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How does cell theory explain the continuance of living organisms

The cell is not only the structural, physiological, and developmental, but also the reproductive unit of life. So far, however, this aspect of the cell has received little attention by historians and philosophers of biology. I will argue that cell theory had far-reaching consequences for how biologists conceptualized the reproductive relationships between germs and adult organisms. Cell theory, as formulated by Theodor Schwann in 1839, implied that this relationship was a specific and lawful one, i.e. that germs of a certain kind, all else being equal, would produce adult organisms of the same kind, and vice versa. Questions of preformation and epigenesis took on a new meaning under this presupposition. The question now was whether cells could be considered as independent agents producing adult organisms of a given species, or whether they were the product of external, organizing forces and thus a stage in the development of the whole organism only. The question was an important one for nineteenth-century biology. As I will demonstrate, it was the view of cells as independent agents which helped both Charles Darwin and Gregor Mendel to think of differential reproduction as a lawful process.Keywords: Cell theory, epigenesis, preformation, specificity, Darwin, MendelThe cell is habitually addressed as the structural, functional, and developmental unit of life. Jan Sapp has aptly and succinctly explained these aspects of the cell by formulating “three tenets” of cell theory: “that all plants and animals are made of cells, that cells possess all the attributes of life (assimilation, growth, reproduction), and that all cells arise from division of preexisting cells” (Sapp, 2003, p. 75; cf. Reynolds as well as Nicholson, this issue). This misses an important fourth sense in which the cell can be regarded as a “unit of life”. The cell is also the reproductive unit of life, not in the sense that cells reproduce themselves by division (this capacity, as can be seen from Sapp’s definition, is already captured by addressing it as the developmental unit of life), but in the sense that all organisms run through a single-celled stage in their life cycles. According to cell theory, one might say, all of life, whether of unicellular, colonial or multicellular organization, is punctuated by periods of minimal organization – whether in the form of spores or zygotes – that not only define the beginning of a new individual life cycle, but also allows naturalists and biologists to think of populations as being structured by the succession of generations. The significance of this aspect of cell theory can hardly be underestimated. Ohad Parnes has argued that thinking in terms of life cycles and generations was the crucial precondition for the emergence of notions of biological inheritance in the mid-nineteenth century (Parnes, 2007). In spite of its significance, the history of the cell as the reproductive unit of life has hardly been written yet. Thus, it remains quite unclear whether the many eighteenth- and early nineteenth-century contenders for priority in laying the foundations of modern cell-theory – from Georges Louis Leclerc Comte de Buffon (1707–1788) over Jean-Baptiste Lamarck (1744–1829) to Matthias Jakob Schleiden (1804–1881) and Theodor Schwann (1810–1882) – really endorsed the idea that all reproductive processes pass through a cell or comparable, fundamental organic unit. The fact that their theories often allowed for some form of spontaneous generation should make us wary, the few historians of biology, on the other hand, who have dealt with the complex history of the reproductive cell, on the other hand, generally agree that the connection between cell theory and reproduction was not forged before the very end of the nineteenth century. Frederick B. Churchill, in a now classic paper, has argued that it “was not until the watershed period of the 1880s [that] cytological advances were brought to bear directly on heredity” (Churchill, 1987, p. 338; cf. Coleman, 1965, pp. 124–126; Mayr 1982, pp. 652–680), and François Duchesneau, in a more recent paper, has spoken of a ‘considerable historical delay’ with which the connection between cell theory and heredity happened, dating this event toward the end of the nineteenth century as well (Duchesneau, 2007, pp. 310–311). Cell theory as we know it thus seems to be a rather recent accomplishment of biology, perhaps not dating back much further than Edmund Beecher Wilson’s pivotal The Cell in Development and Heredity (1896; cf. Dröscher, 2002).Talk about a ‘watershed period’ and ‘historical delay’ makes the prehistory of the confluence of cell theory and theories of reproduction all the more interesting, of course. What complicates matters for such a prehistory is that fundamental categories used today for the analysis of reproduction – most importantly preformation and epigenesis – cannot simply be projected back. As long as the exact nature of the relationship between the fertilized egg and the adult organism had not been defined yet, preformation and epigenesis were bound to mean very different things. As