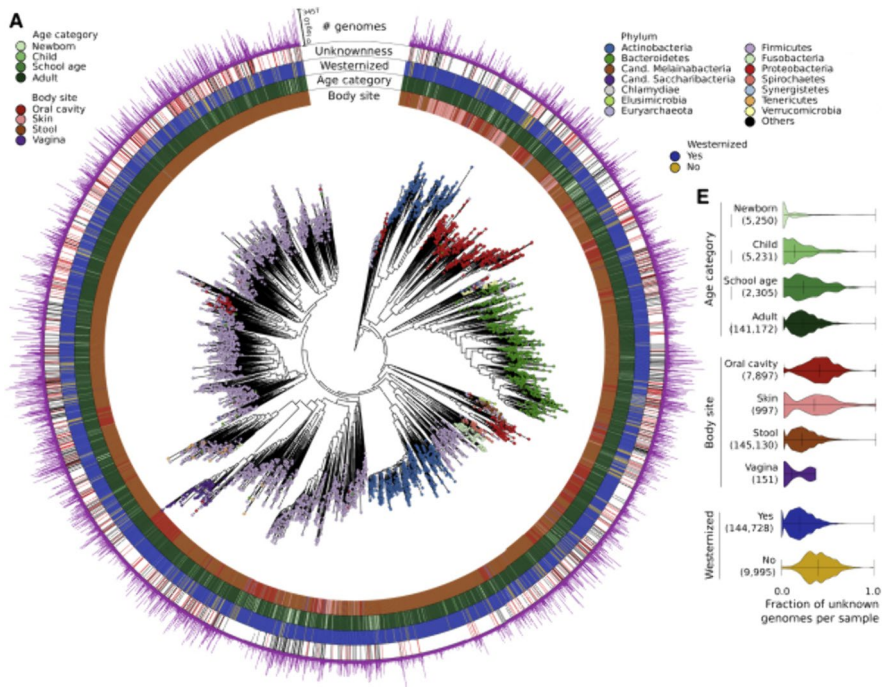
Fig. 5 Radial phylogenetic microbial tree created through the GraPhlAn interface with metadata surrounding genetic data (Pasolli et al., 2019). © 2019 Pasolli et al. Published by Elsevier Inc

This configuration, while giving centrality to the genetic material that identifies individual bacteria, already implies a move beyond gene-centrism, as the presence or absence of a specific bacterium is found to correlate with contextual factors. The outer crown exerts a centrifugal force to the growth of the inner tree of life.

Due to its organizational effectiveness, the radial tree diagram is a structure that has seen great success in scientific iconography: in fact, "it allows us to create conceptual hierarchies through plastic ramifications, to establish coherent links between the whole and the parts, offering a synoptic and panoptic vision of these relationships. It is a very effective taxonomic tool for classifying and ordering knowledge and modeling genealogical relationships" (Dahan-Gaida, 2023, 382, my translation). In its circular form, it makes optimal use of space, whether typographic or digital (Lima, 2014, 123). Moreover, its geological visualization of time is a synthetic vision of diachrony: starting from the center (the origin of life), the concentric circles become wider and wider in order to accommodate an increasing diversity and variety of life forms. Far from being past-oriented, though, the algorithmic basis of this visualization allows it to be a speculative instrument for predictions. Scientific diagrams that scientists use for the visualization of the microbiome are usually interactive tools, allowing the user to manipulate and interpret their object of analysis in different forms and on different scales. As user-data interfaces, they can be used according to Schneiderman's old mantra (1996): "Overview first, zoom and filter, then details on demand". As micro–macro designs (Tufte, 2013), they allow

an overview, making it possible to visualize pan-microbial phylogenies, as well as small-scale analyses: the structure of a species with all its strains.

