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Of atoms, bricks and cells: A historical critique of historical criticisms of classical cell theory

Ariane Dröscher

Università Degli Studi di Firenze, Dipartimento di Biologia, Sezione di Antropologia, Via Del Proconsolo 12, 50122, Firenze, Italy

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ABSTRACT

The essay argues against historical accounts that portray classical cell theory as having established an atomistic and/or building block vision of life and hence as being diametrically opposed to the organismic standpoint. The cell-atom analogy came up in the mid-nineteenth century as a rhetorical creation *against* cell theory. Yet, the historical fact that opponents, such as Thomas Huxley, Adam Sedgwick, and Charles Otis Whitman interpreted and rejected cell theory as an atomistic theory does not mean that it actually was an atomistic theory. Nevertheless, their criticisms passed from one critic to the next over a considerable period and continue to influence present-day ideas about a supposedly reductionist cell theory. A look into the original texts of some protagonists of early cell theory, such as Matthias Schleiden, Theodor Schwann, Franz Unger, Albert von Koelliker, and Rudolf Virchow, shows that no one defended such a view. On the contrary, they explicitly spoke against any form of cell–atom or cell–building block analogy. Nor did they consider cells as completely independent and interchangeable units, or organisms as mere cell aggregates. I demonstrate that their views of cells and their role in vital organization were more complex, more uncertain and more hypothetical than their critics have admitted.

1. Introduction

Several historical accounts and philosophical analyses claim that the founders of classical cell theory entertained an atomistic theory of life. Famously, Georges Canguilhem (2008, p. 37–39 [Canguilhem, (1952), p. 67–70]) asserted that Georges Buffon's eighteenth-century concept of *molécules organiques* represented a form of biological atomism and that “those [nineteenth-century biologists] who located the final element of life in the cell undoubtedly forgot that they were realizing a dream […] of Buffon's” (ibid, p. 38). The missing link between Buffon and Schwann was, according to Canguilhem, Lorenz Oken. He further argued that the view of cells as atoms satisfied the requirement for a scientific analytical tool by explaining the complex visible through the simple invisible (ibid, p. 82). Interestingly, the only nineteenth-century researcher Canguilhem quoted was Claude Bernard, who called the cell “l'atome vital”. Yet, Bernard did so as late as 1874 and, as far as I know, only once (Bernard, 1874, p. 289). General historians and historians of biology, who later considered cell theory as an atomistic theory, are, for instance, R. A. Horne (1963, p. 327), or Silvia Caianiello (2008), who attributes such a view to Schwann, but explicitly excludes Virchow. More recently, Daniel Nicholson (2010) has elaborated a similar view and includes, apart from Schleiden and Schwann, also Turpin, Meyen, Virchow, and Oskar Hertwig, among others. Nicholson defines biological atomism as the postulate “that all life is composed of elementary and indivisible vital units” and that the “activity of a living organism is thus conceived as the result of the activities and interactions of its elementary constituents” (Nicholson (2010, p. 202). Marian Wnuk (2013) and Laurent Loison (2016) adopt a similar reasoning. In this essay, I will show that this definition as well as its attribution to classical cell theorists is misleading.

Canguilhem and Nicholson assert a historical cell–atom analogy. Their biological atomism must thus be distinguished from that of Edward Stuart Russell (1916, 192–194; Russell, 1930) as well as from Rembert Watermann, (1964) “atomism in biology” and Gerhard Müller-Strahl, (2014) “bio-atomism”. Russell mentioned biological atomism in his book *The Interpretation of Development and Heredity*, but, though he was critical of cell theory, only did so in reference to August Weismann's theory of the biophores and similar conceptions of *sub*cellular units (Russell, 1930, pp. 48, 103, 145). Both Watermann and Müller-Strahl define bio-atomism as those views that conceive of organisms from the macroscopic level down to the atomic level. According to Watermann, cell theory profoundly renewed this kind of bio-atomism by inverting and dynamizing the eighteenth-century atomistic view of the globular theories. Cell theory explained cells and cellular processes bottom-up, as

E-mail address: coraariane.droescher@unifi.it.

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based on atoms and molecular processes and followed those up to the level of organisms (Watermann, 1964, pp. 1–5). Schwann's renowned analogy between cell formation and crystallization is but the best-known example of this molecular vision. It is not this concept of bio-atomism that I contest as historically incorrect, but the cell–atom analogy.

The description of cells as the bricks or building blocks of life is today even more popular, in scientific essays (e.g. Ditzler et al., 2022; Lambert, 2006; Tavassoli, 1980), but especially in schoolbooks and biology websites (for a discussion of this metaphor, see Reynolds, 2018, pp. 12–58). The cell–brick analogy has several aspects in common with the cell–atom analogy, but there are also important differences. Both are often traced back to the globule theory, and both consider cells as distinct, independent and interchangeable units of construction. Yet, whereas historians like Timothy Lenoir (1982, p. 147) have shown that Oken, Carus, and Milne-Edwards indeed regarded "granules" or "globules" as building blocks of organic matter, Schleiden and Schwann's cellular view of organic construction was, as I will show, different. My principal critique in the second section of this essay is in fact directed against the strong structural and mechanical connotations of the building block metaphor.

Both analogies were not new – on the contrary. In the third section, I demonstrate that both analogies are based on a long tradition of historical criticisms that rehearse similar arguments at irregular intervals. My principal critique of these historical criticisms is that the newer ones adopt and transmit through time the points of view and assumptions inherent in the older ones as if they were neutral accounts. On occasion, even the same sets of quotes are repeated in them. All historical critiques should be approached with the same critical spirit and understood in their specific historical contexts (as done masterly e.g. by Jacyna, 1984b; Mazzolini, 1988; Richmond, 2000; Reynolds, 2007; Vienne, 2017; and many others). In fact, often the historical critiques do not do justice to the original texts of cell theory and, worst of all, ignore the considerable complexity of the vision they displayed. Presumably, most of the nineteenth-century as well as the recent critics did not even read the originals.

My aim is not to propose a new history of cell theory or to expound a complete list of researchers with original contributions to early cell theory or a complete survey of the *Zellenlehre* with all its far-reaching, multilayered and variegated aspects. I will neither discuss the merits and deficiencies of cell theory or of its originators, nor the question of priority. My aim is much less ambitious and confined to three main arguments: firstly, classical cell researchers opposed the cell–atom analogy; secondly, they did not conceive of cells as building blocks; and thirdly, nineteenth-century critics constructed cell atomism and the cell–building block analogy as rhetorical straw men with which to discredit cell theory. For reasons of space, I will adduce only a small number of quotes from a few proponents of the mid-nineteenth-century cellular viewpoint, mainly from Virchow's papers, because, in contrast to Schleiden and Schwann, he responded to his critics and thus elaborated his position more clearly than others.

2. The vision of cells as atoms

In the first part of this section, I establish that none of the proponents of classical cell theory, except one, adopted a cell–atom analogy. This was deliberate, for they were familiar with Dalton's atomic theory and had many reasons not to compare cells to atoms. In the second part, I show that the cell–atom analogy was created as a charge against cell theory, and I discuss that one of the principal arguments for such an analogy, the supposed atom-like independence of cells, does not capture the vision Schleiden, Schwann, Virchow and others wanted to articulate.

2.1. Atoms, cells and the "fathers" of cell theory

Canguilhem was not the first to assume an analogy between cells and atoms. Precursors exist in the nineteenth century. Yet, and this is my first argument, none of the protagonists in the mid-nineteenth-century cell debate proposed such an analogy in the affirmative. To my knowledge, there were only two exceptions: the embryologist Karl Bogislaus Reichert and, over thirty years later, the experimental physiologist Claude Bernard. However, both deployed the cell–atom analogy in a rather undefined manner. In 1874, in his essay *Phénomènes de la vie communs aux animaux et aux végétaux,* Bernard called the cell "l'atome vital" because of its supposed elementary and irreducible nature:

> Dans l'analyse intime d'un phénomène physiologique on aboutit toujours au même point, on arrive au même agent élémentaire, irréductible, l'élément organisé, la *cellule*, à la même propriété irréductible élémentaire, l'*irritabilité nutritive*, ou simplement la nutrition. [...] La physiologie générale ramène, en somme, tous les phénomènes aux propriétés de l'élément organique, de l'atome vital, de la *cellule* organisée. C'est dans la cellule que réside la vie avec ses caractères essentiels (Bernard, 1874, p. 289).

However, he did so rather late and only once. I have found no additional mention in his other publications. Reichert, who, like Schleiden, Schwann, Virchow, and Brücke was one of the many students of Johannes Müller, initially called yolk-cells "almost chaotically joint atoms" in his famous treatise *Das Entwickelungsleben im Wirbelthier-Reich* (Reichert, 1840, p. 1). While he was full of praise for Schwann and his theory in this book, one year later he objected that he could not go along with Schwann's concept of cell formation – a fundamental aspect of the generalization of cell theory – for the process of the segmentation of eggs. In his argumentation, he adopted the cell–atom analogy:

> However, Nature has many paths that lead to similar formations; but the concept of the simple elementary cell, which is always of the same kind, this organized *atom* at least of all formed organisms, implies something that is at odds with such poorly harmonizing varieties of genesis (Reichert, 1841, p. 524; my translation and my emphasis).

Reichert asserted that the first cells form endogenously, not exogenously, as Schwann believed. His cell–atom analogy was based on the idea that all cells, like all atoms, were essentially of the same kind and should therefore display the same mode of multiplication. His concept of "atom" was rather vague, much like those in circulation up to the eighteenth century. Indeed, none of his fellow Germans borrowed his vocabulary.

They had good reasons not to do so. During the 1830s and 1840s, the period when cell theory was formulated, the term atom was widely known in the German scientific circles. From its origin in Democritean philosophy through to the physics of the day, the term had acquired many meanings. In a strict sense, atomism allows for only one type of matter. For Democritus, composite matter did not really exist, only (invisible) atoms and void. Atoms were characterized by being (1) absolutely indivisible, (2) qualitatively identical, and (3) combinable with each other only by juxtaposition (Melsen, 2023). In the early nineteenth century, atomism was given a concrete chemical definition by John Dalton. In his *A New System of Chemical Philosophy* (Dalton, 1808-1810), he affirmed that atoms could not be subdivided, created or destroyed. He conceded the existence of only one property, their relative weight (see Chalmers, 2019; Banchetti & Robino, 2023). The German chemical circles mostly rejected the theoretical physical aspects of Dalton's atomistic vision. In particular, the analytical and reductionist implications conflicted with the basic beliefs of *Naturphilosophie*. Yet, the practical chemical aspects of atom theory fell on fertile ground (Rocke, 1979). During the 1820s and 1830s, chemistry enjoyed spectacular success in the German-speaking lands. Between 1825 and 1841, Friedrich Wöhler translated into German all thirteen volumes of the chemistry textbook by Jöns Jacob Berzelius, one of the main promoters of atomic theory. This treatise, as well as the works of Wöhler himself, of Justus von Liebig and of other chemists, were likewise widely discussed in biomedical circles, and they decisively contributed, among other things, to the high regard for chemical reasoning in biology – and to a terminological disambiguation. Even if Liebig rarely adopted the word "atom" in his path-breaking textbooks on organic chemistry (Liebig, 1840, 1842), though he frequently used the compound noun "atomic weight", the term acquired a definite meaning. According to Watermann, this was due to Schwann, whose greatest contribution to the history of biology was to finally have established a clear order for all the visible and invisible entities that were discussed in those years – atoms, molecules, granules, nucleoli, nuclei, cells, fibers etc. – and to have introduced modern chemical-physical atomism to biology (Watermann, 1964, pp. 54–55, 65–66, 76). Contemporary studies of the formation of crystals in Berlin, important for Schwann's renowned analogy between cell formation and crystallization, also took into consideration the atomistic theories of Berzelius and René Just Haüy.

Still another debate that contributed to the diffusion of chemical-atomistic thinking among biomedical scholars was concerning Brownian motion. It was first described in 1827 by the Scottish botanist Robert Brown but only became a decisive argument for the existence of atoms several decades later. However, from the late 1820s, the curious and irregular motion of (subcellular) particles and the demonstration that this motion was not due to something alive were actively debated among physicists and chemists as well as naturalists (Dröscher, 2023b, pp. 713–714), contributing to a distinction between particles of living and non-living matter. Schwann, for instance, was convinced to have observed Brownian movement in embryonic cells, and therefore spoke of "molecules" and "molecular motion" *within* the cell (Schwann, 1847, p. 58 [Schwann, 1839, p. 64]). In the same vein, describing his vision of growth and cell formation as a sort of crystallization, Schwann adopted the term "molecules" to connote *sub*cellular entities (ibid, p. 39 [p. 40]).

