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# The Cell and Protoplasm as Container, Object, and Substance, 1835–1861

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**Abstract.** This article revisits the development of the protoplasm concept as it originally arose from critiques of the cell theory, and examines how the term "protoplasm" transformed from a botanical term of art in the 1840s to the so-called "living substance" and "the physical basis of life" two decades later. I show that there were two major shifts in biological materialism that needed to occur before protoplasm theory could be elevated to have equal status with cell theory in the nineteenth century. First, I argue that biologists had to accept that life could inhere in matter alone, regardless of form. Second, I argue that in the 1840s, ideas of what formless, biological matter was capable of dramatically changed: going from a "coagulation paradigm" (Pickstone, 1973) that had existed since Theophrastus, to a more robust conception of matter that was itself capable of movement and self-maintenance. In addition to revisiting Schleiden and Schwann's original writings on cell theory, this article looks especially closely at Hugo von Mohl's definition of the protoplasm concept in 1846, how it differed from his primordial utricle theory of cell structure two years earlier. This article draws on Lakoff and Johnson's theory of "ontological metaphors" to show that the cell, primordial utricle, and protoplasm can be understood as material container, object, and substance, and that these overlapping distinctions help explain the chaotic and confusing early history of cell theory.

**Keywords:** Cell, Protoplasm, Cambium, Primordial utricle, Matter, Coagulation

Without a hint of irony, the eminent American cytologist Edmund Beecher Wilson began the first chapter of his great 1896 textbook, *The Cell in Development and Inheritance*, with a plaintive plea, asking all students of science to stop using the word "cell." "The term 'cell' is a biological misnomer," Wilson (1896, p. 13) insisted, "for whatever the living cell is, it is not, as the word implies, a hollow chamber surrounded by solid walls. The term is merely an historical survival of a word casually employed by botanists of the seventeenth century to designate the cells of certain plant tissues which, when viewed in section, give somewhat the appearance of a honeycomb.''[1] Wilson reproached his cytology students for their grievous terminological and conceptual errors, and, as he emphasized the correctness of the biological theory of recent decades, he outlined the more correct and exacting definition used by only the best and the brightest of students: ''The cell [has come] to be defined by Max Schultze and Franz Leydig as a *mass of protoplasm containing a nucleus*, a morphological definition which remains sufficiently satisfactory even at the present day. Nothing could be less appropriate than to call such a body a 'cell.'''[2] Today the cell theory attributed to Matthias Schleiden (1804–1881) in 1838 and elaborated by Theodor Schwann (1810–1882) in 1839 is celebrated as a watershed moment in the history of science. It transformed a common way of describing the texture of tissues into a grand synthesis of biological theory, by insisting that the cell was the elementary unit of life. But by its centenary in 1939, the cell concept was troubled enough that the American cytologist Edwin Conklin (1863–1952) could travel across the United States and argue that Schleiden and Schwann's scientific legacies were best respected by expunging their names from the annals of cell theory altogether (Conklin, 1939, 1940).

This concern over the conceptual integrity of the ''cell'' had become relatively common as biologists continued to revise their thoughts about what the cell *was*. Of the approximate equivalents to replace the *cell*, however, only *protoplasm* managed to enter common parlance, and protoplasm never fully replaced the cell. Despite the fact that the words *cell* and *protoplasm* roughly corresponded to the same material entity, protoplasm theory always sat somewhat orthogonal to cell theory, both in its historical trajectory and in its contemporary scientific use. Throughout the course of the latter half of the nineteenth century, the cell would become known as the ''elementary organism,'' while protoplasm ascended to the status of ''living substance'' and the so-called

[1] Wilson's textbook had a strong predecessor in Oscar Hertwig's *Die Zelle* (1895, p. 8): ''It is evident that the term 'cell' is incorrect. That it, nevertheless, has been retained, may be partly ascribed to a kind of loyalty to the vigorous combatants, who, as [Ernst von] Brücke expresses it, conquered the whole field of histology under the banner of cell theory.''

[2] In a footnote Wilson (1896, p. 14) suggested that Julius Sachs' neologism *energid*, ''i.e. the nucleus with that portion of the active cytoplasm that falls within its sphere of influence,'' was more appropriate in both morphological and physiological senses, and that, ''It is to be regretted that this convenient and appropriate term has not come into general use.''

"physical basis of life" (Geison, 1969). In its heyday at the turn of the twentieth century, protoplasm theory even surpassed the cell in both popular and scientific importance (Brain, 2015). Yet only the *cell* currently remains as a central feature of biological thought, despite its turbulent history (Reynolds, 2010); in contrast, protoplasm theory and even the word *protoplasm* are all but forgotten. Biologists in the nineteenth and early twentieth centuries spilled considerable amounts of ink arguing over where the former concept ended and the latter began, and yet they agreed on each concept's central importance to modern science. Biologists accepted that the terms *cell* and *protoplasm* had very different meanings, even as they seemed to share the same material referent.

In this article I wish to make two related arguments about the history of the cell and protoplasm concepts. First: that in the 1850s it became possible for biologists to imagine that life could be located in a formless substance, protoplasm, rather than in a discrete organized entity, the cell. Both the cell and protoplasm were conceived as material agents that were responsible for the growth and functioning of living organisms—cells as individual entities, protoplasm as the material basis for such individual entities. After 1839, biologists responded to various shortcomings in Schleiden and Schwann's theories by more closely examining the life of the cell. In so doing, they began to ask questions about whether the material basis of life was better understood as residing in the cell, or if it instead resided in the formless protoplasm that generated the cell in the first place. As I will show, these efforts at theoretical reform began in 1844, when Hugo von Mohl (1805–1872) attacked the material underpinnings of Schleiden and Schwann's definition of the cell. Understood cumulatively, the displacement of the cell concept by the protoplasm concept in the mid-nineteenth century represented a significant shift in the way biologists thought about matter, one much more consequential than a simple problem of vocabulary, be it "cell" or "lump of protoplasm."

Such a significant change to how life and vitality were understood in relation to matter required biologists to also revise what they thought unorganized matter was capable of. This is my second argument: whereas before the 1840s, non-living formless materials were thought to become organized living forms by a process of separation or coagulation of a viscous fluid, after the 1840s formless and viscous fluids were thought to be themselves active, and capable of many of the basic phenomena of life. Historians have previously recognized the existence of a "coagulation paradigm" in biology before the mid-nineteenth century (Pickstone, 1973; Lorch, 1967), manifest as a widespread understanding that pre-biotic or nutritious fluids furnished the material for living organisms through a process of coagulation or separation of fluids from solids. Protoplasm theory, I argue, decisively broke from this older way of thinking about viscous, generative fluids, and it was only after this break that biologists became capable of speaking of "living matter" on nearly equal terms as they could "life forms." Schwann had famously used his theory of cells in 1839 as a vehicle for materialism in biology and physiology, using the individuality of cells to criticize recourses to vital forces (Parnes, 2000; Müller-Wille, 2010). Yet he relied an older materialism, and both his and Schleiden's theories of free cell formation out of the fluid "cytoblastema" had features that could be traced all the way back to Aristotle's biology: that of a primordial, pre-living matter that thickened, hardened, or otherwise congealed into a living organism. As I will show, the idea that unorganized matter could be complex and itself "alive" was only articulated during the 1840s and 1850s, while Schleiden and even Schwann had earlier conceived of the material basis of living cells in terms of a simple, nutrient mucus or slime.

In order to illustrate these transformations in the "cell" and "protoplasm," this article draws on the terminology developed by Lakoff and Johnson (2003) to describe three fundamental types of material entities, or what they refer to as "ontological metaphors," namely the distinction between *container*, *object/entity*, and *substance*.[3] Whereas Schleiden and Schwann had conceived of the cell as a minimal unit of life defined through its boundary, protoplasm was largely defined as the substance from which living cells were made. Lakoff and Johnson's distinction between container, object/entity, and substance explains why the cell concept and the protoplasm concept could each point to the same thing under the microscope, while also providing two separate theories to describe it. Container metaphors define in–out relationships and orient a spatial field: e.g., a cell is defined by the boundary or membrane, enclosing its contents (nucleus, starch granules, vacuoles) within itself against either an exterior environment, or demarcating it from other cells. The cell is also an individuated object/entity, in that one cell can be compared to other cells or other objects; in the same sense, one could say a bathtub is defined by its ability to hold water as a

[3] I prefer to use the term "material" here, although Lakoff and Johnson consistently call these categories "ontological metaphors" in their larger system. The term "ontology" has come under intense scrutiny in science studies, (see especially the June, 2013 special issue of *Social Studies of Science*), but here I am using it in the relatively simple sense of asking questions about the nature of matter or the material world—"what is," or "what exists."

physical and spatial boundary, but a bathtub is also an object that can be counted, repaired, sold, etc. In contrast, protoplasm was always defined as a kind of substance: formless matter from which living cells were made, endowed with specific properties and defined as the material seat of specific physiological processes. These distinctions are inherently overlapping and "partially structured": container, object/entity, and substance metaphors are not mutually exclusive, and combinations serve different cognitive purposes in different contexts. This was certainly the case with the cell and protoplasm concepts in the mid-nineteenth century: there were situations and contexts in which the two terms could be used interchangeably, even if they usually expressed very different ideas. For example, Schleiden and Schwann had initially discussed cells in terms of boundaries and membranes, while later biologists shifted their theoretical discussions towards of the objects within the cell, and eventually the substances that made up different parts of the cell.