Bioinformaticians are keenly aware that the tree is a visualization model, not a representational device. Suppose it is true that, at the beginning, iToL was conceived with the idea that the tree would expand continuously through the placement of every species in the tree of life (Ciccarelli et al., 2006). In that case, it is also true that its authors always considered it a tool and an "updatable reference phylogeny" (Ciccarelli et al., 2006, 1286), never as a "project" for its own sake with the "ambitious goal to once and for all determine every species' evolutionary ancestry" (Gontier, 2015b, 127). Phylogenetic trees, then, are far from inherently inaccurate descriptive illustrations of life's descent. Rather, they are visualization and annotation tools that "represent a backbone for various other biological studies" (Letunic & Bork, 2007, 127). In his notes while reviewing the paper by Bapteste et al. (2009), Ford Doolittle adds: "It's hard for me to see a network as a useful catalog, and so I have no objection to the continued use of an rRNA tree (…) as a conventional tool for classification, provided everybody knows that that is all that it might be, a conventional taxonomic framework" (Bapteste et al., 2009, 14). The status of the tree as a non-representational tool is hence recognized by most of the community of phylogenetic biologists. Thus, we can say that the tree as a tool for visualizing biological data only responds to a diagrammatical and not a representational logic.

Mapping the Microbiome and Naming the Previously Unknown

*In this section, we give theoretical value to one of the most interesting outcomes of the interviews and field observations of scientists' use of the phylogenetic tree: its ability to detect and visualize new, unknown species present in a sample. This data-driven discovery may initiate new research conducted with more traditional methods (*in vitro *cultivation) to isolate and identify these new species.*

Through the inclusion of new data in large databases, most of the advancements in metagenomics depend on the comparison of newly obtained data with those previously collected in these databases. Indeed, newly sequenced genomes, most often belonging to organisms that have never been isolated before, are positioned on maps with their coordinates provided by data from organisms that have already been sequenced and isolated. The tree, then, becomes an organizing principle to manage the huge amount of data arising from a sequencing process. Indeed, part of this data is often "microbial dark matter" (Bernard et al., 2018) that needs to be discovered and identified. According to bioinformaticians, this matter cannot be considered in the same way as dark matter in physics, which has different features from the matter we know. Indeed, "undiscovered microbes have the same molecular basis as the known one" (Thomas & Segata, 2019).

In semiotic terms (Hjelmslev, 1943), initially undetermined molecular matter of life becomes accessible only through its translation into genetic code, a syntagmatic chain from which to extract pertinent and then meaningful units. Life, as "a matter controlled by symbols" (Pattee, 1968, quoted in Barbieri, 2009), becomes readable

through a system equipped with double articulation (Hjelmslev, 1943). Sequence cutting creates meaningful "contigs"[15] from raw sequence data, which are almost unmeaningful units (the proteins): these contigs can be attributed a role, an agency, and a name, depending on their positioning in the system. The increase in genetic information enables scientists to detect, within the continuum of this "dark matter", a finer grain of elements, i.e. microbes, in relation to each other. The more sequencing that takes place, the more species and strains that emerge.

Based on a convention stating that a difference of greater than 5% in the genetic code indicates a species discontinuity, microbiologists have invented a coding system based on what, in semiotics, would be called a commutation test (Hjelmslev, 1943): a certain amount of shared identity between series of bases in a genetic sequence indicates whether or not a microbe belongs to the same class. The tree is thus a map, with its coordinates the genomes of known and cultivated microbes, called "reference genomes". The map of the explored territories becomes the background for what is yet to be discovered. The more the territory is explored, the more detailed and crowded the tangle of the branches becomes.

An attempt to visualize the dramatic expansion of biodiversity obtained through computational techniques in all three domains of life is visible in Hug et al. (2016, 2, Fig. 1). What is striking about this image is not only the small space occupied by the domain of eukaryotes (as we have seen in Micropia's map), but also the quantity of unknowns that emerge from the processing of biological data: the red dots represent lineages with representatives that have never been isolated.

Phylogenetic placement methods such as the PhyloPhlAn program have a role of "contextualizing genomes without prior phenotypic information" (Asnicar et al., 2020, 2) and help to increase the microbiome's mappability and resolution, showing the routes and directions that further research might take (Pasolli et al., 2019, 653; Raffaetà, 2022). The rules of microbiology prescribe that names can be only be attributed to species if a representative of that species is cultivated in a laboratory. In semiotics terms, the form of expression provided by the cutting of the genetic code must be connected to a visible form – another kind of visual codification – to become a meaningful item: a genotype must be linked to an observed phenotype to acquire a name and gain a place in the official taxonomy.[16] Taxonomic assignment, then, depends not only on automatic and numerical criteria but also on the observation of phenotypical features, which calls upon bioinformaticians for a "renaissance of cultivation" (Clavel et al., 2021) to integrate their computational practice. This

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[15] In the Wiley online library, a contig (from *contiguous*) is a set of overlapping DNA segments that together represent a region of DNA that can be identified as a gene.

