

# Chapter 4

## The First Century of Cell Theory: From Structural Units to Complex Living Systems

### A Look from 1940 at 100 Years of Cell-Theory

Jane Maienschein

In his introduction to the volume entitled *The Cell and Protoplasm* in 1940, the editor Forest Ray Moulton noted that the American Association for the Advancement of Science was publishing the volume as the product of a symposium, held in 1939, to celebrate the centennial of Matthias Schleiden and Theodor Schwann's 1838 cell theory.<sup>1</sup> Because of the rich history of thinking about cells up to that time, "In a sense the Cell Theory is not new." Yet, Moulton suggested, "In another sense the Cell Theory is always new, for every discovery respecting this primary and essential unit of living organisms, both plant and animal, has raised more questions than it has answered and has always widened the fields of inquiry."<sup>2</sup> The volume set out to show both what was already well-established and what was new.

By 1940, discussion of cells involved looking at a predictable list of topics, including the way cell walls delineate individual cells, contents of cells including nucleus and cytoplasm and organelles, and environment interactions both internal to and external to each cell. With those came considerations of biochemistry and cell physiology. Less predictable are the chapters on microbiology, viruses, enzymes, hormones, and vitamins. The choice of topics and of contributors makes clear just how many questions remained in the middle of the twentieth century about cells and especially how they interact within organisms.

Cell structure and function clearly affect the organism, but just what the causal connections were remained unclear. By mid-century, two different views co-existed. As Lester Sharp put it in his 1943 textbook *Fundamentals of Cytology*, the first held that cells are the agents of organization of the organism, while the second or

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<sup>1</sup> Schleiden (1838); Schwann (1839).

<sup>2</sup> Forest Ray Moulton (1940), Foreword.

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organismal view placed the agency with the organism as a whole and emphasized, “the primacy of the whole, cells when present being important but subsidiary parts.”<sup>3</sup> In both cases, evolutionary history was thought to have played important roles in shaping the patterns that emerged. But do the cells drive the organism, or does the organism drive the cells? What research and what epistemological assumptions had led to this mid-twentieth century question?

## 4.1 The Standard Story

The familiar story, recounted in textbooks and cell biology courses, declares that Schleiden and Schwann invented the cell theory. Standard accounts tell of these two German innovators, one working on plants and the other on animals, coming up with *the* theory that cells are *the* fundamental unit of life. In 1838, the story goes, they put together the available evidence and reasoning to develop what they called the *Zellentheorie* to ground all of biology, and they were the first to do so.

Everybody likes a good myth, and this one does its job. Schleiden and Schwann did, in fact, respectively study plants and animals and did see and describe cells. They were not the first, however, but drew on earlier observations by Robert Hooke, Anthony Leeuwenhoek, and many others to establish the idea of structural cellular units as bounded by walls. Internally, these seventeenth century microscopists held that cells might consist of some fluid-like or gel-like substance or they might be vesicles full of nothing more than air. What was important is that they each observed vesicles with walls and structure, and came to call them cells.<sup>4</sup>

For decades, textbooks have referred to these two as the fathers or founders of the cell theory, as if they had articulated a theory of the basic units of life. In fact, Schleiden and Schwann saw *basic units of living organisms* but not *basic living units*. That is, they did not clearly consider those cells to be “alive” since they did not reproduce themselves but were thought to arise at least at times through a sort of crystallization. The standard story misses the distinction and ascribes more agency and properties of life to the cell than Schleiden and Schwann did themselves. The myth has not changed much, despite new historical studies after a century of cell biology.

## 4.2 Writing a New History Around 1950

In the mid twentieth century, several researchers set out to look more closely at the historical record by studying what the cell theory meant and what each contributor had actually done. In 1948, Oxford University cytologist John Randal Baker began a series of five essays in the *Quarterly Journal of Microscopical Science*. Under the

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<sup>3</sup>Sharp (1943), p. 21.