By revisiting the history of protoplasm theory, this article travels a well-worn path in the history of biology, now best known from Gerald Geison's (1969) history of protoplasm theory and Victorian vitalist-mechanist debates, James Strick's (1999, 2000) study of arguments over the possibility of spontaneous generation within Darwinian evolutionary theory, Ohad Parnes' (2000) study of Schwann's cytoblastema theory, and Andrew Reynolds' (2008) history of amoebae as "exemplary cells." Geison has shown how the term "protoplasm" developed in German biology to refer to a living substance common in plants and animals, and how T. H. Huxley (1825–1895) transformed the term into the "physical basis of life" in 1868. Strick builds on Geison's history, examining how protoplasm became controversial within Huxley's circle of Darwinists, and how Huxley and his supporters found themselves defending a sharp boundary between life and non-life. Parnes has argued that Schwann's cell theory arose from his reconceptualization of cytoblastema as a "material cause" or "agent" of cell formation, breaking from earlier theories of vital forces. Reynolds has shown that the ascendency of protoplasm theory in the 1860s and 1870s was grounded in the idea that the amoeba was the simplest living organism: the formless amoeba was interpreted as naked and homogenous protoplasm, and thus protoplasm as a formless substance became recognizable as the basis of life itself.

This article builds on Reynolds, Parnes, Geison, and Strick by focusing on protoplasm's earlier history as its definition *vis-à-vis* the cell was still being sorted out, leading up to Max Schultze's (1825–1874) conclusion in 1861 that, "A cell is a clump of protoplasm, in the interior of which lies a nucleus" (Schultze, 1861, p. 11). This article will proceed in four parts. First, I will examine the ideas of formative matter that existed prior to Schleiden and Schwann's development of their cell theory in 1838–1839, and how they did or did not break from older ideas of pre-vital matter. In the following two sections, I will look at Hugo von Mohl's successes and failures to redefine the cell's activity through its internal organization, leading to early development of protoplasm theory in 1846. Finally, I will follow Reynolds and Geison by reexamining the theory proposed by the botanist Ferdinand Cohn (1828–1898) that protoplasm was the common, animating substance in plants and animals.

## Primordial Cell Substances and the Cell as Container Before 1840

One of the enduring problems of the history of protoplasm is who to credit for its conception. The word "protoplasm" was first used in 1839 by the Czech anatomist Jan Purkyně (1787–1869), and it was reintroduced in 1846 by the Württemberger botanist Hugo von Mohl. Before 1846, protoplasm would have been just one of a wide range of pre-vital, primordial substances that were nutritive, but not themselves alive: simple, transparent, viscous, substances that nonetheless were specific to vegetable or animal life and had unique ability to congeal and separate into living tissue. Parnes (2000) lists Albrecht Haller's *tela celulosa* (1754), Theophile Bordeu's *tissu muquex* (1767), Friedrich Tiedemann's *Gallerte* (1808), Samuel Christian Lucae's *Zellstoff* (1810), Ignaz Döllinger's *Tierstoff* (1819), Nees von Esenbeck's *Grundschleim* (1814), Karl Ernst von Baer's *Grundmasse* (ca. 1824) and Carl Krause's *Urtierstoff* (1833)—and this was only in animal physiology. They were all more or less liquid or mucilaginous, primordial substances from which embryos or tissues were thought to be formed. I would argue that one could also add Schleiden's invocation of *Gallerte* or "vegetable gelatin" in 1838, Schwann's neologism *Cytoblastema* in 1839, and Purkyně's use of the word *Protoplasma* in 1839—the first such invocation in a biological context.[4] Schleiden's "vegetable gelatin," Purkyně's "protoplasm," and

[4] Purkyně was likely well aware that the Latin term *protoplastus* was a Catholic liturgical term that referred to Adam, and which could be translated as "first formed" or "first creation." Purkyně had joined the Piarists after completing his *Gymnasium* education, but left the Catholic order shortly before he was to be ordained, in search of a different direction in life (Heidenhain, 1888). There is no indication of whether this religious meaning was known to later, more materialistic scientists who used the term "protoplasm," though it is conceivable that the irony of using a liturgical term for what was essentially a materialist theory appealed to T. H. Huxley's sense of humor.

to a lesser extent Schwann's "cytoblastema" were all conceived as relatively simple substances that congealed, or in Schwann's theory crystallized, into more complex living forms.

Exactly why Purkyně used this vaguely biblical word in 1839 is now somewhat obscure, despite historians' prior attempts to recover it (Baker, 1949, pp. 90–91; Hughes, 1959, p. 41; Geison, 1969, p. 274n4; Harris, 1999, p. 75; Purkinje, 1840, pp. 81–82). The primary extant source for Purkyně's use of the word "Protoplasma" is a short summary of a lecture he gave at the January 16, 1839 meeting of the *Schlesische Gesellschaft für vaterländische Kultur*, which seems to have attracted little notice at the time.[5] The extant remarks suggest that Purkyně used the term "Protoplasma" to refer to a cellular precursor in animals, drawing an analogy to *Cambium*, the pre-cellular, gelatinous or slimy plant substance; they also show that Purkyně knew enough of the outlines of Schwann's forthcoming monograph on his cell theory to give both praise and criticism. J. R. Baker (1949) translated the following relevant passage as part of his historical reassessment of the cell and protoplasm theories (see also Reynolds, 2010, p. 197):

> In plant-cells the fluid and solid elements have separated completely in space, the former as the inner, enclosed part, the latter as that which encloses it. In the animal development-centre [*Bildungskerne*], on the contrary, both are still present in mutual permeation. The correspondence is most clearly marked in the very earliest stages of development [*Um entschiedensten ist die Analogie in den allersten Bildungszuständen*]—in the plant in the cambium (in the wider sense), in the animal in the Protoplasma of the embryo. The elementary particles are then jelly-like spheres or granules [*gallertige Kügelschen oder Körnchen*], which present an intermediate condition between fluidity and solidity. With the advance of development the animal and plant structures now diverge from one another; for the former either tarries longer in the embryonic condition or remains stationary in it throughout life, while in the latter on the contrary the hardening process and the separation of the solid and the fluid progress more rapidly, and come to light first in cell-formation and then in the formation of vessels (Baker, 1949, p. 91; Purkinje, 1840, p. 82).

Despite the relative brevity of Purkyně's reported remarks from 1839, two features are notable, the second of which has been overlooked by

[5] It is not clear if this is a transcript, submitted record, or a summary prepared by someone in attendance.

historians. First, his description of the "*Analogie*" (somewhat mistranslated by Baker as a lesser "correspondence") is meant to suggest that the similarities between the early stages of plant and animal life exist in spite of their other, fundamental differences as they later develop and mature; Purkyně's position was thus contrary to Schwann's claim that plant and animal cells were essentially the same kind of life form throughout the life of the organism (Baker, 1949, p. 91; Hall, 1969, vol. 2, pp. 210–211; Harris, 1999, p. 104). Second, Purkyně's text emphasized that plant life is marked by a transition from an undifferentiated jelly-like state to a state where solid (e.g., woody stem) and fluid (e.g., sap) parts are fully separated, while in animals this transition is halted "in mutual permeation." For Purkyně, the analogy between plant and animal life is incomplete, in part because of the fundamental difference in the kinds of primordial substances plants and animals come from: cambium in plants, and Protoplasma in animals.

Descriptions of development, growth, nutrition, and other physiological phenomena as processes of coagulation were not new: Pickstone (1973, p. 338) long ago argued that "the coagulation paradigm" was an essential feature of nineteenth century animal and plant physiology and an important element of Schwann's thinking in 1839 (Mylott, 2002, pp. 66–78). This emphasis on processes of coagulation and the separation of solids from fluids reaches far deeper in the history of Western science, however. Purkyně's invocation of "cambium" as the precursor to plant tissue development points to an exemplary case of how biological genesis was understood as a process of hardening and separating solid from fluid parts of a primordial sap or jelly. In a lamentably neglected article from 1967, Jacob Lorch demonstrated that while use of the term "cambium" in botany can be traced back to the mid-1600s in writings by Nehemiah Grew and Marcello Malphigi, in medical physiology "cambium" was associated with "dew" and "gluten" as a sort of alimentary humor as far back as Avicenna's eleventh century *Canon of Medicine* (Lorch, 1967, pp. 256–260). Moreover, Lorch argues that the idea of plant development as a "conversion of soft, liquid matter into hard substance" can be traced very far back to the many remaining written fragments of Theophrastus, Aristotle's pupil and the so-called "father of botany" (p. 256), and that the general principle of material condensation could even be credited to Thales if one so desired (p. 261). Lorch also shows that the basic idea that plants mature and grow by a process of thickening and separation of primordial cambium persisted for centuries: disagreements among Western European botanists centered on where or how the cambium congealed, not whether "cambium" was an idea worth retaining or rejecting. Nor was this idea simply very old: in the first third of the nineteenth century it became a common way of thinking about the relationship between vital forces and the material world, with the vital force acting upon matter, causing hard and soft materials to separate out of the mucilaginous fluid (Sloan, 1986). In 1833, for example, the botanist Gottlieb Wilhelm Bischoff (1797–1854) argued that the cambium was ''the fully organized nutrient sap, out from which new plant parts form themselves and which is found everywhere new parts arise'' (Lorch, 1967, p. 271; der völlig organisirte Nahrungssaft, woraus die neuen Pflanzentheile sich gestalten und der sich überall findet, wo neue Theile entstehen).