[16] During this research period, I have followed the process of discovery and naming of a new bacterium at Segata Lab, University of Trento. In the phase of metagenomic practice, an unknown species is put into a phylogenetic context with respect to other known species. If it looks interesting because it is associated with interesting metadata, it is extracted from the sample and isolated in vitro. At the same time, its genetic identity is reconstructed through more accurate sequencing. It is only after the cultivation of the bacterium that a "genome announcement" can be publicly made. This has been the case for the *Catenibacter tridentinum* (Ricci et al., 2023), recently "baptized" in the Segata Lab. The debut in society of the bacterium was even accompanied by the production of a soft toy designed to resemble its phenotypic appearance under the microscope.

equips even the most computational experiences with biosemiotic positions: "without correlation to phenotypic difference, genetic difference is semiotically meaningless" (Salthe, 2007, 142).

Furthermore, since assigning a name means establishing a cultural unit (Eco, 1976, 76), the assignment of a taxonomic label gives a bacterial phylum and its representatives the right to become agents in a scientific discourse. Assigning a microbe to a taxonomy is not automatically decided by a machine that reconstructs kinship based on code similarity; instead, it is a human task involving arbitrariness and decisions that must be taken. For example, some phyla (such as proteobacteria) are not monophyletic: they arise from a combination of different phyla, probably due to horizontal gene transfer. This problem of taxonomic attribution helps us understand why the tree of life is more of a construction than a stable backbone for biological studies emerging from the genetic matter itself. Indeed, microbiologists are often faced with the problem of conflicting taxonomies: the reference databases differ, and there is an important decision to be made in the laboratory with regard to which of them should be used.[17] This decision requires the use of a different background map to evaluate and identify a possible new taxonomic assignment and depends on the confidence one places in the scientists who previously adjusted the database and the resulting tree. Whenever there is ambiguity in the genetic identity of a microbe, the decision to include it in one class or another also depends on bacterial morphology and behavior. All in all, the appearance and structure of the tree used to organize microbial knowledge is not the mechanical result of computational techniques; it arises from encounters between artificial intelligence and careful human pondering, leading to acts of nomination and classification. Some microbiologists thus share a more nominalistic than essentialist approach. In Ford Doolittle's words: "our jobs as systematists is not to discover what an organism truly is (in some essentialist sense) but rather what we should call it" (Doolittle, 2009, 2222).

Mapping Microbial Ecosystems

This section aims to show how the mathematical construction of phylogenetic trees, based on quantifying the distances between one branch and another, also constitutes the numerical substrate on which multidimensional maps are drawn. Maps visually convey kinship relationships between one sample (human or environmental) and another. Through graphical homogenization, they suggest analogies between human and planetary scales.

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[17] Another case I have been discussing in my interviews with the crew of Segata Lab is that of *Lawsonibacter asaccharolyticus*, a microbe that is associated with coffee consumption (Asnicar et al., 2021); its genomic identity corresponds to another taxonomic species (the *Clostridium phoceensis*; see Blanco-Míguez et al., 2023). The bacterium has two different names and affiliations according to the system of classification. As such, deciding what reference taxonomy to use depends, in the words of scientists themselves, on the trust they place in the group of scientists who have previously adjusted the database and the resulting tree.

