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ORIGINAL PAPER

Heredity as a problem. On Claude Bernard's failed attempts at resolution

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Abstract
Heredity has been dismissed as an insignificant object in Claude Bernard's physiology, and the topic is usually ignored by historians. Yet, thirty years ago, Jean Gayon demonstrated that Bernard did elaborate on the subject. The present paper aims at reassessing the issue of heredity in Claude Bernard's project of a "general physiology". My first claim is that Bernard's interest in heredity was linked to his ambitious goal of redefining general physiology in relation to morphology. In 1867, not only was morphology included within experimental physiology, but it also theoretically grounded physiological investigations. By 1878, morphology and physiology were considered as completely independent sciences, and only the latter was perceived as suitable to experimentation. My second claim is that this reversal reflected the existence of two opposite attitudes towards heredity. In the late 1860s, Bernard was convinced that heredity would soon be accessible to experimental manipulation and that new species would be produced in the laboratory exactly like organic chemistry succeeded to do for raw bodies. Ten years later, he ascertained that this was impossible. My third claim is that Bernard was epistemologically ill-equipped to address the issue of heredity. Bernard was strongly committed to a general reasoning scheme that acknowledged only three categories: *determining conditions*, *constant laws* and *phenomena*. This scheme was a key factor in his successes as a physiologist who was able to capture new mechanisms in living bodies. Nonetheless, it also prevented him from understanding how time and history could be endowed with a causal action that cannot be reduced to timeless parameters.

Keywords Claude Bernard · Heredity · Morphology · Species production · General physiology

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1 Introduction

Claude Bernard's foray into heredity is usually ignored by historians and commentators. Bernard was so overwhelmingly concerned with the elucidation of physiological functions in higher animals that it might initially seem that his project of a "general physiology" developed independently of any consideration or interest for the then increasingly floated notion of biological heredity (e.g. Schiller, 1967). Neither Mirko Grmek nor Frederic L. Holmes addressed the subject in their far-reaching and extensive work on Bernard's science. Only in 1991 did the first comprehensive attempt at doing this surface in the form of a book chapter written by Jean Gayon (1991).[1] Since then, only Gustavo Caponi has broached the issue in a 2018 book, albeit more incidentally than Gayon (Caponi, 2018).[2] The aim of the present paper is to reassess the question of heredity in Claude Bernard's work, in order to show how problematic this notion was to him, and how rewarding it can be to follow his theoretical journey from the mid-1860s to the late 1870s.

Gayon was right in emphasizing the fact that heredity was of interest to Bernard and that he started to elaborate on the notion. Caponi also makes a convincing case in showing how Bernard gave up on experimentally explaining the organization and morphology of living things. Yet, none of them seem to take into account that this neglected dimension of Bernard's theoretical work substantially evolved through time, to such an extent that the Bernard of 1878 was in almost complete opposition with the Bernard of 1867. In the present article, I aim to explore this surprising and unheralded reversal in the problematization of the stakes of heredity on both theoretical and epistemological levels. Heredity was a genuine problem for Bernard, first because it directly limited the possible extension of general physiology. In a sense, heredity marked the boundary of physiology. Thus, considering the definition of physiology required a minimal understanding of heredity. But heredity was also a problem to him on a more fundamental and epistemological level, of which he was absolutely unaware. It was a problem because this notion did not fit and even destabilized his standard way of reasoning, a scheme that I will explicitly reconstruct and that proved to be so fecund in his work as an experimental physiologist.

Clearly, Bernard's work on heredity was not prominent. He never performed any experimental work directly linked to heredity or extensively wrote on the subject. He turned to heredity only from 1865 onwards, i.e. after his most important work as an experimental physiologist and when, mostly because of his recurring health problems, he favored synthetic writings over experimental programs (Olmsted & Olmsted, 1952; Grmek, 1979, 1997). Overall, Bernard tackled the issue in no more than twenty pages, scattered in several texts from 1865 to his death in 1878.[3] Quantitatively, this does not amount to much given that he published around 30 volumes and

[1] This text was later reworked in an updated version that contained only minor changes (Gayon, 2013). In the following I will refer mostly to the 1991 text.

[2] I am unable to read Spanish, which means I only have indirect access to Caponi's book, mostly through discussions with colleagues — particularly Ghyslain Bolduc, whom I thank very much for his help.

[3] Some of these texts were published after his death. See for example Bernard, 1879, pp. XIV-XV.

250 research articles in the course of his career.[4] Another problem is that Bernard was so elusive on the issue, and wavered so much in his wording, that interpreting his take on it remains difficult. This is why the present paper includes substantial quotations, in order both to make my case and to show how problematic it is sometimes to get to a satisfying understanding.

This apparently minor output might also explain why this component of his theoretical work remained unexplored during so long. However, while he did not write much on heredity, what Bernard tried to formulate on a couple of occasions is crucial to a better understanding of both his theoretical endeavor and his epistemic engagement and shortcomings. In brief, examining Bernard's positioning on heredity is a useful tool to see how he constantly remodeled the contents of general physiology and to evidence that his profound commitment to his way of reasoning prevented him from formulating the problem of heredity in terms that could set the stage for a credible experimental program.

In the main, my argument relies on three interrelated theses. My first claim is that Bernard's interest in heredity was linked to his ambitious goal of redefining general physiology[5] in relation to morphology. In 1867, not only was morphology included within experimental physiology, but it also theoretically grounded physiological investigations. By 1878, morphology and physiology were considered as completely independent sciences, and only the latter was perceived as suitable to experimentation. My second claim is that this reversal reflected the existence of two opposite attitudes towards heredity. In the late 1860s, Bernard was convinced that heredity would soon be accessible to experimental manipulation and that new species would be produced in the laboratory exactly like organic chemistry succeeded to do for raw bodies. Ten years later, he ascertained that this was impossible. I then discuss several reasons, empirical and theoretical, that might explain this drastic change. My third claim is that Bernard was epistemologically ill-equipped to address the issue of heredity. From the beginning to the end, he was strongly committed to a general reasoning scheme that acknowledged only three categories: *determining conditions*, *constant laws* and *phenomena*. This scheme, which remained remarkably constant in Bernard's work, was a key factor in his successes as a physiologist who was able to capture new mechanisms in living bodies. Nonetheless, it also prevented him from understanding how time and history could be endowed with a causal action that cannot be reduced to timeless parameters. In short, Bernard was unable to conceive historical causation, and this is why heredity and evolution remained unsolvable problems to him.