Thus to Parnes' list of eight different animal substances, Lorch adds a list of ''fluid, raw materials'' in plants: besides ''cambium,'' some more common terms like ''juice,'' ''mucilage,'' ''sap,'' ''dew,'' ''gelatin,'' and ''gluten,'' as well some more colorful terms including ''*Ros*,'' ''*Nahrungssaft*,'' ''*liqueur mucilagineuse*,'' ''nutritious Humour,'' ''caudexes,'' ''*Växtsaft*,'' ''*humus nutritius*,'' ''*succus nutritus*,'' and ''*Bildungssaft*,'' along with several other variations of the same in Latin, German, French, and Italian. While the botanists of the seventeenth, eighteenth, and early-nineteenth centuries might have disagreed over how to name these fluids and how these fluids developed, the long historical consensus posited a relatively simple, gelatinous or sticky substance that thickened and separated to form the more solid and more fluid parts of the larger organism. Lorch goes further to suggest that many of these, in addition to being relatively simple fluids, were ideas that worked to ''save the phenomenon'' (p. 258), providing a material explanation of growth and development by simply referring to the transformation of a mysterious material. The rest of this section will examine Schleiden's notion of ''vegetable gelatin,'' Schwann's more famous ''cytoblastema,'' and how they ''envisioned'' (to use Parnes' term) the process from which cells formed out of these primordial substances. Schleiden and Schwann did not wander very far from this coagulation paradigm in their reliance on relatively mysterious, if apparently simple substances, through which extraordinary forces created living cells.

Schleiden elaborated his cell theory in plants in 1838, in his famous essay, ''Contributions to our Knowledge of Phytogenesis.'' It is best known for its twin arguments: that cells are individual living beings, and that cells are the universal elementary organ of the larger plant. Yet Schleiden also took pains to describe how cells formed and the substance from which they formed. He suggested that starch converts into a slimy substance, which he referred to variously as either "*Schleim*," "*Gummi*," or *"Pflanzengallerte*" (in the English translation "mucus," "gum," and "vegetable gelatin"). This vegetable gelatin was derived from starch, Schleiden suggested, and it was the material precursor to cells, fibers, and all other viscous substances in the plant:

> I shall call it for shortness sake vegetable gelatin, and am inclined to enumerate under this head, as mere slight modifications, pectine, the basis of gum tragacanth, and many of those substances commonly arranged under vegetable mucus. It is this gelatin which is ultimately converted by new chemical changes into the actual cellular membrane, or its thickening layers [*oder ihre Verdickungsbildung*], and into vegetable fibre (Schleiden, 1838, pp. 143–144, 1841, pp. 286–287).

When Schleiden elaborated this theory in his 1842 textbook *Principles of Scientific Botany*, he added that, "Of the nature of the fluid in and out of which the cells originate, we are not yet perfectly cognisant. This much we know, that in some cases…a solution of sugar is present; and, as far as may be decided by the action of alcohol, this is mixed with gum (dextrin?) [*sic*]" (Schleiden, 1842, p. 192, 1849, p. 31).[6]

Thus, despite the fact that Schleiden had begun to think of cells as individual organisms, he still thought of their formation in terms that had long been familiar in biology: matter moving from simple to complex, by means of the separation the fluid and solid parts of a viscous substance. Having described the basic qualities of the vegetable gelatin, Schleiden's continued to describe how the "gum" concentrates into granules, which grow and develop into "cytoblasts"—Schwann later called these "nuclei"—such that the gum becomes cloudy or opaque. Then, "Single, larger, more sharply defined granules now become apparent in this mass; and very soon afterwards the cytoblasts occur appearing as it were like granular coagulations around the granules" (Figure 1; 1838, p. 145, 1841, p. 287). These granular coagulations were the precursor to Schleiden's famous visual analogy of a "watch-glass" covering the cytoblast: "As soon as the cytoblasts have attained their full size, a delicate, transparent vesicle [*ein feines, durchsichtiges Bläschen*] arises upon their surface." This vesicle *is*

[6] The confusion of "gum" with "dextrin" in the English translation of Schleiden's textbook can be traced the translator Edwin Lankester, who elsewhere in the text interjects that the chemist Gerardus Mulder had shown that "the greater part of what has hitherto been called gum is dextrin" (Schleiden, 1849, pp. 19–20). Schleiden predominantly uses "gum," and his text reads, "…bestimmt eine Zuckerlösung, und, wie aus dem Verhalten gegen Alkohol hervorzugehen scheint, vermischt mit Gummi vorhanden ist."

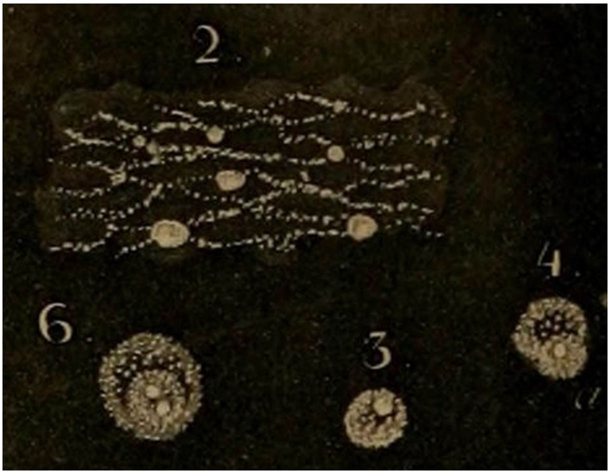


*Figure 1.* Schleiden's (1838) illustration of granules floating in the "vegetable gelatin" (2), growing in size to become (3) a cytoblast, before the cell forms on top of the cytoblast (4)

the cell, sitting on top of the nucleus, "situated on it [*die auf ihm Aufsitzt*] somewhat like a watch glass on a watch" (1838, p. 145, 1841, p. 288). Whereas in its earlier state the cytoblast was surrounded by a cloudy, coagulated substance, the vesicle or cell now has a defined boundary, with the space formerly occupied by the coagulated substance becoming a clear fluid: "the space between [the vesicle's] convexity and the cytoblast is perfectly clear and transparent." All of this echoes prior theories of a separation of juices into solid and liquid parts: the gum or gelatin congeals around the cytoblast before separating out into a clear substance and an opaque cell membrane.

Schleiden's description of this material transformation was not the only older idea in his cell theory: his 1838 "Phytogenesis" essay was also permeated with older terminology and concerns, primarily through the question of whether plants grew by intussusception, i.e. by increasing from within, or juxtaposition, i.e. by increasing by superaddition. His reliance on this older vocabulary of juxtaposition and intussusception shaped his theory of cellular growth. According to Schleiden, after a cytoblast developed into a cell, the cell could grow in one of two ways: by intussusception via the increase of fluid within the membrane's boundary, or by juxtaposition via the addition of layers upon the "primitive membrane," which Schleiden had previously referred to as the "transparent vesicle" (1838, p. 160, 1841, p. 299). To summarize, for Schleiden there were three ways in which a plant could grow: by increasing the number of cells it possessed; by expanding the existing cells from within themselves, (which he notes "can never in any form, not even a remote one, occur in crystals or in animals); and by lignification, whereby, "the walls of the full-grown cells are thickened by fresh-deposited layers" (1838, p. 161, 1841, p. 300).

Throughout the rest of the 1838 "Phytogenesis" article Schleiden dwelled very little on these seemingly-crucial details about the growth of individual cells. Rather, his intellectual labor lay in demonstrating that the cells themselves are agents responsible for the growth and development of a plant's anatomical plan. Nor did Schleiden substantially revise his views on vegetable gelatin, cell genesis, or cell growth in 1842. Both his theory of free cell formation and his conception of the cell *qua* cell remained fairly stable. Reynolds (2010) has argued that Schleiden (and later Schwann) was claiming that the whole organism was a composite of individual cells, and not arguing about the minutiae of the concept of the cell itself. What is clear is that for Schleiden the cell's membrane was its most important physiological and anatomical feature: either the contents inside the membrane increased, or layers were superadded to the membrane's exterior. Furthermore, for Schleiden the development of both the cytoblast and the cell's membrane somehow seemed to be inherent in the chemical properties of the simple vegetable gelatin.

When Schwann adapted Schleiden's cell theory to animals in 1839 in his *Mikroskopische Untersuchungen*, he famously renamed the "vegetable gelatin" to "cytoblastema," while at the same time replacing Schleiden's chemical theory of coagulation with an elaborate and controversial analogy comparing cell formation to crystal formation. If in 1838–1842 Schleiden said much about the chemical properties of vegetable gelatin without going into detail about the congealing process, in 1839 Schwann said much about the congealing process without any chemical detail whatsoever: Schwann hardly knew what cytoblastema was, in contrast to what he believed cytoblastema did. In one overview, Schwann merely used the phrase "structureless substance" to describe a gelatinous cellular precursor:

> The following admits of universal application to the formation of cells; there is, in the first instance, a structureless substance present, which is sometimes quite fluid, at others more or less gelatinous. This substance possesses within itself, in a greater or lesser measure according to its chemical qualities and the degree of its vitality, a capacity to occasion the production of cells. When this takes place the nucleus usually appears to be formed first, and then the cell around it. The formation of cells bears the same relation to organic

> nature that crystallization does to inorganic (Schwann, 1847, p. 39, 1839, p. 45).

In another, Schwann seems content to allow for the existence of different kinds of cytoblastema:

> The chemical and physical properties of the cytoblastema are not the same in all parts. In cartilages it is very consistent, and ranks among the most solid parts of the body; in areolar tissue it is gelatinous; in blood quite fluid. These physical distinctions imply also a chemical difference. The cytoblastema of cartilage becomes converted by boiling into gelatine, which is not the case with the blood; and the mucus in which the mucus-cells are formed differs from the cytoblastema of the cells of blood and cartilage.…in general it is a homogeneous substance; yet it may become minutely granulous as the result of a chemical transformation… (Schwann, 1839, p. 200, 1847, p. 169)

Parnes (2000, 2003) and Müller-Wille (2010) have argued that Schwann was using a distinctive epistemic strategy here, one that had served him well in his previous work on the physiology of digestion. Schwann invented a material agent, and gave it the power to enact physiological processes—pepsin in his digestion theory, cytoblastema in his cell theory. In so doing, Parnes has argued, Schwann was trying to reform the science of physiology around the discovery and elaboration of "'principles' of physiological processes without recourse to vital force" (Parnes, 2003, p. 133; see also Sloan, 1986).