<sup>4</sup>Harris (1999). Chapters 1 and 2 on early microscopists and early theories.

title “The Cell-theory: a Restatement, History, and Critique,” Baker looked closely at the primary sources. He began with the point that “Several zoological text-books published during the last two decades have cast doubts on the validity of the cell-theory.” Baker resolved to review the attacks, the nature of the evidence, and to establish the current status of the cell theory. He found different critiques attacking different aspects of what was lumped together as the cell theory, and he found some of the attacks justified while others were not.<sup>5</sup>

Baker broke down the larger theory into what he called “propositions,” focused on the shape, characteristics, origin, development, and individuality of cells, and claims about the relationships of multiple cells in multicellular organisms. Baker carried out a tremendous service in clarifying what was at issue with cell biology. He showed that Schleiden and Schwann each, in different ways, made assumptions about how cells originate and/or about their structure and nature that went beyond their data. In some cases, they worked with inadequate microscopic tools; in other cases, they started with strong assumptions about what they should see and then somehow persuaded themselves that they actually saw what they wanted – whether it was really there or not. Thus, Schleiden was confident that he actually observed cells crystallizing around a nucleus, even when further investigation using contemporary tools show that that is not true.

Baker’s scholarly essays appeared from 1949 to 1955 and showed who had said and thought what, when, and why. Shortly after, in 1959, the Cambridge University anatomist Arthur Hughes added his *A History of Cytology*. Like Baker, Hughes sought to clarify the development of understanding of cells. Hughes emphasized cytological methods of investigation alongside the theories, with special emphasis on the nucleus and cytoplasm.

In his *The Birth of the Cell* in 1999, Henry Harris went over much of the same ground as Baker and Hughes, but with considerably more subtlety in scholarship and interpretation. He re-read the original sources, and furthermore had the benefit of an additional half century of biological discovery and reflection. Harris pointed to an 1843 quotation from the French microscopist François-Vincent Raspail to show that Schleiden and Schwann did not have the only word even at their time. “Give me an organic vesicle endowed with life,” Raspail said, “and I will give you back the whole of the organized world.”<sup>6</sup> For Schleiden and Schwann, the cells were units of structure, while for Raspail they were units of life. Claiming that the German story focused on cell structure had come to dominate, Harris called for recognizing Raspail’s vision of the cell as a “kind of laboratory” which allowed life to develop and reside within the cell.

Yet despite Raspail’s ideas and Harris’s efforts to revive them, the German interpretation has continued to dominate cell biology and our historical reflections about it. It is therefore worth revisiting again some key historical contributions, and to try to get at the distinction of cells as units of living systems or cells as themselves living systems.

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<sup>5</sup> Baker (1948), page 103.

<sup>6</sup> Raspail (1833), Quoted in Harris (1999), p. 32.

### 4.3 Putting the Life in Cells

Several main themes in the nineteenth and into the twentieth century help illuminate the difference understandings. First is understanding of Schleiden and Schwann's cell theory, then fertilization, the relative roles of nucleus and cytoplasm, cell lineage and development, cell-cell interactions, regeneration, and cell culture outside of the organism. Here, we can look briefly at each of these points.

#### 4.3.1 *Cell Theory*

Schleiden and Schwann in 1838 gave cell theory a name and declared first that cells exist and are constituents of living organisms, and second that the theory might help explain individuality of organisms as clusters of connected cellular units. As Henry Harris aptly puts it, Schleiden's long article on cells in plants "does not make pleasant reading." Fortunately, Harris helps us digest the key points. Schleiden, like Schwann, saw the nucleus (which he called the cytoblast) as centrally important. They each held that the nucleus is the structure that appears first and then generates the cell. From the moment he had encountered Schleiden's ideas during a conversation at dinner one evening, Schwann claimed, "I devoted all my energies to demonstrating the pre-existence of nuclei in the formation of cells."<sup>7</sup> Sometimes the nucleus exists alone and the cell crystallizes around it, sometimes the cells divide and each has a nucleus.

Since this is a central point in the reasoning, it is worth quoting Schleiden at some length, and Harris provides an excellent translation explaining how cells arise:

As soon as the cytoblasts have attained their full size, a delicate, transparent vesicle is formed on their surface. This is the young cell which to begin with appears as a very flat segment of a sphere, with its planar side constituted of the cytoblast and its convex side by the young cell which is superimposed on it much like a watch glass on a watch. ... Little by little the whole cell now grows out over the edge of the cytoblast and soon becomes so big that the latter eventually appears as no more than a small body enclosed within one of the parietal walls.