[4] An exhaustive list of publications is provided in Grmek, 1967.

[5] In France, at the time, general physiology was often synonymous with biology (Grmek, 1979, pp. 14–15).

2 The 1867 research program: Heredity within experimental physiology

In preparation for the upcoming 1867 world exposition, the French minister of public instruction Victor Duruy ordered a series of reports in order to take stock of the situation of the French sciences and humanities (Barbin et al., 2009), especially compared with their German counterparts. As expected, Bernard was in charge of the study on French physiology (Grmek, 1979), and ended up producing a 237-page book, the *Report on the progress and development of general physiology in France* [*Rapport sur les progrès et la marche de la physiologie générale en France*] (thereafter *Report*). This was no standard report, but instead "a scientific autobiography and a finely shaped propaganda instrument" in order to promote experimental physiology as an autonomous science[6] (Coleman, 1985, p. 66). It outlooked a fairly speculative program on what physiology should become over the following decades in Bernard's view.[7] The book also featured Bernard's most detailed and explicit account of the concept of heredity (Gayon, 1991, p. 170). Before that, he had barely touched the subject on a couple of occasions in 1865, first in an article entitled "On progress in physiological sciences" (Bernard, 1865a) and then, incidentally, in his opus magnum, the *Introduction to the Study of the Experimental Method* Bernard 1865b, pp. 140–143). For the sake of simplicity, I mostly rely here on the *Report*, which offers the first assumed synthesis of Bernard's work on the subject.

Before exploring its theoretical contents, it should be stressed that this book, later reprinted under the title *On General Physiology*[8] (1872), is not easy to read because of its structure. The first two thirds of the book are classically composed of thematic sections. What is unusual is that the last third of the text, from pages 151 to 235, consists in no less than 238 endnotes, many of which give substantial indications about Bernard's approach to the issues at stake. In particular, several of these endnotes shed light on Bernard's conceptions of heredity and species formation. This convoluted and unorthodox presentation is certainly an obstacle that gets in the way of anyone seeking a clear view of Bernard's ideas. This has been true for historians and was also true for his contemporaries back in the nineteenth century.

2.1 "Conquering" new territories. Towards a redefinition of morphology and physiology

From the beginning to the end, the *Report* is a complex and subtle dissertation on the nature, definition and goals of general physiology, i.e. the science of "vital phenom-

[6] This aspect, i.e. Bernard-the-discipline-builder, is especially apparent in the manuscript notes and comments that preceded the *Report*. These notes were published in 1979 by Grmek (Bernard, 1979).

[7] For a general treatment, see Grmek, 1979 and Tirard, 2009. The very peculiar form of this text, very focused on Claude Bernard and rather poor in bibliography, certainly owes much to the fact that it was written during a long convalescent stay in Saint-Julien during the winter of 1866–1867, where Bernard had only very limited access to possible documentary resources (Olmsted & Olmsted, 1952, pp. 154–155).

[8] The 1872 text is almost the same as the 1867 version, except for pagination. At first Bernard aimed to produce a reworked version, but he gave up because of health issues.

ena". What is striking for a reader accustomed to Bernard's other classic texts, such as the *Introduction*, is how far Bernard went down a path that was absolutely not pursued either before or after. The context of the book (a series of reports ordered by the French government) might have encouraged him to make risky and speculative choices. We will see in Sect. 2.3. that Bernard was also stimulated by developments in other fields, especially the nascent domain of organic chemistry. Nonetheless, the fact remains that Bernard extensively redefined general physiology in the *Report* by proposing to ground physiology in the process of embryology and thereby in morphogenesis. In 1867, he argued that the "organogenetic or organotrophic[9] movement", i.e. the process responsible for embryological development and the progressive formation of morphology, was no less than the "physiological law per excellence" (Bernard, 1867, p. 137).[10]

The final section of the book ("Phenomena of organization and organic connections") and the general conclusion contain the most part of Bernard's discussion on the subject. His general reasoning was as follows: (a) physiological phenomena are the consequences of biological organization; (b) given that organization is produced during development according to specific "organogenic" laws, (c) these morphological laws are thus the ultimate basis of all physiology.

After a number of paragraphs, where again and again, in various formulations, he repeats that "morphological laws […] govern all the particularities of […] internal organization" and, as such, constitute the "special laws of physiology" (Bernard, 1867, pp. 127–128), Bernard eventually concludes that "physiology is a distinct, autonomous and independent science, which has its own point of view and its special problem: the research of the laws of organization" (Bernard, 1867, p. 229). It is thus undisputable that, around 1867, not only did Bernard make room for morphology within experimental physiology, but he also more fundamentally *based* physiology on the scientific knowledge of "organogenic" laws, i.e. on morphology.

Why such an effort to incorporate morphology within general physiology? The answer is quite straightforward. The experimental impetus was then at its peak: to him, morphology was next territory to conquer. Bernard's standard distinction between two forms of science is well known (Paul, 1985, pp. 98–103; Loison, 2013). At odds with the old practice of descriptive natural history, he constantly pushed experimental science, which he argued was the only way to control phenomena and to understand the causality involved. Bernard always had harsh words for observation and description; only experimentation paved the way beyond empiricism and towards a genuine scientific knowledge. The scope and boundaries of physiology were open to discussion, but in his intent to "*conquer* living nature" (Bernard, 1867, p. 132, my emphasis), the more physiology developed, the more it had to include a

[9] In this text, Bernard used two terms "organogenic" (sometimes "organogenetic") [*organogénique*] and "organotrophic" [*organotrophique*], which he related to "law(s)", "phenomena" and even "force(s)". It is not certain that these two terms express a genuine conceptual distinction, in any case Bernard did not explain himself clearly anywhere. It might be the case that "organogenic" referred to a more fundamental and abstract law, which regulates morphology, and that "organotrophic" designated the protoplasmic processes which make possible the actualization of this law, but this interpretation is not certain. For the sake of simplicity, I do not make any distinction in the article.