Yet the material foundation of Schwann's cytoblastema theory was remarkably old-fashioned, even compared to Schleiden's theory of plant cell genesis from one year earlier. Schwann's cytoblastema was essentially a placeholder for a substance yet to be discovered, very similar to the cambium theory's role in explaining tree growth by means of a mysterious or underspecified thickening fluid. On top of this, however, Schwann also added a theory of organic crystallization, hinted at in the first of the two passages quoted above. This would have been a familiar argumentative strategy in 1839 (Maulitz, 1971). In fact, Schwann conceived of the crystallization process much in the same way that Buffon, Linnaeus, and many others in the eighteenth century did: as layers of two-dimensional particles or molecules deposited onto a central nucleus, analogous to the way lacquerware is made by depositing successive layers of lacquer onto a wooden or bamboo form (Emerton, 1984, pp. 236–237).

> A small corpuscle (the nucleolus) is the earliest formation, that [*sic*] a stratum (the nucleus) is first deposited around it, and then subsequently a second stratum (substance of the cell) around this again. The separate strata grow by the reception of new molecules between the existing ones, by intussusception, and we have here an illustration of the law, in deference to which the deposition takes place more vigorously in the external part of each stratum than it does in the internal, and more vigorously in the entire external stratum than in the internal. In obedience to this law it often happens that only the external part of each stratum becomes condensed into a membrane (membrane of the nucleus and membrane of the cell), and the external stratum becomes more perfectly developed to form a cell, than the nucleus does (Schwann, 1839, p. 213, 1847, p. 180).

Historians have differed widely on how to best interpret Schwann's fixation with this crystallization analogy, both within the context of Schwann's biography (Mendelsohn, 1963; Duchesneau, 1987; Parnes, 2000, 2003; Müller-Wille, 2010), and situated in the broader context of German biology and chemistry (Maulitz, 1971; Mendelsohn, 1965; Lorch, 1972). It appears to have been both instrumental in Schwann's own arrival at a universal cell theory and widely dismissed by subsequent biologists.

What I want to emphasize here instead is that Schleiden's "vegetable gelatin" and Schwann's "cytoblastema"—minus his crystallization theory—bore broad similarities with older theories of generative fluids, even as they stripped out theories of vital forces. Both the vegetable gelatin and the cytoblastema were "structureless," save for their apparent (and sometimes variable) viscosity and gumminess; they were biotic precursors capable of transforming into cells as well as other objects or substances, depending on environmental or other biological conditions; they were either very simple or simply under-defined substances; and they operated through relatively mysterious processes of thickening, condensation, or coagulation. In this particular way, then, neither Schleiden nor Schwann's theories were major departures from what came before them. They envisioned cells as objects arising from a viscous, simple, yet also somewhat mysterious substance.

## Hugo von Mohl's Primordial Utricle Theory

As early as 1835, Hugo von Mohl had proposed that plant cells could multiply by dividing, but between 1838 and 1845 he abandoned cell division in favor of Schleiden and Schwann's broader cell theory, also accepting their theories of free cell formation and juxtaposition of layers of cytoblastema (Harris, 1999, p. 73; Sachs 1890, p. 312; Baker, 1952, p. 425; Mohl, 1837). Schleiden and von Mohl, along with Carl Nägeli, Franz Unger, and Wilhelm Hofmeister, were of a generation of German botanists who sought wholesale reforms to botany as a science (Sachs 1890, pp. 171–172). Whereas Schleiden and Schwann had hoped to reform botany and zoology through bold theoretical statements, von Mohl staked his reputation on terminological and methodological exactitude (Mohl, 1843).[7] After Schleiden and Schwann had established the individual cell as a universal principle, von Mohl became one of the most important theorists of the internal structure and life history of the plant cell.[8]

It was von Mohl's demand for terminological and observational specificity that would lead to his articulation of the "modern" conception of protoplasm in 1846. This same scientific and linguistic rigor that would cause von Mohl to articulate what he believed were two very different theories: the "*Primordialschlauch*" or "primordial utricle" theory in 1844, and his protoplasm theory in 1846. Both of these theories were quietly revolutionary, but the primordial utricle was redefined by other biologists in the late-1850s as "a very thin layer of protoplasm"—partly to recognize von Mohl's priority in discovering or properly conceptualizing protoplasm theory (Sachs 1890, p. 329). In fact, von Mohl's contemporaries failed to understand that these were distinct theories in von Mohl's mind, and historians (Sachs 1890, p. 329; Baker, 1949, p. 92; Geison, 1969, p. 274n4; Lombard, 2011, p. 8) have followed suit; Harris (1999, p. 75), for example, repeats the error that "protoplasm" was the "more specific and…definitive name" for the primordial utricle. For von Mohl, the word "protoplasm" was a way of distinguishing between different kinds of mucilaginous substances within the cell, making his protoplasm theory an anatomical one. The primordial utricle theory, however, was his way of dramatically rewriting Schleiden's cell theory, by arguing for the primacy of a clear, active organ within the cell that was responsible for almost all plant growth and development: it was a physiological theory as well as an anatomical one. Yet von Mohl

[7] Von Mohl was recognized in the 1840s as one of the leading biological microscopists and an expert on reagents and preparation. He wrote one of the earlier microscopy manuals specifically for biologists (Schickore, 2007, pp. 233–235; Mohl, 1846a).

[8] Julius Sachs (1890, p. 226) suggests that after 1839, the botanists who had previously focused on the embryology and development of whole plants turned their focus to the cell.

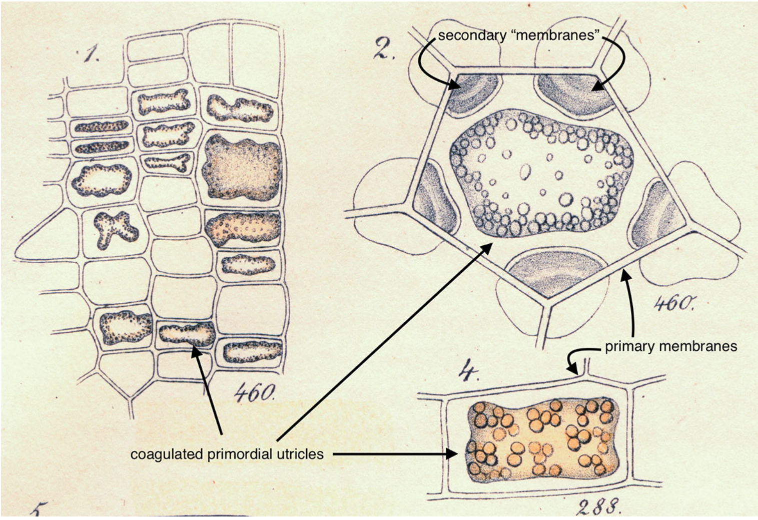


*Figure 2*. Detail from the plate from von Mohl's essay, "On the Structure of the Vegetable Cell" (1844), showing primordial utricles fully detached from the primary membrane after being preserved in alcohol

also undermined his own distinction between protoplasm and the primordial utricle, by changing his opinion on whether the primordial utricle was a "membrane," i.e. a delimiting boundary that oriented a spatial field by defining an inside and an outside or a blobby mass, one of the many objects within the cell, similar in status to the nucleus. This section will address von Mohl's primordial utricle theory in some detail to show how he relocated the vitality of the cell away from the cell membrane and nucleus, into the inner contents of the cell; the next section will address von Mohl's protoplasm theory, his understanding of biological matter, and the confusion and controversy it caused.

Von Mohl discovered the primordial utricle early in 1844, announcing its existence in a long essay entitled, "Some Remarks on the Structure of the Vegetable Cell." This was during a unique transitional period in both his own investigative pathway and the history of cell theory: he still accepted Schleiden's theory of free cell formation, and saw his primordial utricle theory as, "on the whole…confirmatory of Schleiden's theory respecting the formation of cells" (1844, p. 29, 1846b, p. 97). Yet his primordial utricle theory actually overturned many key details of Schleiden's theory of cell formation and growth. Von Mohl had noticed that in tree stems preserved in alcohol, each cell contained an "inner, cell-like structure" that could be stained yellow or brown with iodine (1844, p. 273, 1846b, p. 92). This was the primordial utricle,

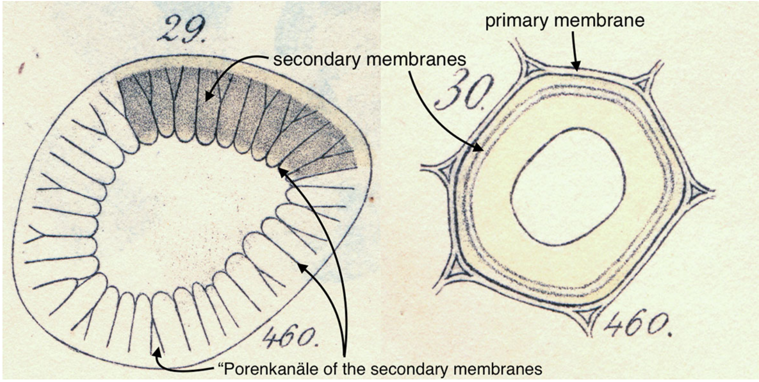


*Figure 3.* Diagrams of woody cells from bald cyprus (*Taxodium distichum*), highlighting the secondary membranes and the "*Porenkanäle*." On the right (30) is a wood cell in its natural state; on the left (29) is a cross section of secondary membrane swollen with sulfuric acid, showing how the secondary membrane separates into lobes. Detail from, "On the Structure of the Vegetable Cell" (1844)

a sac-shaped body that appeared as a single blobby mass (Figure 2).[9] "The question now arises," von Mohl wrote,

> whether the primordial utricle is to be regarded as a cellular membrane [*eine Zellhaut*], or whether it is not rather to be reckoned among the contents of the cell and looked upon as a coagulated mucilaginous coating [*Ueberzug*] on the cellular membrane, for which indeed it has certainly been frequently taken…The substance of which the primordial utricle is constituted [*besteht aus*] appears to be, if not identical, at least nearly allied to the muco-granular substance which usually invests [*umhüllt*] the nucleus as an irregular mass (1844, pp. 293–294, 1846b, p. 99).