Churchill warned fellow historians of biology long ago, any analysis of these two slippery terms ‘must tangle with those intractable questions about the meaning of “novelty”, “emergence”, “coming-to-be” and “form”’ in a given time period (Churchill, 1970, p. 171). What, for example, are we to make of the fact that William Harvey (1578–1657), so well known for having revived Aristotle’s epigenetic theory of embryo formation, claimed in his De generatione animalium (1651) “that the vegetal primordial whence the foetus is produced [...] pre-exists” (Harvey, 1857, p. 465)? And what of the fact, that René Descartes, with his notorious predilection for the animal-machine, referred to male and female seeds as substances that ‘serve each other as yeast’, their interaction ‘giving rise to the formation of one organ after the other’ (Descartes, 1986–1991, vol. 11, p. 253)?In this paper I aim to outline the effects that early cell theory had on theories of reproduction. In a first section, I will turn to Thomas Henry Huxley’s (1825–1895) famous critique of Schwann’s cell theory, to argue that notions of preformation and epigenesis, at this particular point in time, have to be understood against the background of a quest for specific, biological laws, with important consequences for the question whether biological autonomy resided in the organism as a whole, or could be accorded to its parts as well; or, to put it differently, to what degree cells could be considered as independent agents, and to what degree they were subject to external organizing forces. The question was an important one for nineteenth-century biology. As I will demonstrate in the second and third section of this paper, it was the view of cells as independent agents which allowed both Charles Darwin (1809–1882) and Gregor Mendel (1822–1884) to think of differential reproduction as a lawful process. Cell theory, thus the main thesis of this paper, allowed for a subversion of the concept of heredity as a merely conservative force, by portraying the cell as an entity that could escape the grip of the organism and thus form the starting point of a new life.The formulation of early cell theory by Schleiden and Schwann has to be seen against the background of a more general research program that engaged contemporary naturalists and consisted in a quest for biological laws that would elevate botany and zoology to the status of truly scientific disciplines (Nyhart, 1995, pp. 39–47; Gliboff, 2008, pp. 37–53). Schwann in particular, as Parnes has convincingly argued, broke decisively with then dominant approaches to achieve this goal. Rather than assuming that physiological and reproductive phenomena resulted from the interaction of a general, all encompassing life force and environmental conditions, Schwann sought to identify ‘specific material agents exerting specific vital forces’ (Parnes, 2000, p. 82). Schwann’s other major scientific achievement, his discovery of ‘pepsin’, a ‘mucous liquid’ that could be used as a ‘digestive principle’ (Schwann, 1847 [1839], p. xv–xvi; my emphasis). In short, for Schwann, cells and tissues were not the explanans, but the explanandum of a physiological theory of development (Jahn, 2003, pp. 26–27). So what was the common ‘principle of development’ which could account for the development of tissues of diverse histological and physiological type? At this point, most historians of cell theory rest content to quote what is perhaps Schwann’s most famous statement, namely that “[t]he cause of nutrition and growth resides not in the organism as a whole, but in the separate elementary parts – the ‘cells’” (Schwann, 1847 [1839], p. 192). But ‘resides’ (‘liegt in’ in the German original, which a more literal translation would render as ‘lies in’, see Schwann, 2003 [1839], p. 105) is a treacherous term. Firstly, it obscures Schwann’s conviction, that cells grow from the inside-out, so to speak; the ‘nucleolus’, ‘a minute corpuscle’, is formed first from the surrounding nutritive fluid, the ‘cytoblastema’, followed by the formation of ‘nucleus’, ‘cell cavity’ and ‘membrane’ through ‘continual deposition of fresh molecules’ at the periphery. The attractive and metabolic forces – it was Schwann who coined the latter term – do therefore not ‘reside’ in the cell as a whole, but more precisely in the ‘molecules’ it is made from (Schwann, 1847 [1839], p. 193–194; cf. Duchesneau, 2007, 294–297). Secondly, the expression ‘resides’ masks Schwann’s acute awareness of the fact that such a mode of ‘physical (physikalische)’ explanation relies on interactions between molecules, which in turn depend on the latter’s material arrangement. The attractive and metabolic powers of cells are ‘set free only by a certain combination of molecules, as, for instance, electricity is set free by the combination of a zinc and copper plate’ (Schwann, 1847 [1838], p. 189; on the long afterlife of this metaphor see Grote, this volume).These two points are not mere subtleties, but important qualifications if one wants to gain a full understanding of the import of Schwann’s proposal. One way of assessing this import is by turning to the famous critique of Schwann’s cell-theory that Thomas H. Huxley published in 1853, and