[10] All translations from French are mine.

wide range of phenomena, especially morphological and embryological ones. At that time, it would have been an unacceptable failure not to be able to experimentally engage with morphology (Bernard, 1867, p. 110):

> In the phenomena of organic renovation, no more than in others, the physiologist cannot limit himself to contemplating living nature; he must search for the laws of nutrition and evolution,[11] in order to modify and regulate the phenomena of these functions.

The *Report* is moved by a spirit of "conquest"[12] that made such an ambition necessary, as Bernard makes clear in the conclusion (Bernard, 1867, p. 132):

> Physics and chemistry have conquered mineral nature, and every day we see this brilliant conquest extending further. Physiology must conquer living nature; that is its role, that will be its power.

2.2 Heredity as a nutritive and manipulable process

For this to be the case, heredity must be accessible to experimentation. This is the main reason why Bernard elaborated on heredity in the *Report*: it was the key condition that would allow physiology to incorporate morphology. Bernard developed his argument on the matter in the fourth section, entitled "Phenomena of nutrition, generation and evolution". He uses "heredity" and "organic tradition" interchangeably to refer to the phenomenon under discussion. Heredity was responsible for the transmission of what he called a "creative idea" [*idée créatrice*], i.e. the abstract pattern that would be reified into the adult organization (Bernard, 1867, p. 110).[13]

Unsurprisingly, Bernard gave a "nutritive" – i.e. metabolic – account of heredity (Gayon, 1991, pp. 170–171) even though he remained rather cryptic on how precisely he understood the phenomenon. On several occasions, he proposed that heredity could be artificially altered in changing environmental conditions, especially regarding nutrition. He went remarkably far into that direction, to such an extent that he conceived a genuine mechanism of inheritance of acquired characters that relied

[11] "Evolution" is a very common word in Bernard's writings, but he almost always used it in its traditional and old-fashioned meaning, i.e. as a synonymous of development, and only very rarely in reference to species transformation. Being unaware of this is conducive to major misinterpretations (see for example Poupa, 1967 and Schiller, 1967). On the "non-reception" of Darwinism and contemporary evolutionary theories by Bernard, see Bolduc's and Angleraux's joint contribution in the present special issue. See also Roll-Hansen, 1976.

[12] The word itself is repeatedly and purposively used by Bernard: p. 2, p. 132, pp. 138–139, p. 142.

[13] The concept of "creative idea" is especially complex in Bernard's work and would deserve a paper of its own (for a stimulating treatment, see Caponi, 2018). The concept first appears in the *Introduction*, but he does not expand on it then. He alternatively used the phrases "creative idea" or "guiding idea" [*idée directrice*] to designate an entity somewhere in between physics and metaphysics, that "is manifested by the organization" but cannot be seen as an active material cause producing the organization Bernard 1865b, p. 143).

on his concept of an internal milieu, able to transmit nutritive modifications to the reproductive cells (Bernard, 1867, p. 229):

> The experimenter can act on animals in the same way as on plants. When one modifies the nutrition of a living being, one necessarily modifies the constitution of the internal environment and, consequently, the reaction of this environment on the histological elements. These histological elements then behave absolutely like infusoria which are subjected to the gradual influence of a new environment. Now, one can thus modify not only the fixed elements in the formed and adult tissues, but one can also act on the plasmatic elements, which are constantly renewed and which can bring modifications in the ovarian products or in the generative secretions; it is thus possible to understand how these modifications can be transmitted to the descendants of the beings which one subjected to these nutritive modifications.

Bernard's confidence was also based on several experimental results that suggested new forms could be produced in the laboratory. In the 1860s, what would be called *Entwicklungsmechanik* in the end of the 19th century was only nascent,[14] and Bernard had only a few positive results at his disposal. He first referred to Camille Dareste's and Isidore Geoffroy Saint-Hilaire's stimulating work. Dareste took up the research program of Geoffroy Saint-Hilaire in trying to improve what was then called "experimental teratogenesis".[15] Embryos of various species, most frequently birds (and especially chicken), were submitted to unusual conditions and subsequent malformations were carefully observed and listed. By the 1860s, he had already produced and named several standard malformations.[16] Yet, it should be emphasized that in 1867 already, Bernard was not completely convinced by this work because it was more about pathology than physiology, and most of the time it ended in the individual's premature death (Bernard, 1867, p. 112).

More promising to Bernard were the results obtained by Charles Naudin on plants. Naudin was one of the main botanists of the time with an interest in plant hybridization. His work was widely known and has sometimes been credited for having anticipated some of Mendel's findings.[17] Ever since, it has remained a standard used to ascertain Mendel's contributions to the field (Marza & Cerchez, 1967, pp. 391–400; Mayr, 1982, pp. 648–649; Müller-Wille & Rheinberger, 2012, pp. 130–132). Naudin was primarily concerned with the possible perpetuity of new forms. In May 1867, he published new results that supported the indefinite hereditary transmissions of monstrosities (Naudin, 1867). It was those recent results that interested Bernard, which shows that he actively sought out documentation on the subject. Bernard was especially pleased to see that new hereditary forms could be produced in only one genera-

[14] For a recent synthesis on *Entwicklungsmechanik*, see Bolduc, 2021.

[15] For a general treatment, see Fischer, 1973.

[16] On the basis of his extensive experimental work, Dareste published a 600-page synthesis in 1877 entitled *Research on the Production of Monstrosities or Eexperimental Teratogenics*.

[17] For instance by William Bateson himself (Bateson, 1902, p. 30).

tion [“*apparaître tout à coup*”] (Bernard, 1867, p. 112): such a possibility seemed to endow experimentation with a significant power.[18]

2.3 Producing new forms. The challenge of organic chemistry

Bernard’s ultimate goal, in manipulating heredity, was to produce new species and new forms of life, as he made crystal clear on several occasions (Bernard, 1867, pp. 110–111, p. 113, pp. 128–129, p. 230, p. 234). At that time, he was remarkably confident: “To put it briefly, I think that we will be able to scientifically produce new organized species” (Bernard, 1867, p. 113). Note that in the *Report*, as Gayon rightly pointed out (Gayon, 2013, p. 120), he never paid attention to how evolution had occurred on Earth,[19] but only on the human ability to produce new species in a scientific and controlled way. For him, this new ambition was closely related to a strong epistemological commitment: “We can only really know what we create. We will therefore only really know living beings when we can modify them as we wish and remake them in some way” (Bernard, 1867, p. 230). In his will to dominate and conquer nature, Bernard came to think like an engineer: it is only when you can rebuild a system from scratch that you have a true knowledge of it. In order to “dominate” living nature, to “act” on phenomena (Bernard, 1867, p. 142), he saw the ability to produce new living things as necessary.