Von Mohl vacillated throughout the 1840s as to whether the primordial utricle was a "membrane" or a "coagulated mucilaginous coating," two categories that were mutually exclusive in his mind. To follow Lakoff and Johnson's categorization of material types, the primordial utricle in 1844 was an *object,* "among the contents of the cell," much more so than it was a container, membrane, or boundary defining what was inside versus outside itself. It was also clearly not a substance in von Mohl's mind, since the primordial utricle itself was "constituted" by a

[9] The English use of the word "utricle" in botany most often refers to a soft sac, pouch, or bladder-shaped growth near the base of petals and leaves; in animal histology it usually refers to the larger of two sacs in the vestibule of the ear, the other being the "saccule." ("Utricule, *n.*1," *OED Online*).

"muco-granular substance," superficially similar to Schleiden's vegetable gelatin or Schwann's cytoblastema. In order to demonstrate the primordial utricle's existence and importance, von Mohl believed that he needed to both explain its physiological role and describe what kind of material entity it was—hence, his concern about which term to use.

This terminological problem was a manifestation of the larger problem of how to interpret the anatomy and development of plant and plant cell growth. In turn, this was also a methodological issue of how to interpret plant cells that were preserved or treated with diluted acids. If any given plant cell is treated with a diluted acid (von Mohl mentions nitric, hydrochloric, and sulfuric acids) and then stained with iodine, several layers of "secondary membrane" appear to separate off from the outer, "primary" boundary of the cell, showing a range of blues, yellows, and browns (Figure 3, right); this would have been in addition to the appearance of the blobby mass in cells preserved in alcohol (Figure 2). A large portion of von Mohl's 1844 article took the form of a lengthy critique of one of Schleiden's more bitter antagonists, the forestry botanist Theodor Hartig (1805–1880), and an object that Hartig called the *ptychode*, which appeared just like von Mohl's blobby mass.[10] The ptychode was, in Hartig's words, "the innermost membranous limitation of the interior of the cell" (Hartig 1843, p. 8; die innerste häutige Begrenzung des Zellenraumes); or in von Mohl's summary of Hartig's views, "a third inner membrane" (Mohl, 1844, p. 307, 1846b, pp. 101–102; eine dritte, innere Haut). Hartig believed, following Schleiden and Schwann, that the cell grew outward from the nucleus through a layering of membranes in concentric rings: starting with the nucleus, around which was formed the ptychode, which then deposited the outermost layer or layers of "primary" cell membrane, what would today be considered the plant cell wall. Hartig had claimed that when treated with sulfuric acid and stained with iodine, the outermost "primary" layer stained blue, a middle "secondary" layer stained yellow, while the innermost—Hartig's ptychode—stained a dark yellow or light brown. For Hartig, this combination of coloring and layering was evidence that the secondary and primary membranes (especially in lignified, or woody cells) were deposited upon the older ptychode, such that the thick primary membrane would actually be the youngest.

Von Mohl disputed Hartig's interpretation of both the separation of layers and the coloring effects of the iodine, arguing that Hartig's (and

[10] Hartig (1843) did not explain why he decided on this term; it may derive from the Greek *ptyche*, to fold, or *ptualon*, spittle.

by extension, Schleiden and Schwann's) vision of cell growth by a succession of layers had no grounding in the "mechanical conditions" that were visible under the microscope—that is, if preservation was performed correctly and staining was interpreted correctly, both points for which he faulted Hartig. Von Mohl deduced a series of intracellular processes that could be inferred by looking at cells that were more properly preserved. It was these procedural inferences and the resulting microscopically visible structures that he referred to as "mechanical conditions," and which he illustrated with thirty-four schematic, even didactic figures, drawn simply in order to demonstrate the force of his argument. In what follows, I will give a close examination of von Mohl's figures, because they reveal crucial aspects of his argument that he found difficult to express in writing or by definitions alone.[11] Doing so, I hope, will clarify issues that historians have admitted were confusing (Geison, 1969, p. 274n4), and show why von Mohl believed the primordial utricle and protoplasm concepts were very different—the former organized, the latter unorganized.

Von Mohl's first figures show the primordial utricle completely separated from the primary membrane by means of alcohol to demonstrate its existence as an independent anatomical object within the cell; the artificially coagulated primordial utricle, colored pale orange by the iodine, is isolated and exaggerated, shown completely separated from the outer membrane (Figure 2). Hartig had claimed to see this blobby mass as well, and had used its apparent coherence to argue for the ptychode's status as a continuous membrane. For von Mohl, this unity and integrity was important in establishing the primordial utricle's status as a complete, organized organ, but he also argued that primordial utricle's separation from the outer membrane in these figures was the result of overly aggressive acid or alcohol treatment that obscured the nuances of its structure and function. Likewise, the total separation of Hartig's "secondary membranes" was the result of the same aggressive preservation tactic. By using a gentler acid treatment, von Mohl reported seeing these secondary membranes curve and terminate at the boundary of the primary membrane (Figures 3, 4, left), rather than form the even, concentric

[11] Of von Mohl's relatively sparse illustrative practices, Julius Sachs (1890, p. 298) suggested that "von Mohl's microscopic drawings do not aim at giving the collective impression, but at facilitating the understanding of the delicate structure of single cells and their combination by aid of the simplest possible lines. He always despised pictures from the microscope…a kind of artistic restorations of the originals and to some extent a playing with science; and in his later publications he was more sparing of illustrations or omitted them altogether, in proportion as he acquired the power of giving clear verbal explanations of even difficult structural conditions."

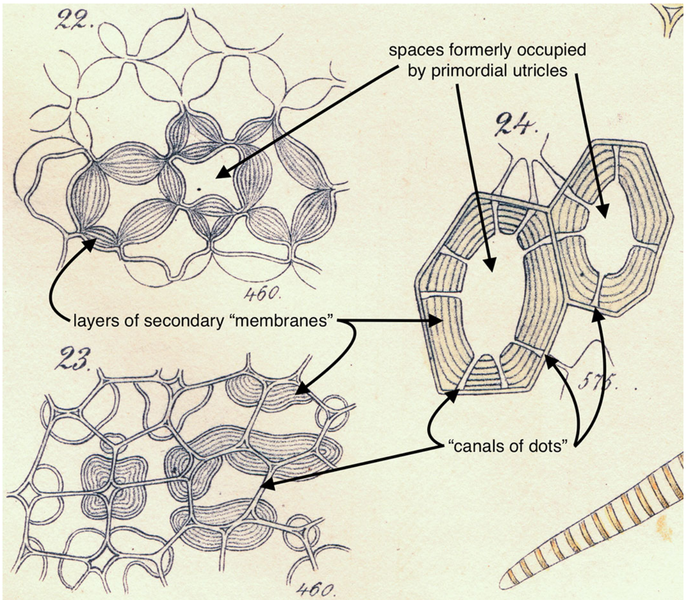


*Figure 4*. Diagrams of ''gelatinous'' cells from spinach stem, showing how the ''curved arches'' of secondary membrane (22) mechanically separate after treatment with hydrochloric acid (23). The right diagram shows woody cells from rattan palm (*Calamus*, 24) treated with iodine, showing lobes of secondary membrane and the ''*Porenkanäle*,'' through which the primordial utricle attached to the primary membrane. Detail from, ''On the Structure of the Vegetable Cell'' (1844)

or parallel layers in untreated cells (Figure 3, right): ''The layers of the secondary membrane do not run parallel to the outer walls of the cell, but exhibit an arched curve directed towards the interior of the cell'' (1844, p. 323, 1846b, p. 106). Seeing gaps or valleys between the lobes of layered secondary membrane, von Mohl then argued that when the cell was still alive the primordial utricle must have extended through these gaps in the secondary membrane, anchoring the primordial utricle to the outermost ''primary'' membrane. He referred to these anchoring points as ''canals of pores'' (*Porenkanäle*) or ''canals of dots'' (*Tüpfelkanäle*), visible on the outer surface of many woodier cells (Figure 4, left). Applying diluted hydrochloric acid to the plant cells would reveal the cleft, finger-like structures surrounding each pore, ''split into many lamellae,'' showing the point at which the primordial utricle was once attached before the woody cell had fully matured (1844, pp. 324–325, 1846b, p. 109).

Throughout all of these diagrams, von Mohl argued that, with the exception of the outermost, primary membrane, the inner ''membranes'' were not continuous layers of deposits or borders, as Hartig, Schleiden, or Schwann's theories of cell growth would suggest. Rather, they consisted of many discrete accumulations deposited by the primordial utricle in clumps or lobes surrounding the canals of pores. For von Mohl, the only "mechanical" explanation for this observation was that the outer parts or membranes of the cell thickened as the primordial utricle retreated inward, while the primordial utricle remained anchored to the primary membrane through the intervening layers it had deposited. Whereas Hartig, Schleiden, and Schwann held that the nucleus created ever-thicker layers of cell, building new layers from the nucleus outward, von Mohl argued that the primordial utricle was responsible instead for creating the outermost membranes or walls of cells first, before retreating inward, depositing successive layers of secondary membrane in the shape of lobes, behind and exterior to itself.