that Martha Richmond has analyzed in great detail. According to her analysis, ‘Huxley viewed Schwann’s theory as a new form of preformationism that posed a threat to the achievement of epigenesis, his discovery of “pepsin”, a “mucous liquid” that could be used as a “digestive principle”’ (Richmond, 2000, p. 250). Epigenesis and preformation are terms that need to be handled carefully, however, as Richmond’s careful analysis of Huxley’s critique reveals. Schwann, as we saw, was not denying that organic structures emerged de novo from a structureless substance, as Huxley was ready to concede (Huxley, 1898 [1853], p. 252). Nor did he deny that vital forces reside in matter, again something Huxley concedes to some extent (Huxley, 1898 [1853], 261–262). What Huxley resisted was more specifically the idea that the ‘primary histological elements (cells) [...] stand in the relation of causes or centres to organization and the “organizing force”’, that vital forces, to put it differently, depend on the prior material conformation of material agents (Huxley, 1898 [1853], p. 253). For Huxley, development was a process that acted from the outside-in; every developmental stage – including the earliest differentiation of a ‘structureless blastema’ into ‘endoplast’ and ‘periblast’ – resulted ‘from the operation of some common determining power, apart from them all’ (Huxley, 1898 [1853], p. 264, my emphasis). Cells were products, not agents of organic change, and vital forces did not reside in specific molecular arrangements, but ‘in the matter of which living bodies are composed, as such’ (Huxley, 1898 [1853], p. 277, my emphasis; cf. Richmond, 2000, pp. 273–276).Schwann’s original proposal from 1839, as well as Huxley’s critique of that proposal from 1853, thus turn out to represent two sides in a debate that had divided naturalists and physiologists across Europe since the turn of the century already. Philip R. Sloan has characterized this debate as one ‘concerning the manner in which “vitality” related to organization’, distinguishing between those who held that vitality was ‘a “superadded” phenomenon, acting externally on inherently inert matter’ and those who held it to be ‘a more immanent power, intimately associated with organization’ (Sloan, 1986, p. 377; cf. Jacyna, 1983; Parnes, 2000, pp. 74–81). In other words, on one side of the debate we find those, like Huxley in 1853, who thought of life as a general phenomenon, and of all its diverse manifestations as brought about by essentially the same vital force; while on the other we find those who, like Schwann in 1839, were convinced that ‘specific life processes have specific causes in the form of specific material agents exerting specific vital forces’ to use a formulation by Parnes (2000, p. 82).Much was at stake in this debate. If one opted for the former position, the continuity of all life was guaranteed but it was difficult to imagine effective causes that could be made responsible for the great for diversity of life forms. Schwann insinuated without further ado, that his opponents would have to take recourse to teleological reasoning to explain diversity (Schwann, 1838, pp. 188–189), and indeed, Huxley at one point admits in his 1853 review, that ‘the “vis essentialis” appears to have essentially different and independent ends in view – if we for the nonce speak metaphorically’ (Huxley, 1889 [1853], p. 267). On the other hand, while diversity was not a problem for a position which presumed from the very start that all manifestations of life were the result of specific conformations of matter, such a solution also opened the possibility for spontaneous generation and transmutation. As a matter of fact, this is exactly, what Schwann suggested in a side remark – that his position made it easier to understand “[t]he first development of the many forms of organized beings’ as well as the ‘progressive formation of organic nature indicated by geology’” (Schwann, 1847 [1839], p. 189; cf. Schwann 1839 [2003]) – and what seems to have turned away Huxley from cell-theory in ‘an abrupt volte-face’ after he had initially endorsed it (Richmond, 2000, pp. 251, 278–279). The extent to which Schwann envisioned cells as endowed with an independent life of their own also allowed him to think of cells as being able to escape what he called the ‘autocracy of the organism’ (Schwann 1847 [1838], p. 188).Positioning Schwann and Huxley in the context of contemporary debates thus reveals that cell-theory from the start attended to the reproductive aspect of the cell. Schwann himself, it is true, remained exceedingly vague about this aspect, and located the predisposing factors that determined the specific reproduction of cells in the cytoblastema, rather than the nucleus (Holmes, 1963, p. 323). Ideas about this aspect should become more concrete only with the increasing realization that cells arise from the union or division of preexisting cells – that is cells, and not some ‘nutritive fluid’, which produce cells – so that the first stage of every new individual organism could be conceived as a self-renewal of the organism itself, endowed with a multiplicity of predisposing characters (Duchesneau, 2007, pp. 295–296). Not much of