Schwann accepted Schleiden's interpretation, even though he saw cell division in addition to what he interpreted as crystallization in the animal cells he studied. Therefore, both emphasized the role of the nucleus as a "cytoblast," or literally cell-developer. Each individual cell emerged and cells then served as structural parts of the organisms in which they resided. And yet, Harris emphatically notes, "I think it is fair to say that no part of the scheme proposed by Schleiden turned out to be correct."<sup>8</sup> Harris provides suggestions about why these German cytologists gained so much attention at the time and later, but for our purposes, the point is that they

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<sup>7</sup>Harris (1999), p. 96.

<sup>8</sup>Harris (1999), p. 98. Translated from Schleiden (1838).

emphasized the structure of the cells and saw them as not the only, but some of the structural parts of the living organisms. In fact, much of what has been credited to Schleiden and Schwann came later.

The decades following brought a great deal of additional observation as well as interpretation. Those years also brought improvements in both microscopes and microscopic techniques, as Hughes discusses in detail. For studying cells, it makes a big difference what one can see and how well one can see it; and making sure that others can see the same thing is especially important. Better lenses reduced chromatic aberrations, and better fixing, staining, and slicing methods improved standardization of specimens to improve consistency of observation. But it wasn't just being able to see more that mattered. It was also looking more carefully, and with a more open mind than Schleiden and Schwann seem to have had.

### 4.3.2 *Fertilization*

Aristotle thought that fluids from the male and female come together and somehow combine, so that form and function emerge only gradually in a way he called epigenetic. The idea of a process of fertilization required first the idea of an egg, so that there was something to be fertilized. Karl Ernst von Baer played an important role here when he observed a mammalian egg for the first time. Chick and frog eggs were big and obvious, but it wasn't clear whether all organisms had eggs or not. Von Baer thought they must and went looking, offering the first clear description in 1827 with an egg from a dog.<sup>9</sup> Animals start from eggs, it seemed.

Furthermore, those eggs seemed to be fertilized by spermatozoa, yet it took a number of people and many observations to observe that a sperm cell actually combines with an egg cell. George Newport wrote three lengthy descriptions of his observations and experiments to discover how the spermatozoa "impregnate" eggs, concluding that they carry some force of "vitalization," or process of coming alive.<sup>10</sup> It took a few more decades for Oscar Hertwig to report observations of sperm cells actually entering into, combining with, and thereby fertilizing egg cells. He observed in detail each step of the entry process, as well as appearance of two nuclei and then reduction and division into one nucleus for the fertilized egg.<sup>11</sup> By the time of Hertwig's work in the 1870s, it had become clear that fertilization involves the process of two cells coming together to make one cell.

Edmund Beecher's *Atlas of Fertilization and Karyokinesis*<sup>12</sup> in 1895 presented the process of fertilization photographically. He showed the details of sea urchin egg cells combining with sperm cells, reduction division of nuclei, chromosomal and cytoplasmic changes in preparation for cell division, and then the process of

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<sup>9</sup> von Baer (1827).

<sup>10</sup> Newport (1851/1853/1854).

<sup>11</sup> For discussion of this point, see for example: Churchill (1970).

<sup>12</sup> Wilson (1895).

cleavage itself. One cell divides into two, into four, and so on. Wilson gave his reader photographs, taken in collaboration with the photographer Edward Leaming, and sketches of the key details to highlight essential features of the process. By the end of the nineteenth century, it was clear to biologists that an individual organism's life began as cells, which underwent fertilization and then divided and differentiated into a complex organism. The egg and sperm cell, and the cells resulting from cell division had begun to have a biological life of their own.