By arguing that the agent of cellular growth worked from the edges of the cell in towards the middle, von Mohl thus reversed Schleiden and Schwann's schema of growth as the layering of gelatinous, hardening substances. More importantly, von Mohl was decisively breaking from the old, possibly ancient view of biological development by a process of coagulation: the primordial utricle, as a clearly defined anatomical object, was now also the agent responsible for growing, expanding, and possibly even generating cells. Von Mohl's primordial utricle theory did not propose any kind of unique, pre-biotic, hypothetical vegetable gelatin, cytoblastema, cambium, etc.; only an object within the cell, the primordial utricle, was active. Nor did he speculate about the substance the primordial utricle was made from; he only speculated that the primordial utricle deposited its layers through a process of denitrogenization, pointing to the fact that iodine stained the primordial utricle brown or orange, young cell membranes yellow, and old woody membranes pale yellow or blue (1844. p. 305, 1846b, p. 100). The high concentration of nitrogen in the primordial utricle and its disappearance in fully mature woody cells even left von Mohl to excitedly speculate: "Ought we not then to conclude that the primordial utricle takes a part in the assimilation of the crude nutritive juices, as well as in the origination of the cell? But enough of conjectures as to the functions of an organ whose very existence has yet to be admitted by other observers!" (1844, p. 306, 1846b, p. 101).

## Primordial Utricle, or a "Thin Layer of Protoplasm"?

Already in the 1844 article, von Mohl had made it clear that he thought the primordial utricle was the primary agent of change, growth, and perhaps even reproduction in the plant. However, he had characterized the material composition and texture of the primordial utricle merely as ''muco-granular'' (*Schleimkörnig*), adding only that it was nitrogenous. Two years later, von Mohl (re-)coined the term ''protoplasm,'' in order to identify and characterize this muco-granular substance—and, just as importantly, in order to differentiate between protoplasm and all of the other gelatinous substances inside the cell. This was a clear break from Schleiden and Schwann's cytoblastema theory, and the coagulation paradigm as a whole in two ways: von Mohl was very specific in his characterization of protoplasm's texture, composition, location, and activity in a way that Schleiden and Schwann were not; and he did not conceive of protoplasm as a pre-biotic or nutrient humor, as in older cambium theories. Unfortunately for von Mohl, having two theories of mucous cell structures confused his colleagues, and his attempt to clarify the problem by reconceptualizing the primordial utricle as either a membrane or a membrane-bound object only led other botanists to abandon the primordial utricle theory altogether.

The title of von Mohl's 1846 essay, ''On the Circulation of the Sap in the Interior of Cells,'' gives no hint of overturning any significant theory of cell structure.[12] Indeed, in this much-heralded paper von Mohl seems more intent on specifying and naming what he believed were two different kinds of gelatinous substances in plant cells: protoplasm, and the inactive, watery ''sap'' (*Saft*). If the cell was ruptured, protoplasm and sap both flowed out, but the two substances would not mix. Von Mohl defined protoplasm as the material precursor to both the nucleus and the primordial utricle, a claim he seems to have made largely based on the fact that the nucleus, primordial utricle, and the ''mucous mass'' preceding each body all stained yellow with iodine.

> …this viscous mass everywhere precedes the first solid formations indicative of future cells where cells are to be formed; since we must moreover admit that it furnishes [*liefert*] the material both for the formation of the nucleus and of the primordial utricle, which stand not only in the nearest relation as to space but react towards iodine in an analogous manner, consequently that their organization is the

[12] The title was also simply not helpful: ''*Ueber die Saftbewegung im Innern des Zelles*'' was a reference to a phenomenon that Treviranus had called the ''*Rotation des Zellsaftes*'' in 1807 (Mohl, 1853, p. 201). Von Mohl was trying to show that granulated *Protoplasma* was distinct from watery, clear *Zellsaft*, and that only protoplasm, not the cell-sap, was rotating.

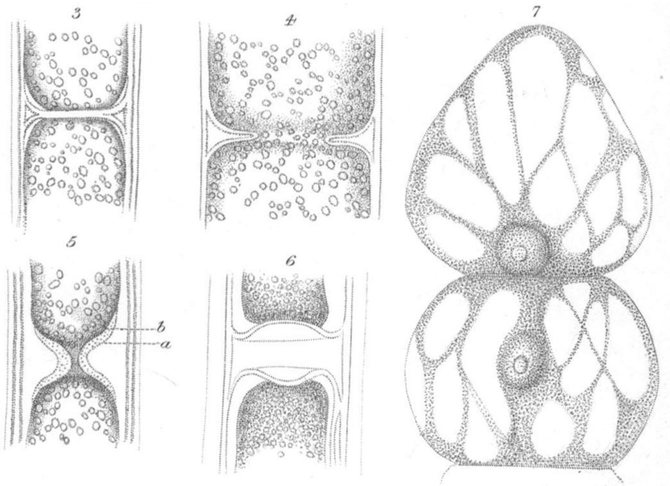


*Figure 5*. Detail from the plate from von Mohl, *Principles of the Anatomy and Physiology of the Vegetable Cell* (1852), showing the constriction of the primordial utricle in filamentous algae (*Cladophora*, left and center, 3–6); nos. 5–6 show the effects of acid treatment, with the primordial utricle (5a) separated from the cell contents (5b). Right (7), protoplasm filaments in two cells from *Tradescantia* (spiderwort) running between the nucleus and the primary cell membrane

> process which induces the formation of the new cell, I trust it will be considered justifiable if I propose to designate this substance by the word *protoplasma*, a term which recalls to mind its physiological function (Mohl, 1846c, p. 75, d, pp. 2–3).

Generating the nucleus and primordial utricle was not the only physiological function von Mohl gave to protoplasm. He also observed that, as young cells matured, their protoplasm developed cavities filled with an "aqueous sap" (*wässerigem Saft*). As the cell grew and became older these cavities merged into one large cavity, such that the protoplasm became stretched into thin filaments, radiating outwards from the nucleus (Figure 5, right). The protoplasm also seemed to exhibit a slow, circulating current, carrying with it the cavities of aqueous sap, granules, and occasionally even moving the nucleus around.[13]

Von Mohl's protoplasm theory was not like earlier coagulation theories in two critical ways: he did not describe protoplasm as "coagulating" or "separating," and protoplasm seemed to play a more active role in the life of the cell than simply being the cell's precursor material.

[13] On the more recent history of protoplasmic streaming, see Dietrich (2015).

Rather than continuing with either the older trope of separating into solid and fluid parts, or increasing by juxtaposition through a kind of crystallization or layering, von Mohl's 1846 essay spoke of protoplasm as alternately "furnishing" material for the primordial utricle and nucleus, as well as giving it a crucial role in the "successive changes of the nitrogenous substances" within the cell. Unlike Schleiden's firm statement that vegetable gelatin was a byproduct of starch, von Mohl argued on the basis of iodine stains that it was some kind of nitrogenous substance; moreover, he had already proposed that one of the primordial utricle's chemical-developmental processes was some kind of denitrogenization, as it transformed into the secondary layers of cell membrane. More importantly, von Mohl gave protoplasm two clear physiological roles: it moved, and it formed sap-filled cavities, what would soon be referred to as vacuoles. Protoplasm was not simply "vegetable gelatin," akin to Schleiden's description of a starch-based gum, but something special and distinctive.

At the same time, he was somewhat ambiguous about whether protoplasm itself possessed the agency to do these things. On the one hand, protoplasm was clearly participating in, or at least allied with the processes of the plant cell's growth and maturation. Protoplasm exhibited motion, one which seemed to sweep up the nucleus, chloroplasts, and other granules along with its current. Protoplasm was also a key feature of the plant cell's distinctive inner anatomy, developing both small vacuoles and the large central cavity within and around itself. On the other hand, von Mohl did not say whether he thought this activity occurred by the protoplasm's own power, or through some other agency, lending his 1846 article a descriptive, acausal sensibility. Most importantly, he was not clear on whether protoplasm possessed the agency to move itself, or whether some other feature of the cell was moving it. "I dare not venture to express the slightest suspicion of the cause of this motion" in protoplasm, von Mohl disclaimed. Yet he was certain enough to note that, "It appears to me however not probable that the nucleus possesses any such influence" (1846c, p. 93, d, p. 9).

After 1846, rather than try to clarify these problems of protoplasm's agency, von Mohl became more insistent that his aim was only to identify protoplasm against other mucous substances in plants; the distinction between protoplasm and cell-sap was but one such distinction. He clearly understood protoplasm as an unstructured mass, whereas the primordial utricle always coagulated into a single body with alcohol or iodine, as noted in the previous section. Von Mohl reported that protoplasm in mature cells treated with iodine "does not solidify uniformly to form a dense globular mass, but in such a manner that some smaller and larger roundish cavities are formed in its interior'' (1846c, p. 77, d, p. 4). The primordial utricle theory was simply much more important to von Mohl, because by 1851 he had identified the primordial utricle as the site of cell division. The primordial utricle theory thus became von Mohl's vehicle to push decisively away from most of Schleiden's cell theory. In brief, von Mohl argued that once the primordial utricle had reached a certain size, it constricted or folded in the middle to divide in two. Then, each half of the primordial utricle would deposit a cellulose cell wall or ''septum'' between themselves, finishing the process of creating two daughter cells (Figure 5, left and center). As he moved the locus of cell genesis, and even the growth of the whole plant to the primordial utricle, von Mohl also had to clarify that he had revised his conception of the primordial utricle, clearly stating that it was a membrane. Recall that he was initially ambivalent about whether the primordial utricle had been merely a ''coagulated mucilaginous coating'' or a true ''membrane'' that delimited an object and held contents within itself—namely, the chloroplasts, nucleus, and starch granules. As both he and Carl Nägeli (1817–1891) were developing more robust theories of cell division in the 1840s, Nägeli had referred to a structureless ''mucilaginous layer'' (*Schleimschicht*) that coated the inside of the cell membrane (''*kleidet die ganze innere Oberfläche aus*''), choosing to ignore von Mohl's neologism (Nägeli, 1846, p. 38). This raised von Mohl's ire, leading him to write this surprisingly revealing clarification: ''No fixed limit can, of course, be indicated between a soft membrane and a compact layer of mucilage, but a layer from which…folds grow out and cause constriction of the contents of the cell, certainly must be regarded as a membrane, and not a layer of fluid mucilage'' (Mohl, 1852, p. 37, 1853, p. 200).