Such a strong stance is understandable in light of Bernard’s own trajectory. From his experimental training in the early 1840s under the guidance of Magendie, Bernard developed an inclination towards the idea of controlling vital phenomena, which led him to formulate the experimental axiom of “determinism” within physiology in the 1850s. His idea of producing new forms of life in the laboratory might accordingly be seen as the peak of a momentum that had started decades before.

Yet, more extrinsic and contextual factors seem to have strongly encouraged him to pursue this particular path. Repeatedly, Bernard mentioned chemistry as an inspiring example that should be followed: “the physiologist will be able, like the chemist, to create new organisms; there is, in fact, no more impossibility in the creation of a living being than in that of a raw body” (Bernard, 1867, p. 234). Even if Bernard never precisely told the reader what kind of chemistry he had in mind, there is little doubt that he thought in the first place of organic chemistry,[20] an emerging discipline that had experienced a rapid boom in the mid-nineteenth century.

Like physiology, organic chemistry benefited from the ongoing competition between Germany and France. In Paris, during the 1860s, one of the main figures in the field was Marcellin Berthelot (1827–1907). Berthelot, like Ernest Renan, was rather close to Bernard and their academic careers ran parallel at the Collège de France. He and Bernard even briefly collaborated in the mid-1850s, when Bernard succeeded in

[18] Apart from Geoffroy Saint-Hilaire, Dareste and Naudin, Bernard also made a brief mention of a recent work on the development of aphids: Balbiani & Signoret, 1867. Note that all these authors cited each other’s work.

[19] See Bolduc & Angleraux in the present special issue.

[20] Here, I owe special thanks to Annie Petit, who suggested with great insight that organic chemistry and especially Berthelot’s work might have stimulated Bernard.

isolating the glycogenic substance (Olmsted & Olmsted, 1952, pp. 98–99). In 1864, a few years before Bernard's *Report*, Berthelot published a 600-page book entitled *Lessons on General Methods of Synthesis in Organic Chemistry*. As the title makes clear, the book was devoted to new techniques enabling the controlled production of a wide range of molecules, most of which do not even exist in nature. The idea of controlling nature recurs in the book, and Berthelot emphasized the "creative power" of this artificial chemistry (Berthelot, 1864, pp. 18–19). One long passage is especially illuminating in order to better understand Bernard's own positioning. In the last four pages (Berthelot, 1864, pp. 521–524), Berthelot expanded on the epistemology of organic chemistry. His argument can be summed up as follows:

(1) Classifications are necessary but not sufficient.
(2) Chemistry goes beyond classifications ("natural history") because it is based on the knowledge of "generative causes". Only chemistry can produce all the possible "species" and "transform then at will into each other".
(3) Such a generative ability "gives man a power over the world unknown to the other natural sciences". This makes chemistry a special science, with a "distinctive feature".
(4) This allows organic chemistry to play a central role for industry in terms of applications. Chemistry is also transformative for human society.

All of the above ideas are reiterated in Bernard's 1867*Report*. In a sense, Bernard took up the challenge of organic chemistry: he could not stand not to be at the forefront. If organic chemistry, as an experimental science, was already able to create new species, physiology had to do the same not to be dismissed as natural history. Heredity was the "generative cause" of organisms, and as such had to be manipulable. Even regarding possible applications for society, Bernard was not ready to give up: to "conquer nature", to "extract its secrets", all this made sense only as long as one could "use it to the benefit of mankind" (Bernard, 1867, p. 142).

3 The final synthesis of 1878: heredity outside of experimental physiology

Bernard's final book *Lessons on the Phenomena of Life Common to Animals and Plants* marks a complete U-turn from the *Report*. The 400-page synthesis recapitulated the main ideas that Bernard had developed in his classes at the Museum of Natural History over the preceding years (Olmsted & Olmsted, 1952). Bernard died on 10 February 1878 during the process of proofreading the book (Bernard, 1878, p., which can accordingly be considered as a reliable approximation of his late-life positions on key questions such as the relationship between morphology, physiology and heredity.

The 1878 *Lessons* did not have the same status as the 1867 *Report*. In the *Report*, Bernard was purposefully speculative and was looking forward to the future of experimental physiology. In the *Lessons*, Bernard was taking stock of a decade of research in order to again redefine general physiology, i.e. the science devoted to "the phenomena of life common to animals and plants". This is why the 1878 synthesis is much more grounded in a wide range of findings which extend far beyond the scope of experimental physiology. All things considered, with the benefit of hindsight (Bernard showed remarkable erudition here) it seemed to him that the 1867 research program was most likely a dead-end.

3.1 On the complete independence of morphology and physiology

The *Lessons* are structured in nine main chapters (called "Leçons"), the ninth offering a general summary of the preceding eight. It is mostly in the eighth chapter, untitled "Organized synthesis, Morphology", that Bernard redefined the relationship between physiology and morphology. In a series of unambiguous and clear-cut formulations scattered across the entire chapter, Bernard argued, in contradiction to his 1867 views, that morphology and physiology study two independent set of phenomena and that the morphological ones are outside the reach of the experimental method (Bernard, 1878, p. 335, my emphasis):[21]

> We want to make clear this essential point that morphology must be *completely distinguished* from the physiological activity of the organs. Morphological laws are laws which we have called dormant [*dormantes*] or expectant [*expectantes*], which do not prevent or produce any vital phenomenon, which do not act and on which one cannot act.

What is a "dormant" law? In order to understand what Bernard meant, it is necessary to go back to the *Report*. In 1867, Bernard had already made a distinction between two kinds of scientific laws, which he then called "effective" [*effectives*] and "contemplative" [*contemplatives*] (Bernard, 1867, p. 36). This distinction was based on the ability of the scientist to modify the phenomena under study. When phenomena were not experimentally controlled, the laws that governed them were called contemplative, like in natural history. In contrast, when phenomena could be manipulated in the laboratory, then laws became effective, because knowledge of them allowed action, a key step for Bernard. A dormant law was equivalent to a contemplative one: the experimenter can do nothing with it.