Schwann’s original theory of ‘free’ cell formation remained intact in the course of the process – except for his intuition that granting cells some degree of independent life would be able to account for differential reproduction.Differential reproduction was a cornerstone of Darwin’s theory of evolution by natural selection. In the Origin of Species (1859), he made it quite clear that variation alone was not enough to account for species transformation; one had to assume that certain variations were heritable, even if the laws that governed inheritance were ‘quite unknown’, and no one could say ‘why the same peculiarity in different individuals of the same species, and in individuals of different species, is sometimes inherited and sometimes not’ (Darwin, 1859, p. 13; cf. Winther 2000). This did not deter Darwin from proposing a very precise, and for its time unusual definition of heredity. Mere similarities between ancestors and descendants were not enough for Darwin to speak about heredity, as it could not tell be excluded that such similarities were ‘due to the same original cause acting on both’ ancestors and descendants; if, on the other hand, Darwin maintained ‘amongst individuals, apparently exposed to the same conditions, any very rare deviation, due to some extraordinary combination of circumstances, appears in the parent – say, once amongst several million individuals – and it reappears in the child, the mere doctrine of chances almost compels us to attribute its reappearance to inheritance’ (Darwin, 1859, p. 12–13). Rather than making heredity out as an essentially conservative force, regulating the reproduction of species, rather than individuals, – the prevailing view among naturalists at the time (Coleman, 1965, p. 125; Parnes, 2007, pp. ##*) – Darwin tied heredity intimately to the occurrence of rare, individual deviations.The Origin of Species, it is well known, did not contain much in the form of speculations into the physiology of reproduction that could have supported Darwin’s peculiar understanding of heredity. I would still like to follow Jonathan Hodge in his claim that Darwin was a lifelong generation theorist (Hodge, 1987, p. 207). According to Hodge, the argument of Origin has to be seen against the background of Darwin’s ‘tendency to try to understand entities above the level of the individual organism – “species” and “trees of life” – as scaled up analogues of individual organisms; and entities below the level of the individual organism – “buds”, “cells”, “gemmules”, “living atoms”, “monads” – as scaled-down analogues to them’ (Hodge, 1987, p. 209). The Origin is framed therefore by notes and printed works that testify Darwin’s continuous interest in topics related to the physiology of reproduction, beginning with his studies in Edinburgh and Cambridge and culminating in the ‘provisional hypothesis of pangensis’ that he presented in the last chapter of Variation of Animals and Plants under Domestication (1868).Darwin’s notebooks from the critical period after his return from the Beagle Voyage in 1836 are of particular interest here, because they document how Darwin’s mind about matters discussed in the previous section, and help us understand the specific role that cell theory should play for his theory of pangensis.For Prosper Lucas, on whose Traité philosophique et physiologique de l’hérédité naturelle Darwin recurred repeatedly, it had been clear already that “der allgemeine Fehler aller alten wie modernen Theorien die Gleichsetzung von Zeugung und Vererbung war.”1However, Lucas made another distinction that in the context of Darwin’s theory of evolution should no longer play a role. He distinguished a “law of heredity” (loi d’hérédité) responsible for the constancy of the specific type from a “law of imateness” (loi d’innéité) responsible for the hereditary transmission of individually acquired or spontaneously arising defects and that could interfere with the regular hereditary process.2 An altered character that had shown up in an individual couldthus be transmitted to its progeny and with that, be “innate” from the perspective of that progeny, and yet it did not affect the hereditary type. “Es ist klar, dass bezogen auf den spezifischen Typus es immer das Angeborene ist, das sich verliert, und das Vererbte, das bleibt.”3 For Darwin’s theory of evolution, which no longer knew the concept of type underlying Lucas’ deliberations, this distinction had become obsolete. In Darwin’s theory, there only was a sum of potentially variable characters and the laws regulating their “correlation” and thus also limiting their independent transmission.4For Darwin, one of the most intriguing phenomena was that of intermitting characters that eventually disappeared in the progeny and reappeared in one of the following generations. Already in the first chapter of the Origin, he stated:The laws governing inheritance are quite unknown; no one can say why the same peculiarity in different individuals of the same species, is sometimes inherited and sometimes not so, why the child often reverts in certain characters to its grandfather or grandmother or other much more remote ancestor; why a peculiarity is often transmitted from one sex to both sexes, or