Most of the German biological and biomedical journals published articles with distinctly chemical content, too, and they used the term "atom" exclusively in chemical contexts. The same terminological distinction also holds in papers on cells (e.g. Schwann, 1839, pp. 242, 246; Schleiden, 1849, p. 28 [Schleiden, 1842, p. 276]; Unger, 1846, pp. 61, 66; Kölliker, 1852, p. 257; Virchow, 1858, p. 148; see also Hoppe, 1983). Moreover, Schleiden's book *Principles of scientific botany* contained two entire chapters on chemical elements and inorganic substances and their assimilation into organic bodies (Schleiden, 1849, pp. 3–30 [Schleiden, 1842, pp. 169–190]). The same holds true for Franz Unger's textbook of plant anatomy and physiology (Unger, 1846, pp. 26–40). It therefore appears that in Berlin and other German scientific circles there reigned general terminological and conceptual clarity about atoms, that the German-speaking cell researchers were familiar with atomic theory, and that they adopted it mindful of its specific chemical meaning. Individuals like the afore-mentioned Reichert or August Franz Joseph Carl Mayer, Schwann's anatomy teacher in Bonn, who still called the globules "elementary atoms" in 1827 (Mayer, A., 1827, p. 50), were but the last to do so.

The decision not to call or compare cells to atoms was thus a conscious choice. The possible reasons were numerous. Firstly, cells are visible with the help of optical instruments and amenable to microscopic observation and experimentation. Atoms are not. For this reason, the Viennese botanist Franz Unger was very clear that cells and atoms were two different things:

> However, these smallest parts [cells] that we want to consider here, are not of the type that belongs to the dimension of almost imperceptible mass particles, to the realm of atoms; on the contrary, they are always of a definite scale [Umfange], of a well discriminable shape, and, even if not always accessible to the naked eye, discernible to the well-armed eye right down to the smallest subordinate details (Unger, 1852, p. 9; my translation).

Secondly, cells were not considered to be indestructible and eternal. Virchow, for instance, noted that "The atom is unchangeable and permanent; the individual is changeable and transitory" (Virchow, 1958b, p. 125 [1862, p. 46]). The idea that cells were *living* entities was crucial for cell theory. Indeed, many treatises of the period described the life cycles of cells, their birth or, in Schleiden and Schwann's case, their *de novo* formation from the amorphous blastema, their growth, their transformations and vital manifestations, and finally their death (e. g. Schleiden, 1842, pp. 191–212, 239–271; Unger, 1846, pp. 64–76). Virchow considered cells to be irreducible, but not in the sense of being indestructible, because it was easy to cut any cell into pieces, but rather in the sense of being individuals.

Thirdly, cells were not seen as indivisible entities. On the contrary, cell division and/or endogenous cell formation was pervasive in descriptions of cells of the period. François-Vincent Raspail (1833, p. 85–86) described the origin of new cells deriving from a "cellule génératrice"; Ferdinand Meyen, 1837, II, p. 339) reported a "continuous production of new elementary organs" i.e. cells; and Unger (1852, p. 25) stated that "daughter cells originate entirely at the expense of the mother cells". The cell's capacity to generate was for Schwann (1847, p. 194 [Schwann, 1839, p. 228–229]) a principle indicator of its autonomy, and for Virchow (1958a, pp. 87–88 [Virchow, 1855, p. 23]; Virchow, 1856, p. 43) an indispensable argument for his cellular pathology. In an essay of 1852, he adopted just this argument to distinguish cells from atoms: "Organic Nature has no absolute individuals, no organic atoms: everywhere we find the principle of divisibility, fissility [Spaltbarkeit]" (Virchow, 1852, p. 378; my translation).

Fourth, the early cell researchers did not conceive of cells as the ultimate component of living bodies. On the contrary, cells were themselves seen as compound bodies. Already in the 1830s, some subcellular structures, namely the membrane, the nucleus and the nucleolus, played fundamental roles in identifying cells in tissues. Other particles, like starch granules, oil droplets, rubber, salt crystals, and similar bodies, even if not that important for cell theory, were nonetheless treated in detail in many treatises, in particular those on plant-anatomy and physiology (Unger, 1846, pp. 26–40; Mohl, 1851, pp. 40–99), and much space was dedicated to the processes of assimilation, processing, incorporation and extrusion of subcellular substances (e. g. Schleiden, 1842, pp. 239–272; Unger, 1846, pp. 64–76; Kölliker, 1845, pp. 54–95). Unger, for instance, explained in his textbook: The plant "does not possess a single atom that it has not received from the outside" (Unger, 1846, p. 61). Besides, some of the subcellular parts were even visibly active. From the late eighteenth century onwards, for instance, cytoplasmic flow was observed inside many cells, especially of algae and root tips. For Schleiden, the fact that such flow never transgressed the cell border was "a phenomenon […] to be connected with [the cell's] perfect individuality" (Schleiden, 1849, p. 94; see also Dröscher, 2023a).

Cells were thus not seen as the final unit, but rather as an intermediate state, between freely moving inorganic substances, on the one hand, and organisms, on the other. Organic organization was not seen as seamless continuity from the atom to the entire organism, but as a discontinuous succession of levels of organization. In the initial pages of his *Manual of Human Microscopical Anatomy*, Albert Kölliker exclaimed:

> If, without pretensions to prescience, it is permitted to speak of the future, this condition of Histology will last as long as no essential advance is made towards penetrating more deeply into organic structure, and becoming acquainted with those elements, of which that, which we at present hold to be simple, is composed. If it be possible that the molecules which constitute cell membranes, muscular fibrils, axile fibre of nerves, &c., should be discovered […] then a new era will commence for Histology, and the discoverer of the law of *cell genesis*, or of a *molecular theory*, will be as much or more celebrated than the originator of the doctrine of the composition of all animal tissues out of cells (Kölliker, 1854, p. 34; his emphasis).

Kölliker dreamt not of understanding cells *as* atoms, but cells as *built up* from atoms, hence of what Müller-Strahl (2014) and Watermann (1964) call bio-atomism. The physiologist Carl Ludwig articulated a similar bio-atomistic view, but one that was, contrary to Schleiden, Schwann, Virchow and others, mechanistic and reductionist. Ludwig's version of vital organization resulted completely from inter-atomic processes. In his *Lehrbuch der Physiologie,* he gave no special place to cells, but sketched a scheme starting with atoms, which aggregated to build higher-level chemical substances. In living beings these substances formed chemically and metabolically active liquids, which could solidify, precipitate or crystallize to assume specific forms, starting with elementary forms, namely granules, fibres and platelets, then cells and other formations, and finally the various tissues (Ludwig, 1856, II, pp. 150–165). Paradoxically, Thomas Huxley and Charles Otis Whitman, hence two of the main authors of the cell-atom critique, were bio-atomists in this sense. Huxley explained at the end of his critical review of cell theory that, in his view, vital forces were at work, which resided in the matter itself and not in structures. These forces were "molecular forces" that "rule the atoms and determine their arrangements into cells and organs" (Huxley, 1853, p. 314). Whitman endorsed the view of Julius Sachs that formative forces resided in all matter (Whitman, 1983, p. 647). Most cell theorists, in contrast, would have agreed with Virchow, when he declared in 1855 that cells were not the ultimate unit, but compound entities that represent the ultimate *living* unit:

> It may be more difficult to isolate the individual substances composing a cell, or a body formed by cells, than to depict a cell or cell-structure, but the cell will always be higher and more important in spite of this. As little as inositol and creatin are more important than the heart in whose muscle they are found are they more significant than the individual, primary, muscle bundles. *The significance of the constituent parts will at all times be found only in the Whole*. If we advance to the last boundaries within which there remain elements with the character of totality or, if you will, of unity, we can go no farther than the cell. It is the final and constantly present link in the great chain of mutually subordinated structures composing the human body (Virchow, 1958a, p. 85; his emphasis).

Fifth, in contrast to atoms, it was immediately obvious that cells were not all of the same kind. On the contrary, one of the early obstacles to the formulation and general acceptance of cell theory was the great variety of cell forms and the existence of cells that coalesce with other cells to form sieve tubes, lactiferous vessels, or myoblasts. Therefore, Schleiden and, even more so, Schwann did not even try to provide a morphological description that encompassed all forms and derivatives of cells in *adult* bodies and instead based their generalization on the assumption of a common pattern of development shared by all cells.

Sixth, cells were not conceived, in the vein of atoms, as entities without their own properties. The only exception conceded by Dalton's atomic theory was that atoms possessed a specific atomic weight. Several contemporary chemical theories, in particular in Germany, attributed other properties and some agency to atoms, but the atoms of Dalton's physical theory were inactive. The idea of cells as elementary units, or, even more so, as elementary organisms, in contrast, grounded on the idea that single cells express multiple if not all vital manifestations. In particular, Schwann, similar to Raspail (1828), conceived of cells as physiological agents (Maulitz, 1971; Parnes, 2003), and Virchow explained how the egg cell, becoming independent from the maternal body, "turns itself to be the seat of ongoing segmentation and scission" to ultimately form the whole organism (Virchow, 1852, p. 377).

As a seventh and last point of distinction, cells were not considered to be freely combinable entities. Cell or tissue transplantation or grafting were not yet practiced in the first half of the nineteenth century. Therefore, cells were never seen as replaceable and interchangeable parts that could be assembled and disassembled at wish. It was unthinkable to remove, for instance, a kidney cell and to transplant it into the heart. Early German cell theory was dominated by organicist conceptions of living bodies as an organically grown togetherness. As Rudolf Virchow clarified, "Atoms can enter into the most complicated combinations and groupings with other atoms, but they can withdraw again at any time with all of their properties intact. The individual depends on separation for its own maintenance" Virchow (1958b, p. 125).

This catalogue of differences between early nineteenth-century conceptions of atoms and of cells explains why Schleiden, Schwann and their contemporaries never proposed an analogy between them. A possible reason for coming up with such a historical artifact might be that some historians have described cell theory as a type or a direct successor of globular theories (e.g. Tyson, 1870, pp. 17–25; Baker, 1948, p. 114; Canguilhem, 2008, pp. 37–39; Nicholson, 2010, p. 204; Loison, 2016). While globular theories took many forms, globules were often indeed considered to be the ultimate structural unit of organic structures and, in Georges Buffon's words, "active particles, whose life is primitive, and perhaps indestructible" (Buffon, 1812, p. 26; see also Lenoir, 1982, p. 147; Vienne, 2014, p. 54). Some themes are indeed common in both globular and early cell theorizing, such as the possession of properties, i.e., the capacity to duplicate, vitality and agency (Hirai, 2016), or the sympathy for epigenetic views. But the possession of properties is enough to set globule (and cell) theory apart from atomic theory, which ascribed no or only the barely necessary properties to atoms. Be that as it may, the interpretation of globular theories as (eighteenth-century) atomistic theories may also have been a reason why some contemporary scholars attacked cell theory as atomistic. They thought cells, like globules, were conceived as "living atoms". Yet, this was a misunderstanding of cell theory. Cell theory diverged from globular theories on exactly this point. Schleiden and Schwann's cells were active, but, as explained above, neither indestructible nor ultimate or exchangeable. The secret of life did not reside in the globule-atom able to explicate processes via vital forces, but rather in cells as the sites of the metabolic processing of atoms. Moreover, cells could be described in their manifold forms, globules could not; and, above all, cells were not envisaged as the atoms of life, but as the smallest living units. François Jacob indeed discerned an important rupture between Buffon's *molecules organiques* and Oken's *cells*. For Oken, at the beginning of the nineteenth century, a living body could

> no longer be imagined as a mere association of elements as Maupertuis and Buffon envisaged. Even when Oken again brought up the idea that beings were composed of elements, he did not contemplate autonomous units bracketed together, but units amalgamated in the wholeness of the complete organism. Oken's new idea, from which the cell theory was gradually to emerge, was to consider the bodies of large animals in relation to microscopic beings and to visualize the latter as elements of the former – in short, to imagine the complex living organism as an association of simple living organisms. […] That unit could no longer be a simple molecule, an inert element or a portion of matter. It was itself a living body, a complex formation, able to move, feed and reproduce, a body, in fact, endowed with the principal attributes of life (Jacob, 2022 [1970], pp. 114–116).