### 4.3.3 *Cells from Other Cells*

The close detailed observations of fertilization and the cell division that followed raised questions about the nature of the living organism. If cells crystallize around nuclei and out of surrounding material, as Schleiden and Schwann had said, then the life of the organism has to come from somewhere. Perhaps it is preformed in the nucleus somehow, or is spontaneously generated, or arises gradually due to some vital force that we have not observed directly. In contrast, if each cell comes only from other cells, then the "life" and the beginnings of the form and function of an individual are in some sense already there from the beginning with that first cell that came from a previously living organism.

Robert Remak rejected Schleiden and Schwann's idea that cells behave like crystals, insisting that they are completely different.<sup>13</sup> The egg is a cell and is the starting point for development of each organism, Remak insisted. Furthermore, that initial cell goes through division to produce more and more cells, which then work together to make up the organism. Finally, since the egg itself came from the previous generation and is alive in the sense of having the capacity to become fertilized and to divide, the living cell comes from another living cell. Life comes from life, and never from some intracellular and inert material.

Rudolf Virchow went further, and Harris discusses the relationship between Virchow and Remak. The two began as friends, but on just this point about the origin of cells and therefore of life, the two diverged vehemently with Remak eventually accusing Virchow (with considerable evidence on his side) of plagiarism.<sup>14</sup> In his work on *Cellular Pathology*, Virchow nonetheless showed decisively through empirical observation that cells divide and give rise to other cells. In his book, quickly translated into English and widely read, Virchow famously declared that "omnis cellula e cellula" and thereby that life comes from other life.<sup>15</sup> Cells had taken on a different status than they had for Schleiden and Schwann: they were not just structural units of living organisms; now they were living in themselves and the living units that make up organisms.

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<sup>13</sup>Robert (1855).

<sup>14</sup>Harris (1999), p. 132.

<sup>15</sup>Virchow (1858). Translated as: *Cellular pathology*, London: John Churchill, 1859.

### 4.3.4 *Cytoplasm and Nucleus*

By the end of the nineteenth century, Theodor Boveri, Oscar Hertwig, and Edmund Beecher Wilson, among many others, were studying cells inside and out. It was clear that the cell has structure, a distinct bounded nucleus, liquid or gel-like cytoplasm, and other internal structures including mitochondria and Golgi bodies, with spindle fibers, asters, and centrosomes playing important roles during cell division. Each cell has a life of its own, and these researchers were showing the ways in which it functioned as a complex dynamic system in itself and in interaction with other cells. The improved microscopic methods and careful observations in the final quarter of the nineteenth century had established this view of the cell.

Understanding the cell's role as a living system involved sorting out what was going on with heredity and development. In his work of 1893 and 1898, Hertwig solidified accumulating evidence and reasoning about the nature of fertilization, observing the details of the way in which the nucleus of the egg and sperm come together to make a new nucleus for the zygote.<sup>16</sup> On the first page of his volume pulling together studies of cells and tissues, he saw the cell theory as an understanding of cells as the "vital elementary units." His volume therefore provided a comprehensive theoretical and empirical framework for understanding cells as living systems. Hertwig paid close attention to the interaction of nucleus and cytoplasm in particular to get at the way that cells are alive.

Edmund Beecher Wilson's masterful 1896 study of *The Cell in Development and Inheritance* appeared about the same time as Hertwig's. For Wilson also, the cell clearly plays a foundational role for life and therefore necessarily for biology. Dedicated to Theodor Boveri, *The Cell* opened by pointing to Schleiden and Schwann and noting that "it has become ever more clearly apparent that the key to all ultimate biological problems must, in the last analysis, be sought in the cell." Furthermore, "No other biological generalization, save only the theory of organic evolution, has brought so many apparently diverse phenomena under a common point of view or has accomplished more for the unification of knowledge."<sup>17</sup>

By his third and final edition in 1924, Wilson acknowledged that a great deal had changed, the volume had grown from 371 to 1232 pages, and had undergone reconceptualization while seeking to retain its synthetic approach. He opened with a slightly different tone: "Among the milestones of modern scientific progress the cell-theory of Schleiden and Schwann, enunciated in 1838–39, stands forth as one of the commanding landmarks of the nineteenth century." Yet their ideas were just a "rude sketch" that led to "opening a new point of view for the study of living organisms, and revealing the outlines of a fundamental common plan of organization that underlies their endless external diversity."<sup>18</sup>

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<sup>16</sup>Hertwig (1893/1898).