Trees and phylogenetic methods underlie other forms of visualization, albeit in a hidden form. While a phylogenetic tree organizes and visualizes the microbial diversity present in a single sample, it is also possible to compare different samples from similar or different environments to understand how distant they are in their bacterial composition. This was the aim of UniFrac, a computational tool invented to identify differences in the composition of microbial communities (Lozupone & Knight, 2005). The metrics measuring differences among samples can be translated into positions on a multidimensional map. This kind of visualization is helpful to access big data and to visualize microbial communities as wholes rather than as analytical combinations of members. It often allows us to discover the factors that influence similarities between samples other than geographical proximity. A visualization tool that exploits these metrics is EMPeror, an interactive web-enabled scatterplot that visualizes the differences between communities of microbes and their covariance with metadata (Vázquez-Baeza et al., 2013; Vázquez-Baeza et al., 2017). It was developed to organize the unprecedented amount of data collected for the Earth Microbiome Project (EMP) and to visualize the results of dimensionality reduction techniques such as Principal Component Analysis (PCA), a method for reducing large and complex distance matrices "into visually manageable two-dimensional or three-dimensional representations of sample distances" (Knight et al., 2018, 417). By adding a color that refers to metadata, it is possible to visualize immediately how microbes that are genetically similar can cluster in the same ecological niche. In Huttenhower et al. (2012, 208, Fig. 1c), for example, this method allows us to visualize the extent of the genetic similarities in the microbes in the noses of different people and the difference between these microbes and those usually present in the gastrointestinal trait. Dysbiosis, an imbalance in the bacterial flora of our gut, resulting in temporary disorders or chronic inflammation, is then represented as a shift of the microbes of a sampled subject from a place of legitimate belonging to another body part (see Vázquez-Baeza et al., 2017, 9, Fig. 1): this means that the dysbiotic subject's bacteria live in a niche where they do not belong. The body, in this representation, is treated as a territory that is safe if its inhabitants do not move from where they are supposed to be. This territorial metaphor has been echoed and made more powerful by Rob Knight, who, during a TED Talk, explained to an audience of non-experts the enormous difference in composition between the microbial communities of different parts of the body (Knight, 2015). In his analogical construction of similarities, Knight also noted that environmental microbiomes – for example those extracted from a prairie and those extracted from a coral reef – are just as different from each other as the mouth and gut microbiomes of one individual. In this analogical construction of similarities, based on scientific evidence, the body and the earth are treated as habitats, hosting, on different scales, a vast diversity of living beings in ecological niches.

Let us return to the tree that opens this paper: Micropia's introductory wallpaper. There, humans are a minority twig, whose class – mammals – needs magnification even to be viewed. Proceeding through the exhibition, however, this peripheral relegation of the human is countered by a powerful interactive body scanner (Fig. 6), allowing visitors to discover the nature of the microbes that populate their body and what they do. The human is given back, with this installation, a centrality that is not

Fig. 6 Visitors scanning their body in search of microbes at ARTIS-Micropia. ©Maarten van der Wal

only related to its position within the exhibition's itinerary, but also to its new role as an inhabited place, a "container of multitudes" (to borrow an expression from Yong, 2016, who in turn has borrowed it from Walt Whitman), and an ecosystem. The human body becomes another map of organization for the living.

In 2012, a phylogenetic circular tree of the human microbiome was redesigned for the pages of *The New York Times*, under the title "Invisible Residents".[18] Taken from the Human Microbiome Project (Huttenhower et al., 2012; Morgan et al., 2013; Turnbaugh et al., 2007), the data visualization invites the reader to think of the human body as a place inhabited by diverse nonhuman agents that can either cooperate or disturb. In their study of the conceptual metaphors used by journalists to explain the microbiome to the public, Nerlich and Hellsten (2009, 27) focus on the presentation of humans as "neighborhoods" to be treated as "unexplored territory that needs to be mapped". Microbes are marked here as "bad" or "good" neighbors: some minimalistic black dots mark pathogens in opposition to harmless or commensal microbes. Pathogenicity is a strongly human-centered category that belongs to the domain of medicine and states the role of microbes in relation to the human host. What is good for the microbe can be harmful for the human: the two *Umwelten* (Uexküll and Jung, 1934) can respond to competing objectives.

By breaking down differences in scale, these types of visualizations attempt to eliminate the "biomedical/environmental dichotomy in microbial ecology" (Ley et al., 2007). We are still far from a satisfactory representation that can help us approach this vertiginous concept, but the invention of new visualization tools and innovative ways of popularizing science strongly suggest unprecedented forms of imagination.

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[18] https://archive.nytimes.com/www.nytimes.com/interactive/2012/06/19/science/0619-microbiome.html. Last accessed April 26, 2024. The visualization is one of the most appealing pieces of information design ever designed regarding the microbiome. I was struck by it for the first time as a poster in Nicola Segata's personal office in Trento. It was this vision that gave me the idea to write this essay.

Conclusions

From a constructivist approach, which we support (Dahan-Gaida, 2023; Drucker, 2020), diagrams are not simple translations of pre-existing data or simple tools for expressing thought. Rather, they "participate in the production of knowledge" (Dahan-Gaida, 2023, 12) and help to shape it (Dondero, 2011; Stjernfelt, 2007). Since they give expression to the relations between things (Mitchell, 1981), they allow us to formulate hypotheses on these relations. Their relationship with their object is thus not mimetical, as they do not look like what they represent, but is instead heuristic and generative: they are prostheses and instruments for the articulation of the thought (Griesemer & Wimsatt, 1989, 76; Burgio, 2021; Dahan-Gaida, 2023, 13).