Concluding this first part, I suggest that corpuscularism, as defined by Fabrizio Bigotti, and the concept of *minima naturalia* are better tools for the analysis of nineteenth-century cell theory than atomism. Bigotti defines corpuscularism as "a set of theories that explain natural transformations as a result of the interaction of particles (*minima naturalia*, *partes exiles*, *partes parvae*, *particulae*, and *semina*). It differs from atomism in that corpuscles are usually endowed with a property of their own and are further divisible, while atoms are neither" (Bigotti, 2020, p. 1). Corpuscles are thus "limits below which, if matter is conserved in quantity, any specific property of it is lost" (ibid, p. 2). Aristotle introduced *minima naturalia* in the fourth chapter of his *Physica,* referring to the smallest parts that combine to form compounds and yet remain in the compounds as components of them (Chalmers, 2019; Murdoch, 2001). For Aristotle, the organization of living beings was bounded by upper and lower (*maxima* and *minima*) quantitative limits. The *minima naturalia* did not necessarily represent the smallest component, but the minimum level of organization below which specific properties are lost. If, for instance, flesh was divided beyond its natural minimum, the residues – water, earth and small amounts of the other elements that blend to form flesh – would no longer have the formal nature of flesh, but of water, earth and the other elements. Accordingly, early cell theorists saw cells not as ultimate, indestructible, indivisible, independent atoms, but as one of several levels of organization and as the minimal level possessing the attributes of life.

2.2. *The atom-like independence of cells*

In the nineteenth century, the cell–atom analogy was deployed almost exclusively by critics and as a charge *against* cell theory. Moreover, I argue, that precisely these critics created the analogy to serve as target of their counterattacks. The main line of criticism was based on the argument that cell theory split organisms into a myriad of atom-like independent cells. Curiously, the first to adopt such a strategy was the aforementioned Karl Bogislaus Reichert, who was probably the only cell researcher to adopt the analogy in the affirmative (Reichert, 1840, p. 1). About fifteen years later, he published a harsh attack against Carl Ludwig and Rudolf Virchow and their supposed atomistic conception of life. Reichert probably felt encouraged by Johannes Müller's warning not to overgeneralize Schwann's cell theory. The process of development in higher animals, Müller had argued, required the multiplication of single cells, but also the transformation of the whole *in potentia* of the germ cell. He thus conceptualized the possibility that each cell is an individual *and* a multiple of the original germ. For him, the body was the result not only of the interaction of the multiples, but also of a force pervading the whole organism (Müller, 1840, pp. 614–617; for this see Lenoir, 1982, pp. 149–152; Zeller & Werneburg, 2024).

In 1855, Reichert published one of his annual reports on advances in microscopic anatomy, devoting the first chapter to the distinction between (Virchow's and Ludwig's) atomistic and (his) "systematic" conception of nature. The term "systematic", as used by Reichert, strongly resembled what was later called the "organismic" or "systemic" view. Reichert applauded Virchow for considering cells as systems, but then faulted him for considering cells as the atoms of bodies. For Virchow, Reichert wrote, the cell was the "absolute empress [*Herrscherin*] of organic nature", "the points of force [*Kraftpunkte*] of the atomists", the exclusive starting point for any consideration of vital phenomena (Reichert, 1855, pp. 3, 4–5; for this see Russell, 1916, pp. 192–194). According to this atomistic conception, Reichert complained, even the most complicated creature was a mechanically assembled aggregate: "One fabricates creatures, as one fabricates houses, ships, clocks, pots – via aggregation using an arbitrary scheme, only that the builders sit inside the cells" (ibid, p. 5; my translation). "Systematists", i. e., supporters of the organismic view, should not fall prey to "the atomistic tyranny" (ibid, p. 6), but rather continue to understand organisms as wholes and study development through the classical concepts of organization, function, germ, irritability etc.

It appears that this discussion was not followed up in German-speaking circles, except through a series of equally polemic counterattacks by Virchow (1856, 1859, 1862) that I consider below, and a voluminous paper by the anatomist August Rauber, who criticized cell theory in an informed and balanced manner (Rauber, 1883). However, similar criticisms surfaced several decades later in the Anglo-American biological communities. In 1893, embryologist Charles Otis Whitman criticized Schleiden and Schwann's exclusive focus on the cell and illustrated the supposed misconception as follows: "Regarded as a primary element of structure, it has come to signify in the organic world what the atom and molecule signify in the physical world" (Whitman, 1893, p. 639). About two decades later, the German anatomist Oskar Hertwig declared that

> As today to the chemists, the atoms of the chemical elements are the ultimate units, to which he is brought by the decomposition of matter, so the species-cell [Artzelle] is the same to the morphologist. Both currently represent the simplest comparable unit of living matter that is the basis for every living being. In these [species cells] the specificity of every organism is expressed, as it were the simplest formula, in such way that we can say that there exist as many varied species-cells as there exist varied living beings in the reign of organisms (Hertwig, O., 1916, p. 28–29).

Yet, Hertwig's concept of the *Artzelle* did not refer to cells in general and cannot be regarded as representing the cell concept of the *Zellenlehre.*

A few years later, the geneticist Leonard Doncaster resumed Whitman's statement when he declared that "the cell was to the biologist almost what the atom was to the chemist – the smallest portion of living matter capable of an independent existence" (Doncaster, 1920, p. 1). Another twenty years later, the American mycologist John Sydney Karling wrote in his (critical) centennial address about the cell theory:

> Biologists are now agreed that the formulation of this doctrine marks an epoch in biological science and that in its far-reaching influence on research the cell concept merits a position beside the atomic theory and the doctrines of organic evolution and Mendelism (Karling, 1939, p. 517).

Neither Whitman nor Karling nor Doncaster contended that cells *were* atoms but rather believed that they were of equal scientific importance. Nevertheless, the close association invited the conclusion that cell theory is an atomistic conception of life. In fact, an explicit statement of this kind can be found in the *Biological Principles* (1929) by the British theoretical biologist Henry Joseph Woodger, who, according to Karl Popper (1981, p. 328), "influenced and stimulated the evolution of the philosophy of science in Britain and in the United States as hardly anybody else". Woodger considered cell theory to be the outcome of an atomistic mode of thought (Woodger, 1929, p. 209). To emphasize his point, he added that "this theory – like other atomistic ones in biology – was hailed as providing biologists with 'units' which were to work the same wonders in biological science as atoms and molecules had done in chemistry and physics" (ibid, p. 210) and that "We are told that the cell is to the biologist as atoms and molecules are to the chemist; an aphorism as misleading as it is crude" (ibid, p. 294). Woodger never revealed who supposedly "told" us this or "hailed" the theory in this way but attributed the authorship of the analogy to unspecified supporters of cell theory.

Like Woodger and Canguilhem, Nicholson bases his thesis of the atomistic nature of cell theory on the statement that the early cell theorists viewed cells as independent individuals (Nicholson, 2010, p. 202). He identifies two neatly opposed factions: the atomistic and the organismic camp. His definition of biological atomism seems to originate in sociological rather than physical theory. The feature of independent agency was not, in fact, part of nineteenth-century (physical or chemical) atomic theory. Instead, in the sociological version, "A social theory is atomistic if it insists that all social institutions and events are to be seen as composed of the actions of individual men and nothing else" (Gould & Kolb, 1964, p. 39). However, the sociological meaning, i.e., the interpretation of classical cell theory as focusing exclusively on the independence and autonomy of cells in tissues, is equally misleading. If one reads the whole texts of German scholars investigating cells in the nineteenth century, the picture is much more complex.

The aforementioned criticism by Reichert, stimulated by Johannes Müller's concerns, shows that cell theory was perceived as a direct contribution to the concept of organismic constitution and organization. It is far beyond the reach of this brief essay to fully appreciate the contribution of cell theory to this debate or to analyse the diversity of the various positions. I will merely shine the spotlight on a few statements by some of the principal authors of classical cell theory to illustrate that the mid-nineteenth-century debate was less extreme and more variegated than the accounts of some historians and philosophers admit. Cell theory did provide a new viewpoint, but it was a position that opposed the reductionist approach of those, who, like Huxley and Ludwig, wanted to explain life exclusively by physical "molecular forces" or by analytical anatomical approaches.

Take, for instance, Virchow's position. According to Nicholson (2010, p. 205), as Virchow also recognized cells as the seats of disease, "the atomistic connotations of cell theory became even more conspicuous" (for this also Zeller & Werneburg, 2024, p. 174). Yet, as demonstrated by Mazzolini (1988) and Reynolds (2007), Virchow's concepts of life and organization were much more complicated. Bechtel (1984, p. 334) has demonstrated that Virchow's main "enemy" was the humoralist school and especially Karl von Rokitansky, who promoted an extremely reductionist physico-chemical programme and attributed disease to chemical factors. In 1859, Virchow responded in his talk *Atome und Individuen* (*Atoms and Individuals*) to Reichert's charge of atomism, defending the cellular viewpoint, but strictly denying that this represented an atomistic view of life. It is true that Virchow stated: "*All life is bound to cells, and the cell is not only the vessel of life but the living part itself*" (Virchow, 1958b, p. 129; his emphasis). Yet, continuing reading, his position immediately turned out to be rather different:

> *Indeed, every organic individual is replete with life.* Life does not have its seat in this or that location; it does not reside only in one or another part. Not so – it is in all parts to the extent that they are of cellular origin. Not only are the nerves alive, not only is the blood, but even in flesh, bones, and hair there is vigorous life-activity, just as the root, the leaf, the flower, and the seed of the plant carry life within (ibid, p. 129–130; his emphasis).

Two years later, Virchow expanded upon this argument, insisting:

> Only atomism knows 'ultimate units without necessary bond'; cellulism, instead, does not in principle behave differently than humorism and solidism, because it considers the parts of the body as formations [Gebilde] which *inevitably belong together*, rely on each other, and relate to each other in mutual solidary dependency. The only difference is that for the cellular viewpoint the bodily parts form a social unity and not, as the humoral and solidist schools maintain, a despotic or oligarchic unity (Virchow, 1860, p. 5; my translation, my emphasis).

Questions about the whole and the parts and about inter-dependence and individuality were pervasive in mid-nineteenth century biological research, in particular in the German-speaking lands (see e.g. Nyhart & Lidgard, 2011). The arguments were very diverse. I return to this aspect in the next section because the argument of independent atomic cells has much in common with the building-block analogy. In its extreme version, arguing for the individualism of parts implies a complete isolation of the parts. Any entity *made up* of individuals would be a pure coexistence or juxtaposition of interchangeable pieces. Müller had warned in 1840 that, *in extremis*, such a view would bring along difficulties for explaining how and why these parts stick together. Schleiden was fully aware of that. It is true that he proclaimed on the first page of his *Phytogenese*, "every plant developed in any higher degree, is an aggregate of fully individualized, independent, separate beings, even the cells themselves" (Schleiden, 1847, p. 231 [1838, p. 137]). Yet, in many other passages, he used the terms "elementary organ" (*Elementarorgan*) or "elementary parts" (*Elementartheile*) as synonyms of cells, implying a concept of cells as parts and not as autonomous individuals.

A few years later, Schleiden devoted a long section of his *Grundzüge der wissenschaftlichen Botanik* (1842) to the "Life of the cell in connection with others" (Schleiden, 1849, pp. 106–123 [Schleiden, 1842, pp. 213–239]). In the methodological introduction to this textbook Schleiden made seemingly contradictory claims about parts and wholes. This introduction – which runs to no less than 166 pages and had not been included in the English translation *Principles of Scientific Biology* (1849) (for this, see Buchdahl, 1989) – probably, best illustrates his ideas. Explaining his conviction that plant cells and animal cells were not the same, he argued:

> Finally, and this is presumably the most important difference, in the animal the independence of the elementary organ, the cell, is completely submerged and dissolved in the individuality of the whole, and every part counts only in association with the other and lives only to serve the whole. In plants, instead, the individuality of the whole is set back with respect to the elementary organ, and the whole plant appears to live only for and through the elementary organ (Schleiden, 1842, I, p. 32, my translation).

Several pages later, however, he declared, "Nature is an organic whole" (ibid, p. 78). He then reflected on plant organisms as systems and as the result of a general developmental plan.

> The plant, however, is a living organism, in other words a definitely ordered system of bodily parts, in which in regular periodicity a self-maintaining interplay of forces causes a steady flow of mutable states [*beständiger Abfluss veränderlicher Zustände*]. It consists, in a certain sense, in three parts: the active of the present, the ruins of the past, and the germs of the future [...], secondly, we can assume in it [in the plant] only the complex of forces in vivid interaction and an association of organs acting on one another, which constitute the ends and the means for their own conservation (ibid, p. 99).

This almost Kantian manifesto casts Schleiden's thought in a more holistic light, as opposed to a purely reductionist-atomistic one (see also Reynolds, 2018, p. 20). Trying for a more concrete approach to decide if certain manifestations were due to single cells or due to the entire body, he recommended to first understand the life of the single cell. At that point,

> we have to subtract from the vital process of the whole plant everything that cannot be already explained through the life of the single cell and appears as modified only because in the plant many cells live side by side and thereby more or less interact with each other. Only what cannot be explained through the concurrence of the vital expressions of the single cells can be considered as a peculiar vital manifestation of the whole plant itself, for which we can then once again search for explanatory reasons (Schleiden, 1842, I, pp. 108–109).