<sup>17</sup>Wilson (1896), page 1.

<sup>18</sup>Wilson (1925), page 1.

In this third edition, Wilson points to three periods since the inception of the idea of cells: focused on the basic ideas about cells and their roles, looking at development and cell division, and then bringing in the chromosome theory of heredity that introduced explanations of the causes of cell division. Wilson pointed to recent successes: “If we are confronted,” he wrote in the final paragraph, “still with a formidable array of problems not yet solved, we may take courage from the certainty that we shall solve a great number of them in the future, as so many have been in the past.”<sup>19</sup>

Together Hertwig and Wilson called attention to the cell and especially to its complexity. They helped to bring attention to, and to stimulate additional interest in, interpreting how cells function as fundamental living units. How does each cell grow, divide, differentiation, and otherwise change over time in ways that add up to a complex organized organism?

Theodor Boveri provided some answers, looking closely at the contributions of the nucleus. In 1902, for example, Boveri demonstrated that chromosomes are defined structures and furthermore that they retain their individuality through cell divisions. They divide, so that each of the daughter cells will have its own set of chromosomes after divisions, but they retain their individuality nonetheless. Observing and carefully describing the details, Boveri added immeasurably to understanding of cell division with his experimental work. He carefully controlled conditions so that he could determine what role the cytoplasm could play on its own and what role the nucleus played. He made clear that a cell without a nucleus is not a living cell, nor is a nucleus alone capable of division and differentiation.<sup>20</sup> The cell as a whole is a complex living system.

### 4.3.5 *Cell Lineage*

Cells each have a cytoplasm and nucleus, but they do not all look or work in exactly the same ways. To get at how differences arise and what they mean, Wilson and others carried out detailed studies of cell lineage, that is study of the lineages of cells, how one cell divided into two and so on. Wilson, Edward Grant Conklin, and others at the Marine Biological Laboratory in Woods Hole, Massachusetts, spent considerable energy collecting specimens from different species, taking them into the lab and observing every stage as each cell divided, one by one.

This work involved observing living cells, and also preserving, fixing, staining, and in short killing them in order to observe what was going on inside. They could see the changes in shape and structure, and they could see the way the chromosomes and other parts behaved during cell division and during differentiation. They could see that it depends on where each cell is located within the organism what shape it takes and how it divides in the next step. But they could only observe for so long in

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<sup>19</sup>Wilson (1925), p. 1118.

<sup>20</sup>For an excellent discussion of Boveri’s work, see: Laubichler and Davidson (2008).



the organism's developmental process; eventually there were too many cells, and the complexity of the whole organism made it impossible with this method to continue observing the individual cellular parts.

### 4.3.6 *Cell-Cell Interactions*

If the individual cells are the fundamental living units, and cell lineage shows that their behavior depends at least in part on their position within the developing embryo, the next question is how they make up a complex multicellular system. Getting at that required studying cell-cell interactions, and doing so required a number of epistemological assumptions about what one is actually seeing. It is challenging to observe processes that occur over time, especially when the methods for observation involve watching sequences of killed and prepared materials. Early studies of transplantation helped illuminate these processes. Cells and tissues taken from their normal placement and role in developing organisms and moved to another place, or to another organism altogether, suggested ways cells communicate with each other.

Clusters of cells that make up the eye vesicle, as Hans Spemann showed for example, could be removed from one embryo and would result in a missing eye. Or they could be transplanted to another part of the organism or to another organism and produce an eye where there would not normally have been one.<sup>21</sup> This work suggested that the individual cells acquire some definition or differentiation themselves fairly early on, and that they also respond to changing conditions both inside the cell and in interactions with other cells. Only gradually in the course of the twentieth and into the twenty-first century have researchers begun to understand the vast range of cell-cell interactions through chemical and hormonal signals, neural signaling across synapses, and diverse messenger systems involved in bringing together the complex cells into a complex organismal whole.