In this paper, we have observed how diagrams participate in the scientific practices of the production of knowledge and how they shape visions about microbes. We have briefly reconstructed the history of the tree of life from Charles Darwin to the dawn of computing practices in order to show how evolutionary models have been used as machines for thinking and explaining the relationships between geological time and the history of life. We have seen how informatics has reenforced the centrality of the tree model as a principle of knowledge organization based on the digital code of genetics. While, in terms of representing evolution, the tree structure has been challenged by new discoveries in the molecular field, it has continued to be one of the most effective forms of visualization for mapping the microbiome in order to explore and position newly discovered species and relate them to contextual factors. We have also emphasized how the overlap of human and environmental microbiome multidimensional maps can foster the imagination of new coexistence scenarios in the future.

Despite apparent objectivity, all topological visualizations – from the tree to the multidimensional map – are conventional models: they are not automatic translations of genetic codes into visual languages mediated by a machine. On the contrary, they are constructions designed according to interpretations and worldviews. Models of statistical algorithms are far from being neutral and automatic: on the contrary, they can be "based on the imitation of an external configuration of space, time, relations and operations" (Pasquinelli, 2023, 247) and thus express a particular vision of the world that comes before and not after data mining. Algorithms are not the only epistemic agents that inform visualization models; these models are organized upstream on the basis of not only digital data but also centuries of research into the laws of evolution, epigenetic theories, and classification decisions.

In this sense, specific ontologies could exist behind different visual models that do not exclude each other but instead co-exist in a kind of multinaturalism (Marrone, 2024). We must keep the phylogenetic tree, a quintessential representation of the paradigm of continuity and unity through differences. This diagram, from Darwin on, links humans and non-humans by reconstructing the filiation of all living things from a supposed common ancestor. However, in some of the visualization tools used in microbiome studies, humans apparently disappear: the tree of life is only used to explore bacteria and archaea, while all eukaryotic domain

is left outside. This does not mean a loss of centrality for humans. On the contrary, they become a superordinate instance – a collective sender establishing and distributing semantic values to microbes. On the one hand, the medical narrative of pathogenicity qualifies microbes from a human point of view, reenforcing the narrative of a "radical divide" (Lynteris, 2017, 474) between humans and nonhumans. On the other hand, the ecological vision of commensality and mutualism between humans and microbes marries the "plenteous, promising, full of potential" world of microbial ecosystems (Paxson & Helmreich, 2014, 166).

From a discontinuist and naturalist approach that fosters the theory of human exceptionalism, it is easy to switch to a more ecological approach where humans, visualized as microbial containers, become hosting ecosystems. Humans dissolve in an emerging non-discontinuist and planetary vision, in which they are "terrestrial" (Latour, 2015; Formosinho, 2022), like any other ecosystem, just on a different scale: they become habitats with specific ecological niches, in a relation of symbiosis with their symbionts where mutualism is accentuated, as microbes often provide the hosts with biochemical substances that the host cannot produce on its own (Gontier, 2015a).

This paper has dealt with trees of life used in metagenomics, yet this diagrammatic structure is becoming the hidden scaffolding for more holistic diagrams that are still very efficient in their heuristic powers. There, some abstracts configurations associate humans with "ecological assemblages" (Haraway, 2016, 58), "super-organisms" (Lederberg, 2004) or – to use a word that is becoming central in biosemiotics studies – "holobionts": entities that are results of symbiotic association and constitute new units of evolution (Margulis & Fester, 1991; Gilbert, 2014, 2020; Lorimer, 2020). In this understanding, microbes are not just residents colonizing a pre-existing territory, but part of a complex eukaryotic metabolism-driven organism in evolution. Tools in science are not designed to represent this idea but succeed in doing so: they help unravel the entanglements of life and name the living substance; they help find connections to which they try to provide causal direction; and they construct visible approximations of the ecological niches that we harbor and create and of which we are part.

Data Availability No datasets were generated or analysed during the current study.

Declarations

Competing Interests The authors declare no competing interests.

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