Affirming hence, on the one hand, his cellular vision, Schleiden however did not exclude the possibility of supracellular organismic explanation. Moreover, one should not overlook that Schleiden, like Schwann, did not aim to provide a theory that explained how cells originate from blastema, but how *organisms* originate from inorganic substances passing through the states of blastema, nuclei, cells, and finally tissues and organs. His focus was on organisms, not on the cell per se.

Nor did Schwann ever use the term "elementary *organism*", either. This was a term and a concept that became notorious about two decades later with Ernst Wilhelm von Brücke's essay *Die Elementarorganismen* (1861) (Liu, 2024). Schwann spoke of "elementary cells" (Elementarzellen) or, more frequently, of "elementary parts" (Elementartheile). It is true that Schwann used the term "aggregate" that was so contested by Huxley (1853, p. 295), Conklin (1940, p. 13), and other critics. Yet, he used it only three times (Schwann, 1847, pp. 2, 190, 212 [Schwann, 1839, pp. 2, 225, 254]), and never as a dogmatic pronouncement but always while reflecting upon opposing views. Historian Russel C. Maulitz opines that we have to be cautious in making judgements about Schwann's supposed reductionist vision: "We must not, of course, be too quick to take Schwann completely at his word" Maulitz (1971, p. 432). Maulitz sees Schwann's seemingly equivocal reflections on the usefulness of a reductionist approach as a contribution to an ongoing debate and part of a personal meditation, not as a final and definite doctrine he wanted to impress onto the scientific community. Similar caution is advisable in approaching Schwann's sometimes contradictory statements on the individuality of cells.

Schwann's presumably most popular quote goes:

> Each cell is, within certain limits, an Individual, an independent Whole. The vital phenomena of one are repeated, entirely or in part,

> in all the rest. These Individuals, however, are not ranged side by side as a mere Aggregate, but so operate together, in a manner unknown to us, as to produce an harmonious Whole (Schwann, 1847, pp. 1–228, p. 2).

This quote calls to mind Schleiden's famous proposal of the "double life" of cells (Schleiden, 1847, p. 231 [Schleiden, 1838, p. 138]). Several historians of cell theory have quoted Schwann's statement. Few (e.g. Watermann, 1960; Jahn, 1987; Lenoir, 1982, pp. 112–136; Vienne, 2017) have further investigated it to elucidate what he meant, whilst many continue to call Schwann's theory an analytical-reductionist approach. But Schwann's reflection on growth is even less atomistic-individualistic: "The cell, when once formed, continues to grow by its own individual powers, but is at the same time directed by the influence of the entire organism in such manner, as the design of the whole [*Plan des Ganzen*] requires" (Schwann, 1847, p. 39 [1839, p. 45]). This quote comes from the third part of Schwann's book, where he also discussed at length the teleological viewpoint. Without completely rejecting this view, Schwann however riposted that exactly this idea of one common force acting throughout the entire organism would mean to lose the individuality of the organism, because all cells would be equal:

> But since the elementary parts of animals bear exactly similar relations, the individuality of an entire animal would thus be lost; and yet precisely upon the individuality of the whole animal does the assumption rest, that it possesses a single fundamental power operating in accordance with a definite idea (Schwann, 1847, p. 190).

Schwann's reflections are difficult to grasp for today's readers if they are isolated from contemporary discussions and the organicist and (anti-)teleological contexts. In any event, I believe they demonstrate that he did not completely dissolve organisms into single atoms. Presumably, his idea about parts and wholes was adequately expressed, when he wrote "The manifestation of the power which resides in the cell depends upon conditions to which it is subject only when in connexion with the whole (organism)" (ibid, p. 193).

I conclude this section by again turning to Rudolf Virchow. He was less equivocal in expressing his position because he could build upon the foregoing discussions and polemics. Indeed, he clearly formulated the dilemma:

> From the beginning, observers of life have been occupied with the peculiar contradiction that recurs in the whole as well as in the particular and that we find again also in cells. Everywhere, there is independence and dependence, both in the mental and in the bodily, in the simple and in the composite of life (Virchow, 1856, p. 49; my translation).

He then explained that life does not have its seat in the single cells, but resulted from the interaction of the parts:

> Life consists in exchange, but it would cease to be life, if this exchange did not have certain limits. These limits require specific facilities for moderation and regulation, in the simple cell as well as in the compound multicellular organism. In the cell, we have come to know the membrane and the nucleus as moderators and regulators; in the compound animal all parts exert such an effect on each other, and, although the blood and the nerves are the most suited to influence other parts, a very effective regulation takes place through the antagonistic behaviour of the single tissue parts on each other (Virchow, 1856, p. 49–50; my translation).

Certainly, these passages do not explain what classical cell theory is, nor can they do justice to all its different aspects and varieties. Nevertheless, they demonstrate that it was not an atomistic-individualistic vision (if not in the sense of Watermann and Müller-Strahl). Regarding the relationship between parts and wholes, the conceptions of Schleiden, Schwann, and Virchow were neither doctrinaire, nor neatly opposed to the organismic viewpoint. Rather, they conceived of cells in multicellular contexts as an intermediate state between the lower levels of molecules and organic substances and the higher levels of tissues and whole bodies. Most German researchers would have agreed with Virchow, when he espoused in his essay *Old and new vitalism* his version of the "double life" of cells:

> I have thus gotten into a position from where I must defend atomism against the vitalists, and vitalism against the atomists. In my view, in biology, both have their share of being right, those who want to trace the history of life back to the ultimate molecular movements as well as those who consider the entire undivided whole to be their object of study. Only, both perspectives can be unified in a single one, if one takes cells as the basis of consideration, because only in cells the molecules find their amalgamation into an actually living unit, and ultimately every organic being is composed from cells (Virchow, 1856, p. 34; my translation).

3. The building block metaphor

The cell–building block analogy, which is very popular these days, shares several aspects with the cell–atom analogy. Both are based on the idea of ultimate structural or physiological units, which are assembled to construct more elaborate forms, like tissues or organisms, yet which exist, before the assemblage and after its dissolution, independently. However, bricks are human artefacts (Reynolds, 2018, p. 25), atoms are not. More importantly, in contrast to atoms, which may also be part of dynamic conceptions, bricks are symbols of stasis, interchangeability, and constancy. Yet, the cells of classical cell theory were everything but static, interchangeable, and constant. Again, I do not discuss whether the cell–brick analogy has traction in present-day biological research and science communication but argue against historical surveys that claim that classical cell theory asserted such a view (e. g. Tyson, 1870; Nicholson, 2010; Lyons, 2020; in part Harris, 1999).

As with the cell–atom analogy, hardly any nineteenth-century scholar of cell research used the building-block metaphor in the affirmative. Neither Schleiden (1838, 1842, 1848) or Schwann (1839), nor Mohl (1851) or Kölliker, (1852) ever adopted this terminology. Again, I argue that they had good reasons not to do so. One reason was that Schleiden and Schwann's papers were not anatomical treatises, at least not primarily, and did not aim to provide descriptions of the structure of plants and animals. Schleiden's work was a by-product of his studies on fertilisation. He was interested in the morphogenetic, not the structural role of cells and cell nuclei (Jahn, 1987, p. 19). Schwann, too, spent few words for cellular architecture. He even invited his readers to distrust visible morphological correspondences in adult cells, but to rely exclusively on the developmental process that showed "that there is one common principle of development for all the elementary particles of organisms" (Schwann, 1847, p. 163 [Schwann, 1839, p. 194]). Many of Schwann's contemporaries recognized the *developmental* premise of classical cell theory (e.g. Remak, 1855, pp. 164–172; Heidenhain, 1907, pp. 4–13), as have some historians of biology (e.g. Harris, 1999; Jahn, 1987; Müller-Wille, 2010; Parnes, 2000), whereas others only noticed the structural implications (Canguilhem, 2008, p. 82; Lyons, 2020; Welch & Clegg, 2012). Yet, there is a decisive difference between saying that an organism is made up *of* cells and saying that an organism is made *by* cells. The former denotes a state of being, the latter a process. The former may be compatible with a mechanical building-block view; the latter is not, because it assumes intimate bonding between the parts that have grown together in mutual interdependence rather than being subjects of assembly at will. Likewise, Schwann's insistence that single cells may be liberated and live independently from the whole, like bees from the swarm (Schwann, 1847, pp. 192–193), has to be understood, according to Gilbert Bourne, as a developmental argument. For Schwann, cells were *in posse* independent beings, but *in esse* subordinate to the whole (Bourne, 1895, pp. 164–165).

A decade later, Brücke did speak about „Bausteine" (building blocks), but he did so while referring to atoms as making up molecules. With respect to cells, he assumed that they had a much more complex structure that profoundly differed from inorganic compounds by showing organization: "Here, the assembled molecules of the organic compounds are only the workpieces, which are not layered up in a uniform manner one next to the other, but artfully fit together to form a living construction" (Brücke, 1861, p. 386; my translation; see also Brücke & Liu, 2024, p. 311).

Ernst Haeckel (1866, p. 528), too, used the term "Baustein" sparingly – once in *Generelle Morphologie*, where it connoted plastidules (i.e. anucleate but vital dots of protoplasm), not cells, and twice in *Natürliche Schöpfungsgeschichte*, where he used it in place of cells and in the sense of bricks (Haeckel, 1868, pp. 244, 285). In the English version, this was translated as "material" and as "unit" (Haeckel, 1876, I, pp. 300, 346). Franz Unger used the term extensively. He even considered replacing the textile metaphor "tissue" with "masonry" (Mauerwerk) (Unger, 1852, p. 14), but then rushed to offer a lengthy discussion of why the cell–brick analogy did *not* work. Firstly, because the process of production is entirely different:

> Every master builder transports his material over remoter or shorter distances; blocks, red-bricks, lime, sand, water and everything else he needs is brought to the construction site and only with these means he is able to implement his opus. From where does the plant take its bricks, its mortar etc., without which, in this case as in the other, a construction made of equal or similar elements is impossible? (ibid, p. 22; my translation).

For Unger, the cell produces its own building material, and is, "like a builder, everything in one and the same person, and, after all, the brick and the artisan at the same time" (ibid, p. 22–23).

Secondly, Unger argued, cells are not solid and homogeneous masses like bricks, but soft and semifluid (ibid, p. 24–25). Thirdly, Unger, as an advocate of endogenous cell formation, was convinced that daughter cells originate at the expense of their mother cells (ibid, p. 25), whereas bricks cannot grow out of earlier bricks. Fourth, he held that the "plant-edifice" continuously self-regenerates itself. Hence, a cell was a dynamic self-organizing entity, not a static, immovable one. Thus, he concluded,

> How different appears to us, after this glimpse into the formative history of the building stones, the masonry of the plant, – which rejuvenates itself continuously – and seemingly grows out of itself. At this point, every comparison vanishes, and we cannot see any construction by human hand and human invention that could resemble the edifice of the plant temple even from afar (ibid, p. 26; my translation).

To my knowledge, advocates of cell theory did not commonly use the cell–brick analogy in the nineteenth century. Again, the analogy was used not to articulate the cellular viewpoint, but in criticism against cell theory. Probably the first scholar who explicitly used the building-block metaphor in this way was Herbert Spencer. In the chapter *The morphological composition of plants* in his *Principles of Biology*, he denied both that all organisms and all parts of organisms are composed of cells. He underscored his opposition by offering analogical reasoning: "Supposing that clay were the only material available for building, the proposition that all houses are built of bricks, would bear about the same relation to the truth, as does the proposition that all organisms are composed of cells" (Spencer, 1867, p. 10). He then built his counterargument on the analogy that he himself had just introduced:

> This generalization respecting houses would be open to two criticisms: first, that certain houses of a primitive kind are formed, not out of bricks, but of unmoulded clay; and second, that though other houses consist mainly of bricks, yet their chimney-pots, drain-pipes, and ridge-tiles do not result from combination or metamorphosis of bricks, but are made directly out of the original clay. And of like natures are the criticisms which must be passed on the generalization, that cells are the morphological units of organisms (ibid, p. 10–11).

The physiologist Martin Heidenhain employed a similar rhetorical strategy. In his book *Plasma und Zelle*, he devoted a short, critical chapter to the "theory of the building block" (Bausteintheorie) (Heidenhain, 1907, pp. 26–29). He defined it as "a theory of tissues and of the body of living creatures, according to which the form of the creature is composed of cells, similar to single building blocks" and considered this to be the morphological correlate of its physiological counterpart, i.e., the theory of the cell-state (ibid, p. 26). Heidenhain presented the morphological and the physiological theories as the classical and still dominant views, and then severely criticized the supposed morphological and, above all, the physiological implications of treating all cells as identical individuals.