### 4.3.7 *Regeneration*

Thomas Hunt Morgan laid out the foundations for modern study of regeneration with his book of that title in 1901.<sup>22</sup> Regeneration provides an excellent source of, in effect, natural experimental material. Observing cell lineage could show what happens in normal cases, but much of the process remained invisible. Experimental approaches such as transplantation could yield additional information, but also had limits. Studying regeneration could reveal cases in which cells change from normal conditions. What makes it possible for a planarian to regenerate a new head or tail,

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<sup>21</sup>Hamburger (1988).

<sup>22</sup>Morgan (1901).

for example? Morgan asked whether existing cells change, that is whether they somehow became re-differentiated into a different kind of cell? Or did they instead generate new cells of the right type to make heads or tails? This raised questions about whether it was something in the organism as a whole that drove the changes, or whether the cells themselves were doing the changing? What was driving the organization of the organism – the cells or the whole of interacting cellular parts? Morgan captured these questions and understood that getting at what causes regeneration to occur in some animals for some conditions could reveal a great deal about development and about the role of individual cells.

### 4.3.8 *Cell Culture*

Ross Granville Harrison removed cells from frogs and transplanted them not to another part of that frog or even to another frog, but rather into a culture dish. The neuroblast cells he transplanted then differentiated as nerve fibers, which he interpreted as developing in just the same way they would have normally within the organism.

This experimental approach allowed a test of how cells develop on their own in an artificial culture medium but not as part of the organism. This kind of tissue and cell culture seemed to answer questions about the extent to which cells are alive and self-differentiating, in contrast to parts of organisms that determine their reactions. Cells must be self-determining to a very large extent, guided by some internal factors and responding to environmental cues. In turn, this conclusion raised questions about how the self-organizing cells then connect physically or communicate biochemically or in some other way with other cells: how do the parts make up the whole interactive and dynamic organism? How does the cellular system work in connection with the organismal system?

One idea held that some sort of protoplasm lies outside the cells and connects them. In the context of his challenges to the cell theory as sufficient explanation for organization in life, Adam Sedgwick was still invoking this idea through the end of the nineteenth century, as Baker discusses.<sup>23</sup> The idea of a reticulum or syncytial connections proved attractive, because it offered an explanation for how cellular parts work together as an whole system. Physical connections could make the parts into a network. This reasoning held for the nervous system in particular. At the end of the nineteenth century, researchers argued about whether the nervous system is there from the very beginning in a sort of reticulum that then grows larger while maintaining its structure. In contrast, the neuronal theory held that individual neuroblast cells develop nerve fibers that grow out and make connections over time. They only gradually make up the nervous system.

Harrison accepted the second, neuronal, theory. His culture experiments described above showed the ways that individual neuroblast cells grow out and

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<sup>23</sup>Baker (1948), p. 175. Sedgwick (1894).

make connections. In fact, his work was taken by many as having resolved the question in favor of the action of individual cells working together. Yet a few such Camillo Golgi never gave up their convictions that the system was inextricably interconnected from the beginning. He simply could not see how to explain the complexity of the nervous system otherwise.

The discussions were part of persistent debates about whether development is more preformationist, that is laid out from the very beginning in a preformed way, or epigenetic, that is arising only gradually over time.<sup>24</sup> The epigenetic view requires an explanation for how the individual cells arise and how they make up a whole organism. Where does the organization and where does the life come from if the separate and individual cells come together to make a whole?

## 4.4 Conclusion

Cells started conceptually as basic structural units of living organisms, arising through crystallization from non-living matter. By the end of the nineteenth century, they had acquired a life of their own and were seen as a complex living system in themselves. As we saw in the reflections after a century of the cell theory, questions persist about the extent to which and ways in which the cells organize themselves and add up into complex organisms, rather than having the organism as a whole organize the cells. Recent research with stem cells and induced pluripotency have complicated the questions still further, suggesting that cells have a tremendous capacity to respond to changing environmental conditions. As Moulton said in 1940 as editor, despite our advances in cell biology, understanding the cell continues to provide us with new insights and to challenge existing assumptions.

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<sup>24</sup>For more discussion of this and related topics, see Maienschein (2014).

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