This is why "the study of morphological laws constitutes the domain of zoology and botanic" (Bernard, 1878, p. 341). Bernard strongly emphasized that, "today [i.e. in 1878], we distinguish vital phenomenology from vital morphology" (Bernard, 1878, p. 342). Morphology could only be "contemplated" whereas vital phenomenology could be "directed" [*diriger*]." (Bernard, 1878, p. 342).

This complete redefinition required giving up on the prospect of experimentally producing new forms of life, a concern that had been a pivotal aspect of the 1867 research program. Species alterations that were empirically obtained were indeed only "fleeting" modifications that did not hold (Bernard, 1878, p. 342). By 1878, Bernard saw no future to such a program (Bernard, 1878, pp. 332–333):

[21] This Bernardian dichotomy was already illuminatingly evidenced by Nils Roll-Hansen in 1976 (Roll-Hansen, 1976, pp. 81–83).

One will not change the rabbit's egg and, making it forget the primitive impulse and its previous states, one will not make it come out a dog or another mammal. The limits between which morphology is fixed, if they are not absolute (there is nothing absolute in the living being), are at least very narrow. If one tries to move a being away from its path, as is done by the creation of artificial varieties, one will be constantly obliged to keep it on the new path. Varieties tend to constantly return to their starting point.

3.2 How to conceive heredity then?

In the process, what happened to heredity? This is a particularly tricky question given that Bernard never performed any research on the subject and that he used fluctuant and equivocal formulations in the *Lessons* and in other related publications. In contrast to 1867, he was then more elusive and touched the notion only in a couple of instances. Another difficulty is that Bernard, in the late 1870s, did not clearly distinguish between heredity properly speaking and what he sometimes called the "vital force", i.e. something close to the morphological laws that ruled organisms. It is very difficult to assess whether heredity was itself that vital force or if it was only the intergenerational channel allowing the transmission of the vital force, whatever this vital force was to him. Depending on the passage under consideration, both interpretations could be supported.

Such a lack of clarity can already be seen on closer inspection of the language he used. In the late 1870s, the terms "heredity" or "organic tradition" were almost absent, with only two occurrences of heredity and none of organic tradition in the *Lessons*. Bernard favored a variety of other words, like "memory", "souvenir" or "previous state". Given that Bernard then saw morphology as a fixed and extrinsic constraint to any living organism, a solution for him would had been to change the epistemological status of heredity. Instead of conceptualizing it as a nutritive and material process, thus within the domain of experimentation, he could have transferred it from the "determining conditions" to the "constant laws" category, i.e. from physics to metaphysics.[22]

This interpretation seems to be supported by a short passage at the beginning of the second Lesson, where Bernard makes a clear-cut distinction between laws and conditions:

"Life is a conflict. Its manifestations result from the intervention of two factors:

1° The pre-established laws which regulate the phenomena in their succession, their concert, their harmony;

2° The determined physico-chemical conditions which are necessary to the appearance of the phenomena.

Regarding the laws, we do not act on them, they are the result of what we can call the previous state; they derive by atavism from the organisms that the living being maintains and repeats, and they can thus be dated back to the very origin of living

[22] Strangely enough, whereas Gayon did not see any difference between 1867 and 1878, he explained that in 1867 Bernard developed a nutritive concept of heredity and that in 1878 he thought of heredity as a "metaphysical conception" (Gayon, 1991, p. 180).

beings. This is why some philosophers and physiologists have seen fit to claim that life is only a memory; I myself have written that the germ seems to retain the memory of the organism from which it proceeds." (Bernard, 1878, p. 66, my emphasis).

Yet the meaning of this passage is largely open to discussion. Strictly speaking, Bernard did not equate heredity with laws; what he might suggest here is that heredity is responsible for the transmission of organic laws. This would be why he used the terms "result" and "derive". It is in another book, the *Lessons in Operative Physiology*, published in early 1879, almost a year after Bernard's death, that one can find the passage that most supports the interpretation that Bernard understood heredity as a metaphysical entity. These lines come from the end of the introductive section, probably written in late 1877 or early 1878, shortly before Bernard's death, at a time when he was also proofreading the 1878 *Lessons*. A brief paragraph is especially significant regarding the issue at stake (Bernard, 1879, p. XIV):

One cannot escape the idea that this unknown atavistic, vital force is the hidden cause of all the phenomena of life. But this is a cause of a metaphysical order which has no action by itself.

If the "atavistic force" was heredity, then it seems logical to assume that Bernard was, in the late 1870s, thinking of heredity as a metaphysical entity. Nonetheless, in my opinion, even if the question remains open, this is not the best interpretation available. It remains an option that makes sense, but, in the remainder of this article, I will favor an alternative reading. It is my view that, even during the 1872–1878 period, Bernard still thought of heredity in material terms, as a nutritive process. To put it shortly (I will come back to this issue in Sect. 4.2), heredity was no longer experimentally modifiable not because it had become a metaphysical entity, but more simply because the determining action of present-day parameters was too weak a force in comparison to the cumulative work of thousands of generations. In other places in the *Lessons*, Bernard seems to lean into that direction. This might be why he was responsive to Haeckel's speculative hypothesis of the "perigenesis of the plastidules" (Bernard, 1878, p. 195). This is also consistent with his idea of a strict material continuity between generations of organisms and their protoplasmic contents (Bernard, 1878, p. 208):

An important remark needs to be made here. We are not witnessing the direct synthesis of primitive protoplasm, nor any other primitive synthesis in the living organism. We are only witnessing the development, the growth of living matter; but some kind of vital leaven must always have been the starting point. At the beginning of the development of any living being, there is a pre-existing protoplasm which comes from the parents and sits in the egg. This protoplasma grows, multiplies and generates all the protoplasmas of the organism. In a word, just as the life of the new being is only the continuation of the life of the beings that preceded it, so its protoplasma is only the extension of the protoplasma of its ancestors. It is always the same protoplasm, it is always the same being.