A few years later, Leonard Doncaster, who (erroneously) maintained that "The cell-theory arose, of course, from observation of the structure of plants", characterized the brick analogy on the opening page of his *Introduction to the Study of Cytology*: "As long as it was generally agreed that all organisms are built up of cells as a house is of bricks, the description of the cell as 'a unit of living matter' was not open to any very grave objection" (Doncaster, 1920, p. 1). He then criticized that vision, replacing the house analogy with that of a horde:

> The cell theory in its original and crude form regarded an organism as composed of a horde of discrete units which co-operate for a common purpose and are modified in various ways to make that co-operation more effective, much as a human community consists of many separate individuals, having different occupation and co-operating for their common good (ibid, p. 2).

Joseph Woodger, too, attacked the supporters of cell theory on these grounds: "We are told that the organism is built up of cells as a house is built of bricks**:** a palpable untruth, since an organism is an organism from the start (if it *has* a start) whereas the house is not a house until it is finished" (Woodger, 1929, p. 294). Like Heidenhain and Doncaster, Woodger did not specify which scholars advocated such a view. Yet, criticizing in the foregoing sentence the cell–atom analogy as "another persistent relic of the days of the 'cell-theory'", he gave the impression that the brick and the house analogies originated from Schleiden, Schwann and their contemporaries. In fact, Russell (1930, p. 234) and the British zoologist Sir James Gray (1931, p. 1) charged classical cell theory with having invoked such an analogy, which was later echoed by the British physician Sir David Waldron Smithers (1969, p. 778).

One of the principal features of building blocks – and atoms – is that they permit a high level of arbitrariness in making compounds. As long as certain constraints are respected, one can decompose a chemical macromolecule, or a house made of bricks, and reuse and recombine the single atoms or bricks at will to construct new and different things. Seventeenth- and eighteenth-century adherents of mechanistic conceptions indeed viewed bodies as machine-like static aggregations of parts. The parts of the body-machines were removable, interchangeable and subordinate to the whole. Cell theory, on the other hand, originated from the anti-mechanist, anti-reductionist organicist currents of the first half of the nineteenth century. Organicist theorists of the early nineteenth century considered bodies as historically grown and therefore indissolubly fused together. They conceived of bodies as composite collaborative entities. Individual parts were meaningless and unviable without their natural context. In a living being, the parts existed only in a dynamic and reciprocal relationship with the whole, and the whole existed only by virtue of its parts. Living bodies were organic units and their investigation required a developmental bottom-up approach, not a static top-down analysis as the mechanists demanded. Representatives of later organismic currents pursued very similar aims. According to Denton, Kumaramanickavel, and Legge (2013) and to Wagoner (2023, p. 1), they shared the romantic roots of the organismic perspective focusing on living, developing, and interconnected wholes, in contrast to mechanical causality, defending the primacy of processes over products, following the genetic and comparative method, with an eye on (dis) continuities and transitions in development.

Most early German cell researchers and those in Britain who, like Carpenter and Goodsir, nurtured sympathies with *Naturphilosophie*, understood and often shared the underlying organicist paradigm (Jacyna, 1984b). Later cell biologists did not, and indeed took at his word Schwann's use of the term "aggregate" and interpreted it as a mechanist manifesto. Yet, in the 1840s, the anti-mechanist Johannes Müller was able to accept Schwann's *Zellentheorie* as consistent with his teleomechanic vision of life. According to Timothy Lenoir (1982, p. 147), Müller maintained that „the relationship of cell to organism is the precise reverse of this 'atomistic' view", because "the cell is the agent operating in the service of the whole, and its structure is determined by the functions that it must carry out in harmony with others to insure the whole". Lenoir emphasises that Müller accepted Schwann's cell theory precisely because it had *not* reduced the whole to an assembly of associated individual parts. Rather, each cell was a replica of the whole, all originating from the same egg cell (ibid, p. 150).

Another example that illustrates how scholars of the mid-nineteenth century conceived of cells as parts and wholes is Karl Marx. For the German philosopher, cell theory was an important scientific inspiration for his socio-economic theory (Jessop, 2018, 2023). He attached great weight to the physiological agency of the individuals in a society, but did so in an organicist, not in an atomistic framework, and considered the "double life" of the citizens. The organic system's "development into a totality consists precisely in subordinating all elements of society to itself, or in creating out of it the organs it still lacks. This is historically how it becomes a totality. Its becoming this totality constitutes a moment of its process, of its development" (Marx, as cited in Jessop, 2018, p. 184).

If Nicholson (2010, p. 205) maintains that "One of the most salient consequences of cell theory's atomistic conception of the cell is that 'organism' becomes a biological category possessing little ontological weight of its own", then he follows the critics, in particular Whitman, in giving too much weight to a cell–organism dichotomy that profoundly misunderstands what researchers like Schleiden, Schwann, Virchow and many others were interested in. In fact, they were not cell researchers in the strict sense. The organism, rather than the cell, was their object of research. The cellular perspective was a novel approach to the investigation of the phenomena of life, but, in the end, their ultimate aim was to understand how life works, not how cells work. Virchow (1860, p. 10) indeed explicitly declared: "[…] the ultimate conception of my pathology is not the cell, but the life of the single parts." Schwann, too, held a position that is far more complex than the simple building block view. Moreover, he seemingly did not arrive at a clear stance but pondered various alternative views. Schleiden's famous quote on the 'double life of cells', too (Schleiden, 1838, p. 138) must be considered in the context of the ongoing German debate on parts and wholes. Franz Unger even took issue with Schleiden's aforementioned conviction in the high level of independence of plant cells, stressing instead that even in ligneous cells there always remained canals that linked neighbouring cells and thus kept them alive. This fact, according to Unger (1852, p. 35), "strikingly attests how, in the body of the plant, one cell cannot subsist without the others, if it wanted to become completely independent".

As explained by Dröscher (2021, pp. 165–169), even the most knowledgeable anatomists and physiologists of the time did not know exactly why the parts of an organism held and worked together with such orderliness. This is true for both supporters of atomistic and of organismic views. The number of explanations proffered cannot conceal that none provided a definite answer. The question of the whole and its parts continued to be passionately debated. A wide range of possible stances were adopted, from, on the one hand, models of loose aggregation of individual parts voluntarily collaborating as long as it benefitted them to models of strict hierarchies of parts that mechanically obey commands or sacrifice themselves entirely for the sake of the unit or a superior good, on the other. Even when, by the 1830s and 1840s, cell theory had more concrete anatomical and experimental results to offer, the lack of evidence about how cells cooperate made answers to the central question of organic theory, i.e., the nature of 'togetherness', necessarily speculative. Discussions about the degree of independence of the parts or their subordination to a higher entity, and about the nature of the tie that held them together, stood on shaky empirical grounds. Models that sounded plausible to some scholars sounded far-fetched to others, and the reasons for favouring one model over another did not reside in scientific proof alone.

Herbert Spencer, for instance, proposed a vision of bodies as "a commonwealth of monads" in 1850, and as liberal, democratic, and anti-dirigiste compound in 1860 (Elwick, 2003, pp. 48–54, 58). In response, Thomas Huxley championed an authoritarian view, in which each part was beholden to a dirigiste authority such as the will or the brain (ibid, p. 54–60). The zoologist Carl Vogt, working on siphonophores, developed a different vision still. According to him, the organization of these small planktonic sea organisms, which live in colonies of closely collaborating units, resembled an anarchy; for his colleague Rudolf Leuckart, they lived together "like in a communist state" because "there are here no poor next to the rich, no hungry next to the sated – but also no lazy next to the industrious. Each contributes its own to the sustenance and health of the whole" (quoted from Nyhart, 2017, p. 620). In France, Edmond Perrier, an expert in marine colonial invertebrates, also favoured an associative view, calling living beings "Republics of plastids" (Thomas, 2017, p. 676).

At the end of the century, the question about the relationship between parts and wholes was still open. Edmund B. Wilson pronounced in 1896:

> There is at present no biological question of greater moment than the means by which the individual cell-activities are co-ordinated, and the organic unity of the body maintained; for upon this question hangs not only the problem of the transmission of acquired characters, and the nature of development, but our conception of life itself (Wilson, 1896, p. 41).

And in 1939 embryologist Paul Weiss opined:

> The state of affairs calls our attention to the general problem of *the relation between the whole and its parts*, as one of the fundamental problems of the developing as well as the developed organism. Much of our further discussion will be devoted to this problem implicitly (Weiss, 1939, p. 109).

In conclusion, I suggest that the atomism–organicism dichotomy is too superficial, too reductive and too artificial and therefore an inappropriate tool for the analysis of classical cell theory. The context of nineteenth-century debate about wholes and parts is key and should never be underestimated, and hence mereology, the theory of parthood relations, or "of the relations of part to whole and the relations of part to part within a whole" (Varzi, 2019) provides a more appropriate framework for understanding these fascinating debates.

4. The role of historical critiques

My argument is not a discussion whether the historical criticisms were correct or not. Critics, as well as supporters, of cell theory had good reasons for querying, or accepting, certain facts and theoretical aspects, and for proposing their own vision. But I object to the tendency of some historians and philosophers to take the historical critical reviews of classical cell theory as if these were neutral, fair and accurate accounts, rather than discussing them in their historical, factual and explanatory contexts. It is questionable if historical criticisms provide valuable arguments for present-day debates. A critic like Reichert, for instance, interpreted and rejected cell theory as an atomistic theory, but this does not mean that it actually was an atomistic theory.

In the foregoing sections, I have tried to show that the charge that classical cell theory promoted atomism and building block views is not justified if one reads the original texts. In this section, I argue that many nineteenth-century criticisms continued to influence twentieth-century and even very recent accounts that reduce classical cell theory to its reductive and mechanistic aspects (e.g. Bechtel & Bollhagen, 2019; Bose, 2013, p. 358; Lyons, 2020; Soto et al., 2016; Theise & Kafatos, 2013, p. 14). These surveys do not represent the mainstream of the recent theoretical discussion, nor do I dispute that there are many excellent works on the *Zellenlehre*, but I maintain that there exists a tradition of critiques that relies on very similar arguments and often uses the same set of quotes.

The reasons why critics objected to cell theory were as varied and complex as cell theory itself and would be worth an analysis in their own right. Most critics (e.g. Rauber, Whitman, Sedgwick, Woodger, Russell) argued from an organismic standpoint. Charging cell theory with atomism served to construct a contrast to their own view and present it as innovative. Tellingly, the critiques were rarely factual alone. External factors were important, too. For instance, favour or rejection may have been based in different thought styles, in particular the underlying – and later misunderstood – assumptions of *Naturphilosophie*. Whitman's arguments against cell theory reveal opposition to Edmund B. Wilson's developmental ideas, and, above all, to Ernst Haeckel's biogenetic law (Maienschein, 1978). Huxley's youthful wish to distinguish himself and find a position in the British academic life (Richmond, 2000) presumably was a reason for publishing an attention-grabbing critique in the *British and Foreign Medico-Chirurgical Review*. Other possible external factors include efforts by the US-American researchers to emancipate and distinguish their views from German "speculation" (Maienschein, 1991), and the anti-German sentiments during and immediately after the Second World War.

Conceptual reasons included a predilection for a chemical-physiological view, the dislike of structuralism, opposition to preformism, rejection of spontaneous generation, a preference for holistic concepts, and many more. To go into these fundamental conceptual divergences in detail would take my argument too far afield. My point is simply to stress that there were good reasons to consider, for instance, cell division a result and not a cause of the organismic activity, just as there were good reasons to prefer the opposite view. There were many good reasons to entertain a view of life as bound to a protoplasmic substance that streams through the whole organism, connecting its parts and thus creating a continuum, just as there were good reasons to limit the focus on the physiological activity of single or a few cells. As Peter Sitte (1992, p. S6) holds, whether a researcher preferred a cellular or an organismic perspective depended on his or her vantage point. But precisely this point brings us back to Schleiden's statement that cells have a double life, as single units *and* as parts of a whole.