In other words, von Mohl insisted that the primordial utricle was structured object, and an object that either had or was itself a clear delimiting boundary that could fold—all the while admitting that the difference between a membranous boundary and a layer of mucilage was both conceptually and empirically blurry. Despite the fact that von Mohl had elevated protoplasm to have a unique status in the life of the cell, he was not willing to concede that a mere viscous fluid could be an independent living agent. This status he reserved for the primordial utricle exclusively. ''The protoplasm bears the same relation to the cell-sap as a frothing fluid does to the air contained in its bubbles,'' von Mohl wrote around 1851. ''The unceasing flow and continued transformation of the mass of the protoplasm, furnish the most distinct proof that we have to do with a fluid, and not with an organized structure'' (Mohl, 1852, p. 40, 1853, p. 202). Thus, when the Berlin botanist Nathaniel Pringsheim (1823–1894) argued that the primordial utricle did not exist and that the protoplasm alone was the material basis of the plant cell's life (Pringsheim, 1854), von Mohl strenuously objected, again insisting that there was a reason that he made the distinction between the organ and the substance from which it was made. Von Mohl reiterated that his aim in 1846 was not to articulate a radical new theory of living matter, but only to distinguish one mucilaginous substance from others, writing,

> With this term I designated a particular *anatomical* part of plants, independent of its chemical composition, which is still not yet accurately known; under no circumstance did I want to coin a collective name for the protein substances, which are present in the most diverse anatomical proportions, and which shall be named by the chemists, who are studying them in far greater detail. To employ the term protoplasma as an overall designation of the plant proteins, of legumins, diastases, etc., is as useful as to subsume animal fibers, casein, etc. all under the term "blood" (Mohl, 1855, p. 690).

Reading von Mohl's attempts to clarify what he meant by "primordial utricle" and "protoplasm," it is possible to see that these two concepts belonged to two different theoretical projects in his mind: the former to explain the development and structure of mature cells, the latter to differentiate between different substances of the cell. He seems to have explicitly illustrated protoplasm in a cell only one time, where the moving protoplasm is stretched out into thin filaments connecting the membrane and the nucleus (Figure 5, right). The contrast between this diagram and his diagrams showing the constriction of the primordial utricle is stark, with the primordial utricle clearly shown as a coherent and bounded object, and the cell's protoplasm shown as a strung-out net of slime. One does not get the impression that these two images are obviously related to each other, despite appearing next to each other on the same lithograph and in a single work.

Von Mohl resisted associating protoplasm too closely with the primordial utricle, in spite of the fact that they were similar both texturally and topographically. While his contemporaries like Nägeli and Pringsheim were willing to accept that protoplasm could be thought of as an independently active substance, responsible for many of the vital phenomena shown by organized cells, von Mohl's thinking had nearly the opposite trajectory. When von Mohl initially engaged with Hartig and Schleiden in the 1840s, he was intent on showing that a blobby mass of "muco-granular substance" could be seen as a single coherent object—an object that was only in part characterized by its composition or substance, to use Lakoff and Johnson's terminology. When others misread von Mohl as arguing that a small amount of slimy substance was itself capable of driving changes in the cell, he reacted by emphasizing the primordial utricle's status as a bounded object, and tried to dissociate the object from its composition—i.e, the substance from which the primordial utricle and nucleus were made. Despite the fact that von Mohl had essentially given "protoplasm" its enduring biological and physiological meaning, and despite the fact that he had put an end to the so-called coagulation paradigm, he did not believe it was possible to divorce life from the form it took. Von Mohl would have rejected the idea that formless, unstructured protoplasm itself could be "living substance" or "the physical basis of life," as biologists would come to believe in the 1860s and 1870s. The equation of the phenomena of life with formless matter happened instead in other areas of biology with different aims and interests.

## Sarcode and Protoplasm

Von Mohl had given protoplasm six primary characteristics in "On the Circulation of the Cell Sap" in 1846: it was an unstructured slime, it contained granules, it was nitrogenous in a way that the wall or membrane were not, vacuoles appeared inside of it, it did not mix with other fluids, and, most importantly, it exhibited an irregular flow or circulation. Neither protoplasm theory nor the primordial utricle theory were originally conceived of as a replacement for the cell; the idea of the cell as both a container and as an individual unit of life was still crucial, even as Nägeli, Pringsheim, and von Mohl argued over the cell's functional anatomy. In the hands of other biologists in the 1850s and early-1860s, formless protoplasm was recognized as being the primary locus of the cell's activity, elevating protoplasm to the point where the cell was redefined around a frothing lump of mucus.

As histories on the subject have long noted, one of the protoplasm theory's origins can be traced to 1835, when the French protistologist Félix Dujardin (1801–1860) identified the *sarcode* in *Foraminifera*, a class of amoeboid protists that produce a shell or test (Fauré-Fremiet, 1935):

> I propose to name sarcode that which other observers have called living jelly (*gelée vivante*), this diaphanous, glutinous substance, insoluble in water, contracting into globular masses, attaching itself to dissecting-needles and allowing itself to be drawn out like mucus;

> lastly, occurring in all the lower animals interposed between the other elements of structure (Dujardin, 1835, p. 367).

Sarcode's texture was not the only characteristic that made it similar to von Mohl's protoplasm. The most important features of sarcode for Dujardin were its ability to generate, contract, and dilate vacuoles. It was also important to Dujardin that sarcode was distinguishable from other mucilages, as it had been for von Mohl: "Its properties are distinct from those substances with which it might have been confused because its insolubility in water distinguishes it from the albumins that coagulate in nitric acid, and at the same time its insolubility in potash distinguishes it from mucus, gelatin, etc." (p. 368).

Yet despite their many outward similarities, the connection between sarcode and protoplasm was not made until 1850—not only because von Mohl and Dujardin were studying very different organisms, but because they were pursuing materialistic strategies within relatively confined, sub-disciplinary contexts. In 1835 Dujardin was more narrowly concerned with showing that what he called "vacuoles" in amoebae were not their "stomachs," as his contemporary Christian Gottfried Ehrenberg (1795–1876) was claiming (Churchill, 1989). This was an issue of ranking and classification, and at stake for Dujardin and Ehrenberg was whether the visible structures in amoebae were more physiologically important than the unstructured slime surrounding them. Ehrenberg wanted to understand the *Infusionsthierchen* as complete microscopic animals, with distinct nervous, digestive, motor, and sexual organs. This would have allowed Ehrenberg to establish a firm division between plants and animals, and had the added benefit of giving even the smallest animalcules an irreducible complexity, foreclosing the possibility of spontaneous generation (Farley, 1977, pp. 55–56). In contrast, Dujardin saw them as far lower organisms, composed of little more than undifferentiated slime, arguing that these simple organisms were neither plant nor animal, but rather belonged in their own taxonomic category, *Infusoria*. Dujardin thus had a fairly specific ideological motivation to assign the physiological capacity to grow and control vacuoles to a very simple mucus.

Dujardin's sarcode concept was not unheard of outside of German and French protistology, and the term seems to have been introduced more broadly into German zoology by the Swiss-German anatomist Alexander Ecker (1816–1887) in 1846, in a short essay on contractility in hydras and other lower animals. Ecker believed that studying hydras might illuminate the relationship between infusoria and higher animals, and he found the sarcode concept useful because it could explain hydras' immense powers of contraction and movement in the absence of anything resembling fibrillar muscle tissue. Thus, Ecker was predisposed to think of unstructured substance as the site of physiological activity, and he was not alone: Ecker cited not only Dujardin, but also Carl Theodor von Siebold, Thomas Rymer-Jones, and the plant physiologist Franz Meyen as having reported a lack of structure in the lowest organisms—despite the fact that the word ''sarcode'' was not in wider use (Ecker, 1846, p. 5). Extrapolating from Dujardin's theory that sarcode was the mucous substance that controlled the contraction and dilation of vacuoles, Ecker argued that sarcode ought to be thought of as at least analogous to muscle tissue in higher animals. ''It thus appears suitable to me that the German designation, 'unformed contractile substance' [*ungeformte contractile Substanz*] describes the most essential properties of the same'' (p. 18). Contractility, long an essential concept in animal physiology as the most general type of organismal motion, was thus attached to sarcode.

These discussions about sarcode, the contractility of lower animals, and controversies over whether lower animals had stomachs were relatively distant from the botanists' arguments about the structure of cells and the growth of woody cell walls; the identification of these lower organisms with cells or the cell theory more broadly remained controversial even at the turn of the twentieth century (Richmond, 1989; Hertwig, 1902). It should thus not be surprising that the connections between the cell, sarcode and protoplasm were made within botany, where arguments about the structure of the cell were more vigorous, rather than in zoology or animal physiology, where contraction and movement were more important. When Ferdinand Cohn made the theoretical synthesis of sarcode and protoplasm in 1850, not only was he engaged in cell theories, but he was finishing his habilitation research on the classification of unicellular algae (Klemm, 2003, p. 37). Thus, when Cohn wrote that ''The *protoplasm* of the Botanists, and the contractile substance and *sarcode* of the Zoologists, if not identical, are at all events in the highest degree analogous formations'' (Cohn, 1850, p. 664, 1853, p. 535), he was in a unique position to survey the shifting landscape of cell and substance theories that had developed throughout the 1840s.