Finally, at the end of the *Lessons*, Bernard still explicitly stated, when he renounced to the possibility of producing new forms of life, that heredity was the "essential *factor*" of morphology and that "one can consider heredity as an *experimental condition*" (Bernard, 1878, p. 342, my emphasis), which seems to suggest that he saw it more as a determining factor than as a law in itself. In sum, even if Bernard was especially cryptic, it is possible to assume that he was still making a distinction between heredity (as a determining condition) and morphology (as a – now "contemplative" – law). Were my reading to be accurate, what changed between 1867 and 1878 was not the epistemological status of heredity: in both cases, heredity was a material property of the living and not an abstract law. Why, then, did Bernard turn his back on his 1867 research program?

3.3 Why such a drastic reconfiguration?

The answer to this question could not be simple and straightforward, and posits a variety of causes that pertain to two intertwined levels: empirical and theoretical. Most importantly, this reconfiguration, drastic as it was, should not be interpreted only as a renouncement[23]. True, Bernard had to give up his experimental program on morphology, but in the process, what he got in exchange was also a purer type of physiology that in the end could focus only on vital phenomenology without any need to consider the morphological side. Bernard seemed perfectly happy with that; his tone was never one of disappointment. On the contrary, the *Lessons* embraced this new rebuilding of general physiology.

3.3.1 Empirical reasons

The first set of reasons directly concern the results obtained during the 1870s regarding the possibility to experimentally alter the course of embryological development. Although he did not cite any specific publications, Bernard found no empirical results that might support his 1867 program. To a large degree, development is strongly determined and any experimental action would usually destroy the organism (Bernard, 1878, p. 333):

> The egg already is in the adult state, and its formation takes place in such determined conditions that one cannot change beings without killing them. It is therefore not surprising that in such circumstances the species and types perpetuate and preserve themselves, and that experimental intervention cannot be carried beyond certain limits.

Another set of results was positive and crucially contributed to shaping his new theoretical positioning. Bernard was particularly interested in the possible discovery of new living things whose organization would be so simple that they would be deprived of any morphological feature. Here, Bernard specifically referred to a variety of findings, including in the first place the famous *Bathybius haeckelii* (Bernard, 1878, p. 189) — whose existence Bernard regarded as proven (Bernard, 1878, p.

[23] Nevertheless, in the last years of his life, we find at least one written trace where Bernard showed a form of nostalgia towards his former project. Thus, in a letter to his close friend, "Mme" Raffalovich, he wrote in August 1876: "Could nature be taught a new lesson and would its memory reproduce it in a series of new beings? I think so. It is still my old idea, to remake beings not by spontaneous generation, as one dreamed, but by the repetition of organic phenomena of which nature would keep the secret" (Bernard, 1950, pp. 108–109).

190), Haeckel's moneres (Bernard, 1878, p. 297), and Balbiani's work on amoebae (Bernard, 1878, p. 298). These forms of life were so simple that they were non-cellular; to Bernard, they showed the phenomenon of life "naked" (Bernard, 1878, p. 297), in its most fundamental essence. In accordance with Huxley, whose work had recently been translated into French (Huxley, 1877)[24], Bernard thought of the protoplasma as the "physical basis of life" (Bernard, 1878, p. 192).

3.3.2 Theoretical reasons

If the *Report* can be characterized as a reconceptualization of general physiology in relation to an engineering perspective stimulated by the success of organic chemistry, the *Lessons* reflect a different impetus. In the main, it can be said that at the end of his life, Bernard was redefining physiology in the light of the new protoplasmic theory[25]. This makes the *Lessons* an in-depth reflection on the many implications of the protoplasmic theory for the main categories that had structured Bernard's thought for years, namely "organic destruction", "organic creation", "irritability", "sensitivity" and, lastly, "morphology". Here, I am focusing only on morphology.

First, it should be stressed that the protoplasmic theory of life very much echoed Bernard's own obsessions. It gave legitimacy to a processual and reductionist account of life that was tailor-made for Bernard's nutritive perspective. Life was only about the "universal properties of living matter, apart from the specific molds [*moules*] in which it has entered" (Bernard, 1878, p. 126). This is the aspect that is crucial in order to understand Bernard's last shift: the protoplasma was thought as a "substratum without form" (Bernard, 1878, p. 184), i.e. as a substance whose properties did not require morphological features. In other words, life "starts before the cell", "the cell is already a complex organism" (Bernard, 1878, p. 187). In the *Lessons*, and once again in contrast with the *Report*, Bernard distances himself from standard cell theory by promoting a strong version of the protoplasmic theory.

The protoplasmic theory allowed Bernard to draw a clear line between life and morphology: unlike in 1867, morphology was no longer a necessary attribute of the living. Life was only about a specific albuminoid substance: "The morphological notion thus disappears here to make way for the notion of physicochemical constitution of the living matter" (Bernard, 1878, p. 192). This "disappearance" of morphology was a blessing for Bernard, because, finally, he could get rid of morphology on scientific basis and ground general physiology only on the nutritive dynamics of the protoplasma. Morphology became only a secondary "complication", an "epiphenomenon" (Bernard, 1878, p. 203, emphasis in the original):

The fundamental phenomenon of organic creation consists in the formation of this substance, in the *chemical synthesis* by which this matter is constituted by means of the materials of the external world. As for the *morphological synthesis* which shapes

[24] During the second half of the nineteenth century, many important foreign books and authors were translated into French. Thus, even if French biologists were not fluent in English or German, they had at that time a direct knowledge of some key works thanks to this huge translation effort.

[25] On the history of the protoplasmic theory, Geison, 1969 is still informative. For a modern treatment, see especially Liu, 2017.

this protoplasm, it is, so to speak, an epiphenomenon, a consecutive fact, a degree in this indefinite series of differentiations which lead to the most complex forms; in a word, a complication of the essential phenomenon.

4 Epistemic lessons. What we can learn about Bernard's reasoning

That Bernard changed his mind so dramatically regarding the relationship between morphology and physiology is in itself a gain in historical knowledge. Nonetheless, his intellectual trajectory on the subject of heredity is illuminating also because it allows to highlight a central pattern in Bernard's reasoning, which dated back at least to the early 1850s and remained remarkably constant until the end of his life. Recognizing this scheme and its centrality in turn sheds light on why Bernard was ill-equipped to address the issue of heredity. Evolution, history and heredity were indeed categories that did not fit into his thinking, which was geared towards allowing experimental action in the laboratory.