And yet it seems that many scholars already had a negative opinion of classical cell theory before they delved into the details. A recurring argument by the early critics, especially among Anglo-American scholars, was the supposedly dogmatic and scarcely proven character of classical cell theory. As early as 1874, John Drysdale complained that the Germans have "a perverted idea of patriotism and pietas toward Schwann and Schleiden" (Drysdale, 1874, p. 104). In 1896, the embryologist Adam Sedgwick lamented in his essay *On the inadequacy of the cellular theory of development* that cell theory "is now holding men's minds in an iron bondage" and that it blinds men's eye by "the domination of this fetish" (Sedgwick, 1895, p. 88). William Emerson Ritter and Leonard Doncaster complained that cell theory contradicted the simplest observations, there to see for anyone who could free his mind from the prevailing indoctrination (Ritter, 1919, pp. 166, 185; Doncaster, 1920, p. 2). Similarly, Woodger (1929, p. 209) denounced an "accompanying intolerance of criticism […] accompanied by a good deal of metaphysical speculation". Some criticisms even included personal attacks, calling Schleiden "arrogant" (Mayer, J., 1939, p. 482) and "caustic" (Huxley, 1853, p. 296), charging him of "bluff and brag" (Mayer, J., 1939, p. 482) and "fanciful descriptions" (Conklin, 1940, p. 12), and assessing his and Schwann's publications as "their most serious blunders" (Conklin, 1939, p. 538) and "absurdly wrong" (Conklin, 1940, p. 12). At the dawn of the Second World War, on occasion of the celebration of the first centennial of cell theory at the *American Association for the Advancement of Science*, three historical papers set out to dethrone cell theory's "fathers", claiming that "these two men added nothing either in content or in clarity with respect to the theory as such, and that they in fact lent support to a general view of cell formation which was completely erroneous" (Mayer, 1939, p. 482; similar is Karling, 1939, p. 517; Conklin, 1939, p. 538; Maximow & Bloom, 1942, p. 2). Similar negative statements are echoed in recent historical surveys, such as Henry Harris, who blames the "unquestioning acquiescence of German textbooks" for having propagated cell theory "against all criticism and circumspection" (Harris, 1999, p. 106), and Maienschein (2017, pp. 45–47). Welch and Clegg (2012, p. 643), too, adjudged cell theory to be a "superficial perspective that dwelled on the mere housing of life's basic processes".

Adherents of the cellular viewpoint, like the British zoologist Gilbert C. Bourne, on the other hand, were taken aback by the critic's accounts of cell theory, such as Sedgwick's and Whitman's. Bourne responded that, possibly, some cell researchers have attributed

> too great and too fundamental importance to the cell as an independent vital unit (Lebenseinheit). But, in point of fact, I am unable to find, in the writings of any reputable biologist, any statement to the effect that an organism is composed of independent and isolated units. One may, it is true, find passages here and there which, when removed from the context, might be made to bear such an interpretation. […] I am therefore far from being satisfied that the independent-life-unit theory has had such a dominant influence as Mr. Sedgwick would have us believe (Bourne, 1895, pp. 144–145, 147).

Bourne, like other supporters, did not see any doctrinaire connotation. He did not view cell theory as an incontestable truth: "Our concept of a cell must be an 'Allgemeines bild,' the generalized idea of a cell, derived from our experience of many kinds of cells" (ibid, p. 165–166). Likewise, early British supporters of cell theory did not consider Schwann's *Zellentheorie* as a revolutionary break, but rather as an interesting framework to be tested by their own research (Jacyna, 1984a, p. 27). A major figure of cytology around the turn of the century, Edmund B. Wilson maintained a similarly pragmatic attitude (Dröscher, 2002, pp. 361–363; Dröscher, 2009), and the anatomist Günther Hertwig likewise did not see why cell theory should be abandoned because it could not explain everything (Hertwig, G., 1929, pp. 18–21). Historian Russel C. Maulitz reminds us that in 1839, Schwann "intended the *Theorie der Zellen* section as something less than an ultimate synthesis uniting the theoretical elements of a lifetime of investigation" (Maulitz, 1971, p. 231). The American pathologist Arnold Rice Rich went even further, complaining that too many scholars discussed Schwann without having read his book. He deplored that

> curiously enough, in spite of the immense popularity of a part of its contents, the book itself was read by relatively few persons. There was not even a demand for it sufficient to encourage the printing of a second German edition. The kernel of truth contained in it seems to have been passed on from person to person, and quoted from book to book (Rich, 1926, p. 333).

Rich's suspicion was that most critics as well as many adherents had not read the original texts by Schleiden, Schwann, Virchow and others. Thomas Huxley is a case in point. Notwithstanding his ignorance, Huxley proceeded to tell his readers what "Schleiden and Schwann teach implicitly" (Huxley, 1853, p. 295). His review of cell theory of 1853 was a major break in the British debate, which until then had been rather positive (Jacyna, 1984b), and exerted an enormous influence on the future generations of critics, at least in the Anglo-Saxon world. He opposed cell theory for a number of reasons. Marsha Richmond (2000, p. 276) argues that the focal point of his criticism was his idea that cell theory expressed the new version of preformationism. She has shown that Huxley's view of cells relied not on Schleiden and Schwann, but on Kölliker's treatise, which included an updated and personal version of cell theory. At the time, he was translating Kölliker's *Handbuch der Gewebelehre des Menschen* (1852) into English (Kölliker, 1854). His review was originally meant to become an appendix to it. He criticised Kölliker's "preformistic" focus on cellular structures like membranes and nuclei (Richmond, 2000, pp. 264–265).

Besides this, I would add that Huxley's review was a response to his colleague Walter Benjamin Carpenter, rather than an in-depth analysis of Schwann's book, and probably foreshadowed their later dispute on the nature of mind and soul of the 1870s (Anger, 2009; Stanley, 2014). Carpenter was convinced of a fundamental difference between living and non-living bodies. He welcomed physical and chemical analyses but could not see how these would ever explain cell growth and reproduction (Hall, 1979). Similar to Justus von Liebig, Carpenter assumed a 'vital force' that depended on a certain arrangement of elementary particles. Cells were the instruments of that special force, a mechanical "cell force", as he called it (Carpenter, 1850, p. 737). Huxley took issue with this view, maintaining, "that the cells are not machines by which alone further development can take place" (Huxley, 1853, p. 314). In 1840, Carpenter had published a lengthy and detailed review of Schwann's book in the same journal in which Huxley's review appeared thirteen years later. Carpenter, in contrast to Huxley, had read Schwann's book. Whereas Carpenter dedicated much space to the first part of Schwann's book, containing his studies on cartilage and the chorda dorsalis (Carpenter, 1840, pp. 496–520), Huxley, as well as subsequent critics, did not even mention the first two parts of the *Mikroskopische Untersuchungen.* He concentrated exclusively on Schwann's theoretical reflections and reported those in a very selective manner, omitting Schwann's doubts and hesitations, his frequent weighting of different points of view, and all of his explicit signposting of certain deductions as hypotheses. Instead, Huxley provided an idiosyncratic and reduced selection of talking points, and sometimes subtly distorted Schwann's words. One example will suffice to illustrate my point. Huxley stated that "For Schwann the organism is a beehive, its actions and forces resulting from the separate but harmonious action of all its parts" (Huxley, 1853, p. 295), and referred readers to the passage in Schwann's German text (Schwann, 1839, p. 229). He himself had probably taken the quote from Carpenter's review (Carpenter, 1840, p. 524). In the original text, however, Schwann had not referred to a beehive, but used the example of the bee to illustrate that he saw no contradiction in saying that the cells of multicellular organisms are independent but at the same time cannot survive independently:

> The failure of growth in the case of any particular cell, when separated from an organized body, is as slight an objection to this theory, as it is an objection against the independent vitality of a bee, that it cannot continue long in existence after being separated from its swarm. The manifestation of the power which resides in the cell depends upon conditions to which it is subject only when in connexion with the whole (organism) (Schwann, 1847, pp. 1–228, p. 192–193).

Rather than attending to Schwann's view, Huxley probably reminded himself of Buffon's analogy of beehives as an emergent property of countless mechanical interactions. Buffon, in turn, had responded to Réaumur's reasoning that the social structure and the regular shape of the cells in beehives are proofs of divine wisdom (Canguilhem, 2008, p. 37; Kleiman-Lafon & Wolfe, 2021, pp. 263–264). In this way, Huxley transmuted Schwann's reflection on the part–whole relation into proof that Schwann "teaches implicitly […] that the whole organism is the result of the union and combined action of these primarily separate elements" (Huxley, 1853, p. 295). Schwann never stated that the cells of a body were originally separate. In order to make plain his own epigenetic view, Huxley overemphasized Schwann's thoughts about cellular independence, an aspect that Schwann had strongly qualified precisely in this above passage.

A second example of an author who constructed the arguments to serve his own needs is the physiologist Martin Heidenhain. He dedicated his book *Plasma und Zelle* to the centenary of Schwann's birthday, but nevertheless adopted a critical, though respectful attitude. He argued against the idea that organic products were "a mere sum of the individual performances of discrete cells" (Heidenhain, 1907, p. 54). Yet, no one defended such an extreme particulate position. A collaboration between parts, as Schwann proposed, was not a mere summing up. Moreover, it was difficult to demonstrate whether a cellular product was the result of the agency of the parts or of one whole. Heidenhain adduced the argument that certain continuous fibrous structures were "the communal product of a multitude of cells" (gemeinschaftliches Erzeugnis einer Vielzahl von Zellen) rather than of a "collaboration of cells" (Kollaboration der Zellen) (ibid, p. 53). Contrary to his firm conviction, however, it was (and probably still is) impossible to experimentally establish whether a substance was produced by a continuous protoplasm streaming through many cells, or by single cells working together. Crucial for Heidenhain's conviction was that, while he admitted that at the outset all cells are derived from the egg-cell, he maintained that during later developmental stages structures are formed that cannot be regarded as cells any more, but *sui generis* component parts: muscle fibres, neurons and other structures. He also took for granted the existence of an intercellular substance possessing its own metabolism and its own developmental potentiality (ibid, p. 55). If confirmed, this would have been a powerful proof of non-cellular activity. But without confirmation, it was as speculative as Schwann's view.

The visions of Huxley and Heidenhain exhibited equally dubious and speculative aspects as Schleiden and Schwann's theory. My essay does not aim to judge which of these historical actors was right and who was not, but it recommends caution in taking (polemical) criticisms as historical truths. Critics such as Huxley, Whitman, Sedgwick and Heidenhain were not historians who *super partes* analysed scientific theories of the past, but scientists involved in a, sometimes, fierce contemporary debate. Several misunderstandings are indeed due to the fact that Schleiden and Schwann, as is only normal, tended to overemphasize certain aspects in order to stress their own (real or imagined) innovative contributions. In the same way, the critics tended to overemphasize the points of (real or supposed) disagreement. It is therefore inopportune to use the criticisms as if they were a neutral source for historical research on these very items, without checking whether their historical interpretations were correct.

5. Conclusion

In this essay, I have sought to demonstrate that the historical criticisms of classical cell theory as atomistic and/or presupposing a building block view were constructed as such by the critics themselves, and that these charges were then passed from one critic to the next over a considerable period. Opponents like Huxley, Sedgwick, and Whitman adopted a rhetorical strategy of erecting a straw man, which could be easily knocked down by first reducing the complexity of cell theory to a few simple statements, and then criticizing these very statements. In order to persuade their readers, many critics also emphasized the erroneousness of parts of Schleiden and Schwann's theory, the heavy style of their texts, and some even impugned their character. This process produced a set of arguments and quotations from the texts of classical cell theory, that were echoed again and again, while much of the body of the work was ignored. In contrast, reading the entire original publications and considering the contemporary debates reveals that the authors' standpoints were more variegated, more complex and less extreme than the critical surveys imply.

I do not question that classical cell theory contained issues, nor is my aim to dissect specific points of contention, but I argue against the wholesale characterisation of classical cell theory as promoting an atomistic and/or building block vision of life, and as being diametrically opposed to the organismic standpoint. Schleiden, Schwann, Virchow, and almost all other cell researchers of the time investigated the cell to answer long-standing questions about organic organization, not to establish an exclusive and isolated research field for cell studies. Therefore, I argued in section 2.2, what today we call the cell-cell interactions and higher order systems were actually part of their reflections, albeit in a rudimental form. For reasons of space, I have limited my argumentation to two aspects, the supposed aggregate-like independence and the supposed brick-like nature of cells, and adduced only a small number of quotes by a few authors. However, I hope to have provided a salve against the uncritical assimilation of historical criticisms, and in particular, to have emphasized that many criticisms do not do justice to the complex reasoning of the early protagonists of cell theory. Far from representing definite conclusions or sacrosanct dogmas, the texts of Schleiden, Schwann, Virchow and many others are extraordinarily rich in reflections, new visions and even contradictions. I suggest that it was this which made their texts so inspiring for their contemporaries, and a success that went beyond the errors in their publications that later became apparent.