to one sex alone, more commonly but not exclusively to the like sex.5Here we see clearly what it was that caught the attention of Darwin. It was the ‘independent life’ of qualities whose distribution in the progeny obviously could not be explained by external circumstances, but that had to be attributed to a hidden mechanism. The epistemic space in which such peculiar characters circulated could no longer be restricted to the individual relation between parental progenitors and their children.In 1868, Darwin published a two-volume treatise on The Variation of Animals and Plants under Domestication that first had been intended to be a part of the Origin, but then had occupied the author for another ten years. Here he collected everything he could find on variations and their transmission in the variegated literature of breeders, physicians, and natural historians. And here, in the 27th Chapter, he tried to “connect by some intelligible bond” the observations that he deemed the most important ones on sexual procreation, graft-hybrids, xenia, development, the functional independence of the elements or units of the body as well as variability and inheritance. He found this bond in his “Provisional Hypothesis of Pangensis” that he introduced with the following words:It is almost universally admitted that cells, or the units of the body, propagate themselves by self-division or proliferation, retaining the same nature, and ultimately becoming converted into the various tissues and substances of the body. But besides this means of increase I assume that cells, before their conversion into completely passive of ‘formed material’, throw off minute granules or atoms, which circulate freely throughout the system, and when supplied with proper nutriment multiply by self-division, subsequently becoming developed into cells like those from which they were derived. These granules are always already being a complex organism itself, endowed with a multiplicity of predisposing characters (Duchesneau, 2007, pp. 295–296). Not much of Schwann’s original theory of ‘free’ cell formation remained intact in the course of the process – except for his intuition that granting cells some degree of independent life would be able to account for the sake of distinctness may be called cell-gemmules, or, as the cellular theory is not fully established, simply gemmules. They are supposed to be transmitted from the parents to the offspring, and are generally developed in the generation which immediately succeeds, but are often transmitted in a dormant state during many generations and are then developed. Their development is supposed to depend on their union with other partially developed cells or gemmules which precede them in the regular course of growth. [...] Gemmules are supposed to be thrown off by every cell or unit, not only during the adult state, but during all the stages of development. [...] Hence, speaking strictly, it is not the reproductive elements, nor the buds, which generate new organisms, but the cells themselves throughout the body. These assumptions constitute the provisional hypothesis which I have called Pangensis.6According to Darwin’s hypothesis of pangensis thus not only all relevant characters of a given organism were collected as gemmules in the sexual cells, but also countless gemmules stemming from more remote ancestors. They could be transmitted over generations in a dormant state, before they – according to whatever circumstances – were activated again. For Darwin, with this assumption one of the most pressing problems of inheritance appeared to be explained, a problem that haunted breeders in the form of reversion or atavism, and on which Darwin came back again and again. Just as the spontaneous and unpredictable appearance of sports, for Darwin they were hints at the autonomy, if not capriciousness and irregularity that characterized life and its evolution.7 The stronger or weaker expression of characters could also be attributed to the gemmules in terms of their variable quantity and their more or less penetrating power. And not least, the problem of development was also grounded in the material substrate of inheritance, since gemmules represented all the stages of its course. It is characteristic for theories of heredity in the second half of the 19th century that they progressively separated the phenomena of inheritance and development, but that they continued to try to explain them together and in a unitary fashion.Mendel and Darwin closer to each other than one might think, and both eccentric Hereditary variations thus pointed to an autonomy of life that was neither compatible with the view that organisms were always already adapted to their environment nor with an unlimited plasticity and perfectibility of life.I would like to thank the organizers of the British Academy sponsored workshop on the history and philosophy of cell research – Staffan Müller-Wille, Maureen O’Malley, Dan Nicholson and Pierre-Olivier Méthot – for inviting me and for making my stay so enjoyable and productive. I am also grateful to Staffan and Maureen for comments and suggestions that led to significant improvements to the paper. 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