4.1 On Bernard's central reasoning scheme: an overview

At least from the early 1850s, and probably during most, if not all, his scientific life, Bernard based his reasoning on a general scheme that acknowledged only three types of epistemological entities: (1) *material and determining conditions*, (2) *pre-established laws* and (3) *phenomena*. Here, I am only focusing on the scheme's epistemic structure and I will not get into its historical genesis in Bernard's early writings. What is certain is that it was already well entrenched back in the 1850s (Bernard, 1856, pp. 129–130).

For Bernard, experimentation was only about manipulating the *determining conditions* in order to produce or prevent *phenomena*. The *pre-established laws* were always thought as an extrinsic constraint, and as impossible to alter. The scientist can know them, he might use them, but he cannot modify them. Only the *determining conditions* are materially alterable. Hence his distinction between two forms of sciences and two types of laws. When the *determining conditions* are modifiable, then Bernard uses the term "efficient laws", as we have seen (Sect. 3.1). In contrast, when, for various reasons (technical limitations, dimensional issues, etc.), they are not under control, then they are "contemplative laws", because they cannot be used for action.

Importantly, all these three categories were tightly linked by what Bernard always emphasized as the first axiom of experimental science, the "principle of determinism" (Gayon, 2009). If certain *conditions* are set, a given *phenomenon* will necessarily occur according to a *pre-established law*. Faith in determinism was central to Bernard; it was his main weapon against all forms of vitalism that endowed living matter with inner spontaneity.

In sum, Bernard's central reasoning scheme could be diagramed as follows (Fig. 1):

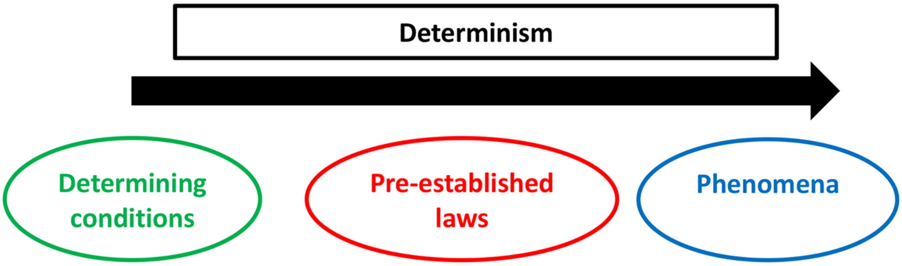

Fig. 1 The general epistemic structure of Bernard's central reasoning (see the text for explanations)

4.2 From a thought experiment to an experimental goal and backwards. On "cosmic conditions" and "forms of life"

This scheme was unsurprisingly at the root of his 1867 experimental program on morphology. As detailed in Sect. 2.3, Bernard's ambition then was, as in organic chemistry, to produce new forms of life, i.e. new living beings. But what was meant exactly by "new"? At first sight, and this was for example Gayon's reading (Gayon, 1991, pp. 171–172), it could seem that Bernard was trying to launch a genuine program of "experimental transformism" which set the stage for French Neo-Lamarckism.[26] Such an account, in my view, misses a crucial aspect: Bernard was unable to think of historical causation as a creative process (see the next section), being stuck in his reasoning scheme from the outset.

In 1867, he thought that heredity could be dominated by new environmental (nutritive) conditions. Both heredity and the nutritive treatment were thought as *determining conditions*, that, according to morphological *laws*, would produce more or less new forms of life (*phenomena*). Thus, these "new" forms were new in a very restricted sense: only inasmuch as their determinism had not yet been realized. This is how he expanded on the issue in the *Report*. Special attention has to be paid first on the comparison with chemistry and, second, on the argument's epistemic structure (Bernard, 1867, p. 234):

"We have said somewhere that the physiologist will be able, like the chemist, to create new organisms; it is in fact, no more impossible to create a living being than it is to create a raw body. But only the physiologist will have to start from organized matter in order to imprint on it, through special conditions, physiological modifications and new phenomenal directions.

All the creations of the chemist and the physicist are in reality only exhibitions. They do not create the physical-chemical forces; they only provide them with conditions to manifest themselves in forms which are new to man, but which existed in a latent state in the eternal laws of nature. In the same way, the physiologist, in giving birth to new living beings, cannot imagine that he has created the vital force: what he has done, like the chemists and physicists, is only to discover particular conditions

[26] The difficult issue of the relationship between Bernard's 1867 program and the subsequent French neo-Lamarckism will be dealt with in a forthcoming work. On French neo-Lamarckism, see Loison, 2011 and Loison & Herring, 2017.

in which the vital germ will be able to take new directions and develop organisms hitherto unknown."

For once, Bernard is especially clear in his formulation. The "new" forms of life were already potentially contained in the morphological laws; what the scientist might do could only be producing the determining conditions that would dominate heredity and allow their "exhibition" (as in crystallography for instance). Crucially, the issue of time is completely absent: either the new conditions are stronger than the ancient ones (heredity) and then new forms are produced (1867); either hereditary conditions are almost indelible, and then morphology and species are fixed once for all (1878). Such a positioning is consistent with the view, which I have endorsed in Sect. 3.2, that heredity remained a determining condition, but one too strong to be experimentally altered (Bernard, 1878, pp. 332):

The morphological law does not have its reason for being at each moment: it translates a hereditary or previous influence of which we could not erase the influence, a primitive action which is related to a general cosmic whole that we are impotent to reach.

Remarkably, then, Bernard remained faithful to his reasoning scheme in the *Lessons*. If in 1867 he thought in terms of an actual research program that should rapidly be launched in the laboratory, in 1878, the exact same reasoning had a different epistemological status: it was no longer a feasible program, but a mere thought experiment (Bernard, 1878, pp. 332–333):

In another cosmic balance, the vital morphology would be different. I think, in a word, that there exists virtually in nature an infinite number of living forms of which we are not aware. These living forms would be dormant or expectant, as it were; they would appear as soon as their conditions of existence came to be manifested, and, once realized, they would perpetuate themselves as much as their conditions of existence and succession would perpetuate themselves.