Cohn's made his analogy in a very long essay on ''The Natural History of Protococcus Pluviais,'' where he was trying to clarify a problem in the classification of unicellular algae, *Protococcus pluvialis* (now known as *Haematococcus pluvialis*).[14] Prior investigators had be-

[14] The English version of Cohn's substantial and difficult treatise was published as a significantly shortened summary, with several interjections by the English translator. Citations for both are provided.

lieved that there were ten different species of the organism; Cohn's primary goal in the essay was to show that this one species could show ten different forms, as the organism underwent a complicated cycle of alternation of generations.[15] Cohn believed that examining the anatomy and physiology of *Protococcus* could not only clarify its taxonomic identity, but also say something important about the essential difference between plants and animals. Because some of *Protococcus pluvialis*' forms were motile, Cohn argued that the traditional division of sessile plants and motile animals was too crude to provide a basis for classifying what he believed to be one species. Carefully following *Protococcus* across several seasons and in different freshwater environments, Cohn reported that the organism in question displayed different morphological features depending on its immediate physiological needs: it became green when its vegetative powers were needed and turned bright red when it was about to reproduce (1850, p. 611, 1853, p. 519); it became motile or sessile depending on light and temperature, and it could even have a stronger or more gelatinous cell membrane (1850, pp. 620–621, 1853, p. 520).

Having argued that all of these forms could belong to one species, Cohn then sought to dramatically redefine the boundary between the plant and animal kingdoms, and it was to this end that Cohn united Dujardin's sarcode and von Mohl's protoplasm (Klemm, 2003, pp. 119–120). Cohn began by reviewing the fundamental similarities between the two: both sarcode and protoplasm were recognized to possess motion, both could generate vacuoles, and they both had a similar appearance and texture, reacting similarly to stains and fixatives. Then, with great flourish, Cohn attacked the traditional basis for the division between plants and animals that had prevailed since Aristotle, writing: "*It is not the animal organism itself which is contractile, but only a single tissue in it*; all the rest, skin, bones, connective tissue, etc., are as rigid as the vegetable membrane, or at most elastic; in the higher animals only the

[15] Cohn argued that *Protococcus pluvialis* was a unicellular *plant* ("*eine einzellige Pflanze*"), with a motile form and a sessile form, and not merely a unicellular alga: Cohn argued that only plants went through a genuine alternation of generations, but others (including the English reviewer) did not accept this claim. Still others had suggested that certain stages of *P. pluvialis'* life cycle were multicellular, but Cohn wanted to demonstrate that an alternation of generations was possible with a strictly unicellular organism. The species Cohn wanted to unite into one included: *Protococcus coccoma, P. pulchur, P. minor, Gyges granulum, P. turgides,* "perhaps" *P. versatilis, Gyges bipartitus, P. dimidiatus,* some varieties of *Gonium, Pandorina Morum, Botryocystis Volvox,* and members of either *Uvella* or *Syncrypta, Microhaloa protogenita,* some form of *Euglenae, Astasia,* and *Bodo*. Cohn found this situation intolerable, "a state of complete anarchy in the domain of microscopic organisms" (1853, p. 560).

muscles are contractile, and only in the lowest, namely the Infusoria, is the entire body contractile'' (1850, p. 662, 1853, p. 533). Thus Cohn sought to redefine plants and animals on the basis of the location of motion and contraction within the organism, rather than the whole organism's capacity to move in general—and if the organism was very basic or unicellular, then its taxonomic status was based on the location of the protoplasm within the cell.

> Whence, the distinction between animals and plants, viewed in the above light, must be thus understood; that in the latter, the contractile substance, as the primordial utricle, is enclosed within a rigid, ligneous membrane, which permits only an internal motion, evidenced in the phenomena of circulation and rotation; while in the former it is not thus enclosed. The protoplasm, in the form of the primordial utricle, is, as it were, the animal element in the plant, in which it is *confined,* being *free* only in the Animal kingdom (1850, pp. 664–665, 1853, p. 535).

For Cohn, it was thus completely within reason to think of *Protococcus* as a motile plant, because its motion was generated by protoplasm from within a more-or-less rigid membrane. He made it clear that he took his understanding of protoplasm's contractile powers from Dujardin and Ecker (Cohn, 1850, pp. 662–663, 1853, pp. 533–534), but his notion of the primordial utricle and protoplasm's activity as enclosed within a non-active cell membrane is clearly traceable to von Mohl. To again borrow Lakoff and Johnson's terms, the critical aspects of Cohn's understanding of substance came largely from Ecker's definition of sarcode as ''unformed contractile substance.'' Cohn's understanding of the relationship between the cell as a container and the objects and substances it contained, on the other hand, relied on von Mohl's ideas from the 1840s: that the cell as a container was generated by the primordial utricle, and the motion of the contents of the cell was located in its protoplasm.

As Margot Klemm has noted (2003, pp. 120–127), such a synthesis between plant and animal kingdoms was a rare event in nineteenth century, and Cohn's contemporaries quickly recognized him as both an important new biological theorist and an expert in lower organisms. Cohn's protoplasm theory reinforced the idea that protoplasm was the truly vital part of the plant cell, and the cell was merely the container that confined it. Unicellular plants may not be able to reach out into the world with pseudopodia like an amoeba, but it was no longer unimaginable that they could swim towards light through ciliary protrusions running across their solid membranes. And yet, despite Cohn's impressive synthesis and his very thorough attempt to reshape both biology and natural history, in the next decade protoplasm theory became detached from Cohn's subtle analysis of the relationship between cellular anatomy and life's taxonomic divisions. Cohn had emphasized the role of the membrane in unicellular algae as what defined it as a plant, confining its moving protoplasm—but was it possible to believe that, using Cohn's own definition, an unbound organism could exist?

This was Max Schultze's premise (1861, p. 11), when he provocatively argued a decade after Cohn that, "A cell is a clump of protoplasm, in the interior of which lies a nucleus." Cohn had made protoplasm essential to all plant and animal life, but had noted that only in plants was protoplasm necessarily bounded in a rigid structure. If animals were still to be thought of as being composed of cells, and if the movement of their cells were not confined by a rigid membrane or wall, then the definition of the cell could no longer be predicated on its having a boundary, or being essentially a container. As Andrew Reynolds (2008) has shown, Schultze's redefinition of the cell as a unit of protoplasm gained traction among biologists not only because of its logic *vis-à-vis* cell theory, but also because of other ideological forces active within biology. Schultze's redefinition of the cell was premised on the amorphous nature of the amoebae that Schultze studied, and the amoeba in turn became "exemplary" of both cells and of organisms precisely for its lack of form. For Schultze and many others, amoebae were life at its simplest: amoebae, and by extension "formless" protoplasm came to be seen as exhibiting all of the necessary phenomena of life, while resting at the bottom of the evolutionary tree or chain of being (Reynolds, 2008, p. 317). By itself, Schultze argued, protoplasm was capable of changing shape, performing autonomous movement, nourishing itself, even merging with other materials in order to create the rest of a larger organism; anything else around or embedded in the protoplasm existed only in service to the protoplasm's unique activity (Schultze, 1861, p. 17). Stripped of form, the most basic cell—and therefore the most basic unit of life—became nothing more than a mass or unit of a substance endowed with basic vital functions.

## Conclusion: Protoplasm as the "Physical Basis of Life"

As Andrew Reynolds has argued, "It was through protoplasm's new status as the *Urstoff* of life that amoebae could be seen as exemplary of cells (and of life) in general" (2008, p. 317). But before Schultze could make his extraordinary argument that the amoeba was exemplary of both cells and life itself, a crucial, earlier step had to be taken: the concept of an *Urstoff* or the substance of life had to be redefined first. As I hope I have demonstrated through the early history of protoplasm, by denying the necessity of the cell membrane, Schultze had brought to completion an effort to shift biologists' attention to the material basis of the cell—a project that began with von Mohl's initial clarification of Schleiden's cell concept in 1844. The distillation of the cell down to a single substance would have been novel to Dujardin, patently incorrect to von Mohl, and beside the point for Cohn: in each of their own contexts, protoplasm was merely useful for fulfilling other agendas. Yet, as they sought to refine or create new ideas in taxonomy, anatomy, and physiology, Dujardin, von Mohl, and Cohn were all investing more and more importance in this slimy, viscous substance, one which had nearly been an afterthought in Schleiden's cell theory in 1838 and Schwann's in 1839.

The transformations of the cell into a formless substance, protoplasm, could be seen as a series of theoretical reductions of vital phenomena to smaller and smaller parts, belonging to a long history of scientific reductionism, attacks against vitalism, and a triumphal march toward mechanistic and materialist approaches to life. What this history of the cell and protoplasm shows instead, however, is that these kinds of major conceptual changes are often tied to other, more immediate, and often more diverse agendas. One of the advantages of Lakoff and Johnson's distinctions between ontological metaphors of container, object, and substance, is that it allows material concepts like *cell* and *protoplasm* speak to different purposes. There were specific contexts in which it might be useful to speak of organisms as being "made of protoplasm"—e.g, in making claims about the unity of life, or the material basis of vital phenomena—rather than explaining the activity or location of protoplasm inside the cell. By being attentive to these three, overlapping categories of material entities, we can see that the early and confusing history of the cell and protoplasm theories was not simply a matter of making the right observation, or finding the newest cellular structure. Rather, by closely scrutinizing the early history of the cell and protoplasm, I hope I have shown that biologists' fundamental notions about matter and materialism could change rapidly in response to local contexts, and that these changes had far reaching consequences in biological theory.

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