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References

Anger, S. (2009). Thomas Huxley, "On the hypothesis that animals are automata" (1874). *Victorian Review, 35*(1), 50–53.
Baker, J. R. (1948). The cell theory, a restatement, history and critique. Part I. *Quarterly Journal of Microscopical Science, 89*, 103–125.
Banchetti, M., & Robino, G. V. (2023). John Dalton and chemical atomism. In Ibid, & ibid (Eds.), *From the atom to living systems: Chemical and philosophical journey into modern and contemporary science*. Oxford University Press. https://doi.org/10.1093/oso/9780197598900.003.0007. . (Accessed 5 May 2024).
Bechtel, W. (1984). The evolution of our understanding of the cell: A study in the dynamics of scientific progress. *Studies in the History and Philosophy of Science, 15*(4), 309–356.
Bechtel, W., & Bollhagen, A. (2019). Philosophy of cell biology. In Zalta E.N. (Ed.), *The Stanford encyclopedia of philosophy*. https://plato.stanford.edu/archives/win2019/entries/cell-biology/ [Accessed 5 July 2025].
Bernard, C. (1874). Phénomènes de la vie communs aux animaux et aux végétaux. *La Revue scientifique de la France et de l'étranger, 13*(26 Septembre 1874), 289–295.
Bigotti, F. (2020). Corpuscularianism. In D. Jalubeanu, & C. T. Wolfe (Eds.), *Springer encyclopedia of early modern philosophy and the sciences* (pp. 1–13). Cham: Springer. https://doi.org/10.1007/978-3-319-20791-9_133-1. . (Accessed 1 May 2024).
Bose, B. (2013). Systems biology: A biologist's viewpoint. *Progress in Biophysics and Molecular Biology, 113*(3), 358–368.
Bourne, G. C. (1895). A criticism of the cell-theory; being an answer to mr. Sedgwick's article in the inadequacy of the cellular theory of development. *Quarterly Journal of Microscopical Science, 38*(149), 137–174.
Brücke, E. (1861). Die Elementarorganismen. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften Mathematisch-Naturwissenschaftliche Classe, Abt. 2, 44*(2), 381–406.
Brücke, E., & Liu, D. (2024). The elementary organisms. *Journal of the History of Biology, 57*, 305–330.
Buchdahl, G. (1989). Leading principles and induction: The methodology of Matthias Schleiden. In R. Giere, & R. S. Westfall (Eds.), *Foundations of scientific method: The nineteenth century* (pp. 23–52). Bloomington: Indiana University Press.
Buffon, G.-L. L. de (1812). *Natural history, general and particular: The history of man and quadrupeds, translated, with notes and observations, by William Smellie* (New edition, Vol. 3). London: T. Cadell & W. Davies.
Caianiello, S. (2008). La federazione delle parti: Sul concetto di individuo in Rudolf Virchow. *Medicina nei Secoli, 20*(1), 43–89.
Canguilhem, G. (1952). *La connaissance de la vie*. Paris: Librairie Hachette.
Canguilhem, G. (2008). Knowledge of life, ed. by P. Marrati & T. Meyers, transl. by S. Geroulanos & D. Ginsburg. New York: Fordham University Press.
Carpenter, W. B. (1840). Mikroskopische Untersuchungen über die Uebereinstimmung in der Struktur und dem Wachsthum der Thiere und Pflanzen, von Dr. Th. Schwann. *British and Foreign Medico-Chirurgical Review, 9*(18), 495–528.
Carpenter, W. B. (1850). On the mutual relations of the vital and physical forces. *Philosophical Transactions of the Royal Society*, 727–757. London.
Chalmers, A. (2019). Atomism from the 17th to the 20th century. In Zalta E.N. (Ed.), *The Stanford encyclopedia of philosophy (spring 2019 edition)*. https://plato.stanford.edu/archives/spr2019/entries/atomism-modern/ [Accessed 15 April 2024].
Conklin, E. G. (1939). Predecessors of Schleiden and Schwann. *The American Naturalist, 73*(749), 538–546.
Conklin, E. G. (1940). Cell and protoplasm concepts: Historical account. In F. R. Moulton (Ed.), *The cell and protoplasm* (pp. 6–19). The Science Press.
Dalton, J. (1808). *A new system of chemical philosophy, 2 vols*, 1810. London: R. Bickerstaff.
Denton, M., Kumaramanickavel, G., & Legge, M. (2013). Cells as irreducible whole: The failure of mechanism and the possibility of an organicist revival. *Biology and Philosophy, 28*(1), 31–52.
Ditzler, M. A., Popović, M., & Zajkowski, T. (2022). From building blocks to cells. In R. Thombre, & P. Vaishampayan (Eds.), *New frontiers in astrobiology* (pp. 111–133). Elsevier.
Doncaster, L. (1920). *An introduction to the study of cytology*. Cambridge: Cambridge University Press.
Dröscher, A. (2002). Edmund B. Wilson's the cell and cell-theory between 1896 and 1925. *History & Philosophy of the Life Sciences, 24*, 357–389.
Dröscher, A. (2009). »Was ist eine Zelle?« Edmund B. Wilsons Diagram als graphische Antwort. In J. Kaasch, & M. Kaasch (Eds.), *Natur und Kultur: Biologie im Spannungsfeld von Naturphilosophie und Darwinismus* (pp. 191–201). Berlin: VWB.
Dröscher, A. (2021). *Plants and politics in Padua during the age of revolution, 1820-1848*. Cham: Palgrave Macmillan.
Dröscher, A. (2023a). Die Zelle, das Leben und der Organismus: Giuseppe Meneghini und die Frühphase der Zelltheorie im habsburgischen Venetien. In M. G. Ash, & J. Mikoletzky (Eds.), *Von einer Wissenschaft des Lebens zu den Lebenswissenschaften in Zentraleuropa* (pp. 31–45). Wien: LIT Verlag.
Dröscher, A. (2023b). Inspiring imagination – Embarrassing analogies: Coping with the causes of cytoplasmic streaming. *Intellectual History Review, 33*(4), 703–725.
Drysdale, J. (1874). *The protoplasmic theory of life. London: Baillière, Tindall, and Cox*.
Elwick, J. (2003). Herbert Spencer and the disunity of the social organism. *History of Science, 41*, 35–72.
Gould, J., & Kolb, W. L. (Eds.). (1964). *A dictionary of the social sciences*. New York: The Free Press of Glencoe.
Gray, J. (1931). *A textbook of experimental cytology*. Cambridge: Cambridge University Press.
Haeckel, E. (1866). *Generelle Morphologie der Organismen: Allgemeine Grundzüge der organischen Formen-Wissenschaft*. Berlin: Georg Reimer.
Haeckel, E. (1868). *Natürliche Schöpfungsgeschichte. Gemeinverständliche wissenschaftliche Vorträge über die Entwickelungslehre im Allgemeinen und diejenige von Darwin, Goethe und Lamarck im Besonderen, über die Anwendung derselben auf den Ursprung des Menschen und andere damit zusammenhängende Grundfragen der Naturwissenschaft*. Berlin: Georg Reimer.
Haeckel, E. (1876). In *, 2. The history of creation: Or the development of the earth and its inhabitants by the action of natural causes. A popular exposition of the doctrine of evolution in general, and that of Darwin, Goethe, and Lamarck in particular. Translation revised by E. Ray Lancaster*. London: Henry S. King & Co.
Hall, V. M. D. (1979). The contribution of the physiologist, William Benjamin Carpenter (1813-1885), to the development of the principles of the correlation of forces and the conservation of energy. *Medical History, 23*, 129–155.
Harris, H. (1999). *The birth of the cell*. New Haven: Yale University Press.
Heidenhain, M. (1907). *Plasma und Zelle*. Jena: G. Fischer.
Hertwig, O. (1916). *Das Werden der Organismen: Eine Widerlegung von Darwin's Zufallstheorie*. Jena: Gustav Fischer.
Hertwig, G. (1929). Historische Übersicht über die Bedeutung der mikroskopischen Anatomie zur Erforschung der lebenden Masse. In G. Hertwig, F. K. Studnićka, & E. Tschopp (Eds.), *Die lebendige Masse. 1: Allgemeine mikroskopische Anatomie und Organisation der lebendigen Masse* (pp. 3–31). Berlin: Julius Springer.
Hirai, H. (2016). Mysteries of living corpuscles: Atomism and the origin of life in Sennert, Gassendi and Kircher. In P. Distelzweig, B. Goldberg, & E. R. Ragland (Eds.), *Early modern medicine and natural philosophy* (pp. 255–269). Dordrecht: Springer.
Hoppe, B. (1983). Chemophysiologie zwischen vitalistischer und mechanistischer Biologie im 19. Jahrhundert. *Medizinhistorisches Journal, 18*(3), 163–183.
Horne, R. A. (1963). Atomism in ancient medical history. *Medical History, 7*(4), 317–329.
Huxley, T. H. (1853). The cell theory. *British and Foreign Medico-Chirurgical Review, 12*, 285–314.
Jacob, F. (2022). In *The logic of life: A history of heredity. Translated by B. E. Spillmann*. Princeton: Princeton University Press.
Jacyna, L. S. (1984a). Immanence or transcendence: Theories of life and organization in Britain, 1790–1835. *Isis, 74*, 311–329.
Jacyna, L. S. (1984b). The romantic programme and the reception of cell theory in Britain. *Journal of the History of Biology, 17*(1), 13–48.
Jahn, I. (1987). Einführung und Erläuterung zur Geschichte der Zellenlehre und der Zellentheorie. In I. Jahn (Ed.), *Klassische Schriften zur Zellenlehre von Matthias Jacob Schleiden, Theodor Schwann, Max Schultze* (pp. 6–44). Leipzig: Akademische Verlagsgesellschaft Geest & Portig.
Jessop, B. (2018). 'Every beginning is difficult, holds in all sciences': Marx on the economic cell form of the capitalist mode of production. *Consecutio Rerum. Rivista critica della postmodernità, 5*(1), 173–192.