In 1878, this "other cosmic balance" could not be achieved in the laboratory. The new forms were forced to be "dormant", because they will never be produced. This theoretical positioning, which is a major shift in comparison to the view endorsed in 1867, is indeed identical to Bernard's thought in 1865, before he was asked to reflect on the future of general physiology. In an article published in August 1865, Bernard gave another instance of his reasoning scheme applied to species formation and, in contrast to his writings of 1867 but in perfect accordance with his final account of 1878, he proposed a speculative thought experiment that could absolutely not be turned into a tractable research program Bernard 1865a, p. 655, my emphasis):

"As a consequence of the above, we see that all phenomena, of whatever order, exist virtually in the immutable laws of nature, and that they only manifest themselves when their conditions of existence are realized. The bodies and beings on the surface of our earth express the harmonious relationship of the cosmic conditions of our planet and atmosphere with the beings and phenomena whose existence they permit. Other cosmic conditions would necessarily bring about the appearance of another world in which all the phenomena which would meet their conditions of existence would manifest themselves, and in which all those which could not develop there would disappear; but whatever the infinite varieties of phenomena that we conceive on earth, placing ourselves in *thought* in all the cosmic conditions that our imagination can produce, we are always compelled to admit that all this will happen according to the laws of physics, chemistry and physiology, which have existed without our knowledge for all eternity, and that out of all that would happen there would be nothing created either in force or in matter, that there would only be the production of different relations, and consequently the creation of new beings and phenomena."

4.3 Time, causation and historicity. Heredity as an unsolvable problem

Thus, as expected, Bernard's central reasoning scheme remained unaltered from 1865 to 1878. What changed in the process was only his faith in our human abilities to overcome heredity, i.e. past determining conditions. As suggested in the previous section, such a way of thinking was an insurmountable obstacle to conceiving historical causation – i.e. cumulative change and contingency – and conceptualizing heredity. In my view, because Bernard was so completely stuck in this epistemic rut, he was unable to properly understand the stakes of species evolution and heredity.

In the standard meaning of the concept, which was shared for example by Darwin but also by the French Neo-Lamarckians that were active from the 1880s onwards, heredity was a cumulative force able to produce or at least stabilize a truly new biological organization, i.e. organisms that are the transient consequence of the historicity of the evolutionary process (whether the main factor was natural selection or Lamarckian inheritance). In other words, evolutionary causation was embedded within time. Time was (and still is today) a necessary component of the causal explanation.

Bernard's thinking was timeless. This was true for heredity and evolution, as I have argued, but this was a so deeply entrenched component of his work that it was also the case when he elaborated on another form of history — namely, the history of science. Annie Petit has masterfully showed that Bernard thought of past figures like Plato, Aristotle, or even Magendie, not as historical individuals, but as "symbols", i.e. timeless essences that work, in her words, "for all time" (Petit, 1987, p. 210). According to Petit, in Bernard's version of history of science, "time becomes timelessness" (Petit, 1987, p. 210) because he saw historical events "as forming repetitive patterns" (Petit, 1987, p. 211). This also very much applies to his 1867 ambition to produce new forms of life: they would have been produced almost instantly, as soon as the determining conditions were realized, as in organic chemistry or crystallography. This is why his short-lived program, despite appearances, never belonged to experimental transformism.

Ultimately, heredity remained equally embarrassing to Bernard in 1867 and in 1878 alike because his timeless reasoning scheme, which proved to be so fecund within standard physiology during decades, also made him unable not only to find a tractable solution to the problem, but more fundamentally to even truly grasp it.

5 Conclusion

This paper has aimed at providing a detailed and problematized picture of Bernard's changing position on heredity from the mid-1860s to the end of his life. Since Bernard was especially difficult to understand, which paved the way to what I see as incorrect interpretations (Gayon, 1991), this conclusion sticks to a summary of the main findings:

(1) First, the issue of heredity was important to Bernard because it was closely connected to the matter of what an experimenter can do in the laboratory with the morphological features of a living being. In 1867, speculatively, Bernard proposed that morphology would be accessible to experimentation, i.e. that heredity, as a set of determining conditions, could be modified using appropriate "nutritive" treatments. At that time, his view was that general physiology should be grounded on morphology. In 1878, he drew a firm line between physiology and morphology, downgrading the latter to the status of a "contemplative science".

(2) While Bernard drastically changed his mind with respect to the human ability to alter heredity, in my reading, this reversal did not cause a change of epistemic status for heredity. Heredity, as a material and nutritive process, remained in the category of determining conditions, even if in some cryptic formulations, Bernard sometimes appears to think of heredity as a metaphysical entity. For various reasons, which I have tried to make explicit, Bernard, in the late 1870s, was far less confident in the possibility to overcome heredity in artificial configurations. But this was just a factual judgment, not an impossibility in law.

(3) This interpretation is supported by the fact that what I have called Bernard's *central reasoning scheme* remained remarkably unaltered during the shift. This scheme was at the basis of his numerous successes within experimental physiology and acknowledged only three types of epistemic categories: determining conditions, pre-established laws and phenomena. In a strongly deterministic understanding, the control of determining conditions would allow, in accordance to universal laws, to produce or suppress any given phenomenon. This is exactly what Bernard tried to do in the laboratory during his entire career. Unsurprisingly, this is how he framed the issue of heredity (determining conditions), morphological laws and new forms of life (phenomena). In 1878, still, Bernard explained that in other cosmic conditions, other forms of life would be produced according to eternal and pre-established morphological laws. What changed in the process was only the feasibility of experiments. In 1867, they were thought as a tractable and promising research program. In 1878, they were only thought experiments, as Bernard already briefly suggested in a 1865 article.

(4) Finally, as I have suggested in the final section, heredity was a problem for Bernard on a more fundamental level in that he was especially ill-equipped to conceptualize the issue at stake. Whereas his reasoning scheme was tailor-made for standard physiology, his conception of determining parameters as timeless proved insurmountable obstacle to approaching historical causation and gradual change. This is why, even in 1867, what Bernard had in mind was not a genuine project of experimental transformism. Bernard's experimental practice was throughout driven by a philosophy of action. The mastery of a phenomenon required not only the inte-

gral control of the determining parameters, but even more fundamentally its *immediate* control. All his experimental activity testifies to this, a frenetic activity that led to his physical exhaustion. Hence his inability to think about biological phenomena in the long term, first and foremost that of heredity. Strictly speaking, Bernard was not even able to understand what the problem of biological heredity was or could be.

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