Jessop, B. (2023). The economic cell form. In R. Bellofiore, & T. Redolfi Riva (Eds.), *Marx: Key concepts* (pp. 49–66). Edward Elgar Publishing.
Karling, J. S. (1939). Schleiden's contribution to the cell theory. *The American Naturalist, 73*(749), 517–537.
Kleiman-Lafon, S., & Wolfe, C. T. (2021). Unsystematic vitality: From early modern beeswarms to contemporary swarm intelligence. In P. Fratzl, M. Friedman, K. Krauthausen, & W. Schäffner (Eds.), *Active materials* (pp. 259–298). De Gruyter.
Kölliker, A. (1845). Die Lehre von der thierischen Zelle und den einfachern thierischen Formelementen nach den neuesten Fortschritten dargestellt. *Zeitschrift für wissenschaftliche Botanik, 1*(2), 46–102.
Kölliker, A. (1852). *Handbuch der Gewebelehre des Menschen. Leipzig: Wilhelm Engelmann*.
Kölliker, A. (1854). *Manual of human microscopical anatomy. Translated by G. Busk & T. Huxley, edited with notes and additions by J. Da Costa. Philadelphia*. In Lippincott, Grambo & Co.
Lambert, G. (2006). Assembling the building blocks of cell theory. *Cellular and molecular biology (Noisy-le-Grand), 51*(8), 789–795.
Lenoir, T. (1982). *The strategy of life: Teleology and mechanics in nineteenth-century German biology*. Dordrecht: Reidel.
Liebig, J. von (1840). *Die organische Chemie in ihrer Anwendung auf Agricultur und Physiologie*. Braunschweig: Vieweg und Sohn.
Liebig, J. von (1842). *Die organische Chemie in ihrer Anwendung auf Physiologie und Pathologie*. Braunschweig: Vieweg und Sohn.
Liu, D. (2024). The schema and organization of the cell: An introduction to Ernst Brücke's Die Elementarorganismen (1861). *Journal of the History of Biology, 57*, 281–304.
Loison, L. (2016). The microscope against cell theory: Cancer research in nineteenth-century Parisian anatomical pathology. *Journal of the History of Medicine and Allied Sciences, 71*(3), 271–292.
Ludwig, C. (1856). Lehrbuch der Physiologie des Menschen. Zweiter Band: Aufbau und Verfall der Säfte und Gewebe. Thierische Wärme. *Leipzig und Heidelberg: C. F. Winter'sche Verlagshandlung*.
Lyons, S. L. (2020). *From cells to organisms: Re-envisioning cell theory*. Toronto: University of Toronto Press.
Maienschein, J. (1978). Cell lineage, ancestral reminiscence, and the biogenetic law. *Journal of the History of Biology, 11*, 129–158.
Maienschein, J. (1991). *Transforming traditions in American biology, 1880-1915*. Baltimore: The Johns Hopkins University Press.
Maienschein, J. (2017). The first century of cell theory: From structural units to complex living systems. In F. Stadler (Ed.), *Integrated history and philosophy of science* (pp. 43–54). Berlin: Springer.
Maulitz, R. C. (1971). Schwann's way: Cells and crystals. *Journal of the History of Medicine and Allied Sciences, 26*, 422–437.
Maximow, A. A., & Bloom, W. (1942). *A textbook of histology*. W. B. Saunders Company.
Mayer, A. F. J. C. (1827). *Supplemente zur Lehre vom Kreislaufe*. Bonn: Adolph Marcus.
Mayer, J. (1939). The cell theory: its past, present and future. *The American Naturalist, 73* (749), 481–484.
Mazzolini, R. G. (1988). *Politisch-biologische Analogien im Frühwerk Rudolf Virchows*. Marburg: Basilisken-Presse.
Melsen, A. G. M. van (2023). Atomism: Philosophy. In *Encyclopedia Britannica*, 3 Nov. 2023 https://www.britannica.com/topic/atomism. (Accessed 30 April 2024).
Meyen, F.J.F. (1837-1839). Neues System der Pflanzen-Physiologie, 3 Bände, Berlin: Haude und Spenersche Buchhandlung.
Mohl, H. von (1851). *Grundzüge der Anatomie und Physiologie der vegetabilischen Zelle*. Braunschweig: Friedrich Vieweg und Sohn.
Müller, J. (1840). Handbuch der Physiologie des Menschen für Vorlesungen. *Zweiter Band. Coblenz: Verlag von J. Hölscher*.
Müller-Strahl, G. (2014). Matter, metaphors, and mechanisms: Rethinking cell theories. *Studies in History and Philosophy of Biological and Biomedical Sciences, 48*, 130–150.
Müller-Wille, S. (2010). Cell theory, specificity, and reproduction, 1837–1870. *Studies in the History and Philosophy of the Biological and Biomedical Sciences, 41*(3), 225–231.
Murdoch, J. E. (2001). The medieval and Renaissance tradition of minima naturalia. In C. Lüthy, J. E. Murdoch, & W. R. Newman (Eds.), *Late medieval and early modern corpuscular matter theories* (pp. 91–132). Brill.
Nicholson, D. J. (2010). Biological atomism and cell theory. *Studies in the History and Philosophy of the Biological and Biomedical Sciences, 41*, 202–211.
Nyhart, L. (2017). The political organism: Carl Vogt on animals and states in the 1840s and '50s. *Historical Studies in the Natural Sciences, 47*(5), 602–628.
Nyhart, L. K., & Lidgard, S. (2011). Individuals at the center of biology: Rudolf Leuckart's Polymorphismus der Individuen and the ongoing narrative of parts and wholes. With an annotated translation. *Journal of the History of Biology, 44*(3), 373–443.
Parnes, O. (2000). The envisioning of cells. *Science in Context, 13*, 71–92.
Parnes, O. (2003). From agents to cells: Theodor Schwann's research notes of the years 1835-1838. In F. L. Holmes, J. Renn, & H.-J. Rheinberger (Eds.), *Reworking the bench: Research notebooks in the history of science* (pp. 119–140). Kluwer Academic Publishers.
Popper, K. (1981). Obituary: Joseph Henry Woodger. *British Journal for the Philosophy of Science, 32*(3), 328–330.
Raspail, F.-V. (1828). Second Mémoire de physiologie et de chimie microscopique sur la structure intime des tissus de nature animale. *Répertoire général d'anatomie et de physiologies pathologique et de clinique chirurgicale, 6*, 135–164.
Raspail, F.-V. (1833). *Nouveau système de chimie organique, fondé sur des méthodes nouvelles d'observation*. Paris: J.B. Baillière.
Rauber, A. (1883). Neue Grundlagen zur Kenntnis der Zelle. *Morphologisches Jahrbuch, 8*, 233–338.
Reichert, K. B. (1840). *Das Entwickelungsleben im Wirbelthier-Reich*. Berlin: August Hirschwald.
Reichert, K. B. (1841). Ueber den Furchungs-process der Batrachier-Eier. *Archiv für Anatomie Physiologie und wissenschaftliche Medicin*, 523–541.
Reichert, K. B. (1855). Bericht über die Fortschritte in der mikroskopischen Anatomie im Jahre 1854. In *Archiv für Anatomie. Physiologie und wissenschaftliche Medicin,1-75*.
Remak, R. (1855). *Untersuchungen über die Entwickelung der Wirbelthiere*. Berlin: G. Reimer.
Reynolds, A. S. (2007). The theory of the cell state and the question of cell autonomy in nineteenth and early twentieth century biology. *Science in Context, 20*(1), 71–95.
Reynolds, A. S. (2018). *The third lens: Metaphor and the creation of modern cell biology*. Chicago: The University of Chicago Press.
Rich, A. R. (1926). The place of R.-J.-H. Dutrochet in the development of the cell theory. *Bulletin of the Johns Hopkins Hospital, 39*, 330–365.
Richmond, M. L. (2000). T.H. Huxley's criticism of German cell theory: An epigenetic and physiological interpretation of cell structure. *Journal of the History of Biology, 33*, 247–289.
Ritter, W. E. (1919). *The unity of the organism, 2 vols*. Boston: R.G. Badger.
Rocke, A. J. (1979). The reception of chemical atomism in Germany. *Isis, 70*(4), 519–536.
Russell, E. S. (1916). *Form and function: A contribution to the history of animal morphology*. London: John Murray.
Russell, E. S. (1930). *The interpretation of development and heredity: A study in biological method*. Oxford: Clarendon Press.
Schleiden, M. J. (1838). Beiträge zur Phytogenesis. *Archiv für Anatomie, Physiologie und wissenschaftliche Medicin*, 137–176.
Schleiden, M. J. (1842). *Grundzüge der wissenschaftlichen Botanik nebst einer methodologischen Einleitung als Anleitung zum Studium der Pflanze. 2 Teile. Leipzig: Wilhelm Engelmann*.
Schleiden, M.J. (1847). Contributions to phytogenesis. In Schwann, *Theodor: Microscopical researches into the accordance in the structure and growth of animals and plants* (pp. 229-268), translated from the German by Henry Smith. London: Sydenham Society.
Schleiden, M. J. (1848). *Die Pflanze und ihr Leben: Populäre Vorträge*. Leipzig: Wilhelm Engelmann.
Schleiden, M. J. (1849). In *Principles of scientific botany, or, botany as an inductive science, translated by E. Lankester*. London: Longman, Brown, Green, and Longmans.
Schwann, T. (1839). *Mikroskopische Untersuchungen über die Uebereinstimmung in der Struktur und dem Wachsthum der Thiere und Pflanzen*. Berlin: Sander.
Schwann, T. (1847). *Microscopical researches into the accordance in the structure and growth of animal and plants. Translated from the German by Henry Smith* (pp. 1–228). London: Seydenham Society.
Sedgwick, A. (1895). On the inadequacy of the cellular theory of development, and on the early development of nerves, particularly of the third nerve and of the sympathetic in Elasmobranchii. *Quarterly Journal of Microscopical Science, 37*, 87–101.
Sitte, P. (1992). A modern concept of the 'cell theory': A perspective on competing hypotheses of structure. *Journal of Plant Sciences, 153*(3), S1–S6.
Smithers, D. W. (1969). No cell is an island. *British Medical Journal, 3*(5673), 778.
Soto, A. M., Longo, G., Miquel, P.-A., Montevil, M., Mossio, M., Perret, N., Pocheville, A., & Sonnenschein, C. (2016). Toward a theory of organisms: Three founding principles in search of a useful integration. *Progress in Biophysics and Molecular Biology, 122*(1), 77–82.
Spencer, H. (1867). *The principles of biology* (Vol. II). London: Williams and Norgate.
Stanley, M. (2014). *Huxley's church and Maxwell's demon: From theistic science to naturalistic science*. Chicago: The University of Chicago Press.
Tavassoli, M. (1980). The cell theory: A foundation to the edifice of biology. *American journal of pathology, 98*(1), 44.
Theise, N. D., & Kafatos, M. C. (2013). Complementarity in biological systems: A complexity views. *Wiley Periodicals, 18*(6), 11–20.
Thomas, M. (2017). Biological and social new orders: Charles Robin (1821-1885) and Comteanism in the Third republic. *Historical Studies in the Natural Sciences, 47*(5), 653–677.
Tyson, J. (1870). *The cell doctrine: Its history and present state, for use of students in medicine and dentistry*. Philadelphia: Lindsay & Blakiston.
Unger, F. (1846). Grundzüge der Anatomie und Physiologie der Pflanzen. *Verlag bei Carl Gerold*.
Unger, F. (1852). *Botanische Briefe*. Wien: Verlag von Carl Gerold & Sohn.
Varzi, A.C. (2019). Mereology. In Zalta E.N. (Ed.), *The Stanford encyclopedia of philosophy (spring 2019 edition)*. https://plato.stanford.edu/entries/mereology/ [Accessed 15 April 2024].
Vienne, F. (2014). Organic molecules, parasites, Urthiere: The controversial nature of spermatic animals, 1749-1841. In S. Lettow (Ed.), *Reproduction, race, and gender: In philosophy and the early life sciences*. Suny Press.
Vienne, F. (2017). Worlds conflicting: The cell theories of François-Vincent Raspail and Theodor Schwann. *Historical Studies in the Natural Sciences, 47*(5), 629–652.
Virchow, R. (1852). Ernährungseinheit und Krankheitsherde. *Archiv für Pathologische Anatomie und Physiologie und für Klinische Medicin, 4*, 375–399.
Virchow, R. (1855). Cellular-pathologie. *Archiv für Pathologische Anatomie und Physiologie und für Klinische Medicin, 8*, 3–39.
Virchow, R. (1856). Alter und neuer Vitalismus. *Archiv für Pathologische Anatomie und Physiologie und für Klinische Medicin, 9*, 3–55.
Virchow, R. (1858). *Die Cellularpathologie in ihrer Begründung auf physiologische und pathologische Gewebelehre*. Berlin: August Hirschwald.
Virchow, R. (1859). Reiz und Reizbarkeit. *Archiv für Pathologische Anatomie und Physiologie und für Klinische Medicin, 14*, 1–63.
Virchow, R. (1860). Die Kritiker der Cellularpathologie. *Archiv für Pathologische Anatomie und Physiologie und für Klinische Medicin, 18*, 1–14.

Virchow, R. (1862). Atome und Individuen. Vortrag, gehalten im wissenschaftlichen Vereine der Singakademie zu Berlin am 12. Februar 1859. In *Vier Reden über Leben und Kranksein* (pp. 35–76). Georg Reimer.

Virchow, R. (1958a). Cellular pathology (1855). In L. J. Rather (Ed.), *Disease, life, and man: Selected essays by Rudolf Virchow, translated and with an introduction* (pp. 71–101). Stanford University Press.

Virchow, R. (1958b). Atoms and individuals (1859). In *Disease, life, and man: Selected essays by Rudolf Virchow, translated and with an introduction by L. J. Rather* (pp. 120–141). Stanford University Press.

Wagoner, B. (2023). The organismic theory of development: Romantic roots of a vital concept. *Theory & Psychology, 34*(1), 1–23.

Watermann, R. (1960). *Theodor Schwann: Leben und Werk*. Düsseldorf: L. Schwann.

Watermann, R. (1964). *Vom Leben der Gewebe: Ein kleines Geschichtsbuch. Köln: Kölner Universitätsverlag*.

Weiss, P. (1939). *Principles of development: A text in experimental embryology*. New York: Henry Holt and Company.

Welch, G. R., & Clegg, J. S. (2012). Cell versus protoplasm: Revisionist history. *Cell Biology International, 36*, 643–647.

Whitman, C. O. (1893). The inadequacy of the cell-theory of development. *Journal of Morphology, 8*, 639–658.

Wilson, E. B. (1896). *The cell in development and inheritance*. The Macmillan Company.

Wnuk, M. (2013). Geneza i rozwój idei elementarnej jednostki życia – W kierunku filozofii nanobiologii [The Genesis and Development of the "Elementary Unit of Life" Idea: Towards the Philosophy of Nanobiology]. *Lublin: Wydawnictwo KUL*. https://www.kul.pl/the-genesis-and-development-of-the-elementary-unit-of-life-idea-towards-the-philosophy-of-nanobiology,art_46012.html. (Accessed 20 April 2024).

Woodger, J. H. (1929). *Biological principles: A critical study*. Kegan Paul, Trench, Trubner & Co., Ltd.

Zeller, U., & Werneburg, I. (2024). A life dedicated to research and ideal: Johannes Müller between empirical universality and idealistic vitalism mirrored in lecture notes from 1851. *Theory in Biosciences, 143*, 161–182.