

## Darwin and Inheritance: The Influence of Prosper Lucas

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**Abstract.** An important historical relation that has hardly been addressed is the influence of Prosper Lucas's *Treatise on Natural Inheritance* on the development of Charles Darwin's concepts related to inheritance. In this article we trace this historical connection. Darwin read Lucas's *Treatise* in 1856. His reading coincided with many changes concerning his prior ideas on the transmission and expression of characters. We consider that this reading led him to propose a group of principles regarding prepotency, hereditary diseases, morbid tendencies and atavism; following Lucas, he called these principles: *laws of inheritance*.

**Keywords:** Darwin, Prosper Lucas, inheritance, variation, atavism

### Introduction

Darwin's ideas on inheritance were elaborated from diverse sources.<sup>1</sup> The influence on Darwin of horticulturists, hybridologists,<sup>2</sup> breeders,<sup>3</sup> and English physicians,<sup>4</sup> as well as German and French naturalists,<sup>5</sup> has been amply discussed. However, an important historical aspect that has scarcely been investigated is the relation between Darwin's ideas and the

<sup>1</sup> For example, Andrew Knight, William Yarrel, Carl von Gärtner, James Prichard, Henry Holland, Giorgius Gallesio, Joseph G. Kölreuter, among others.

<sup>2</sup> See Wells, 1971.

<sup>3</sup> See Bartley, 1992.

<sup>4</sup> See López-Beltrán, 1992.

<sup>5</sup> See Weinstein, 1977.

concepts of Prosper Lucas (1805–1885), a renowned French physician.<sup>6</sup> Darwin reserved a special place for him when he referred to matters of inheritance, and he recognized the *Treatise on Natural Inheritance* as the fullest and the best upon subject.<sup>7</sup>

With the purpose of establishing which ideas this work elicited in Darwin, this paper compares various concepts and terms that are found in the *Treatise on Natural Inheritance* (Vol. 1, 1847, and Vol. 2, 1850) and in Darwin's texts written before and after he read the *Treatise* in September, 1856. This comparative analysis indicates that Darwin's reading of Lucas's work triggered a re-elaboration of his ideas on character transmission and expression in crossings, and led him to propose, after reading Lucas, *laws of inheritance* that explain regularities and irregularities in the transmission and expression of prepotency, constitutional vigour, hereditary diseases and latent characters determining reversions. These ideas are analyzed and discussed fundamentally in *The Variation of Animals and Plants under Domestication*, 1868 (herewith referred to as *Variation*). The development of Darwin's ideas on heredity can be conceived in two periods: (1) from 1837 to 1856 when he started to analyze regularities and irregularities in the transmission of characters, and (2) after 1856 when he articulated these ideas on laws of inheritance explaining constancy and variation in the transmission and expression of characters.

Darwin's ideas on inheritance have been analyzed by many historians of Darwinism. For example Olby (1966), Mayr (1982) and Bowler (1989) have studied Darwin's hypothesis of pangenesis as a scheme of transmission ideas. Hodge (1985, 1989),<sup>8</sup> Winther (2000)<sup>9</sup> and Endersby

<sup>6</sup> This relation has vaguely been shown by different historians, for instance, Churchill, 1987; López-Beltrán, 1992, 2004a; Mellon, 1996; and Bulmer, 1999.

<sup>7</sup> See Darwin, p. 12; 1868, Vol. 2, p. 1.

<sup>8</sup> Hodge states that between 1837 and 1838 Darwin elaborated the concepts related to generation that determined the development of his theories during the next four decades (Hodge, 1985, p. 218).

<sup>9</sup> Winther suggests that Darwin considers the origin of variation and its transmission (inheritance) as two separate facts, variation as the production and existence of intergenerational differences and inheritance as the production and existence of intergenerational similarities. However, he affirms that Darwin eventually conceived these facts sometimes as opposites and other times as part of the same process of development. He states that for Darwin the origin of variation is a consequence of the laws of development and reproduction. This interpretation coincides with Peter Bowler's conclusion: "Darwin never gave up the belief that variations are caused when external conditions disturb the reproductive system" (Bowler 1984, p. 161).

(2003) have analyzed the pangenesis ideas in a theory-of-generation program framework. Other authors who have proposed important ideas of Darwin upon inheritance are Gayon (1998, 2000)<sup>10</sup> and Churchill (1987), and this last one is the only writer who has suggested how Lucas may have influenced Darwin. Churchill identifies in Darwin's work two fundamental interests: in the origin of modifications and in organic stasis. The first is expressed as variation and the last as inheritance, both of which explain genealogical patterns. Churchill considers that these ideas are similar to Lucas's concepts. He states that in *Variation*, Darwin follows Lucas's line of reasoning but to a greater depth by proposing pangenesis, a physiological explanation of the process of transmission. In this paper we shall expand this landscape about this dynamic scheme of stasis and modification.

### Prosper Lucas

Prosper Lucas was born in Saint-Brieux in 1805 and died in Mennecy in 1885 at the age of 77 years old. He was a physician, a psychiatrist, an alienist and a French republican, brother of the entomologist Pierre-Hippolyte Lucas. Prosper Lucas studied medicine in Paris and received his doctorate in 1833 at the age of 25 with the thesis *On Contagious Imitation, or the Sympathetic Propagation of Neurosis and Monomanies*.<sup>11</sup> He worked as a psychiatrist in asylums of Bicêtre and Sainte-Anne. In 1879 he was secretary of the Société Médico-Psychologique.<sup>12</sup>

Lucas wrote various texts. His most influential work was his *Philosophical and Physiological Treatise on Natural Inheritance in Healthy and Ill Conditions of the Nervous System, with the Methodical Application of*

<sup>10</sup> Jean Gayon affirms that, even though Darwin did not have a complete theory of inheritance when he proposed descent with modification, his explanation of modification by variation and natural selection is based on the idea of inheritance, mainly the genealogy concept. Gayon points out that Darwin used this term to understand how the force of inheritance explains likeness between ancestors and descendants, the sudden appearance of capricious characters, and the connections between variation and inheritance (1998, 2000).

<sup>11</sup> Lucas, P. *De l'imitation Contagieuse, ou De la Propagation Sympathique des Névroses et des Monomanies*, thesis presented in the Faculty of Medicine at the University of Paris, the 28th of August of 1833 to obtain a doctorate degree in medicine.

<sup>12</sup> Some society minutes of that year can be found in the Bibliothèque Interuniversitaire de Médecine: <http://www.bium.univ-paris5.fr/>.

*the Laws of Procreation to the General Treatment of Affection of which it is Principle. Work on Matters and Consideration of Reports. Primordial laws, Theories of Generation, Determinant Causes of Sexuality, Acquired Modifications of Original Nature of Beings, and Distinct Forms of Neuropathy and Mental Insanity*<sup>13</sup> (herewith referred to as *Treatise on Natural Inheritance*). He also published other books that had great impact, such as *On the Freedom of Teaching*<sup>14</sup> (1831), and *On Matters Included in the Complex Expression: Animal Magnetism* (1837).<sup>15</sup>

The importance and influence of Lucas's work is shown in the concepts utilized by the most important physicians, naturalists and intellectuals of the second half of the nineteenth century, such as Darwin, Galton, Morel and Ribot.<sup>16</sup>

Diverse historians have been interested in Lucas's work recently, for example, Churchill (1987), Balan (1989) and López-Beltrán (1992, 2004a, b). Vedder (2005), in his analysis upon Lucas influences in Emile Zola, briefly summarizes the schematic structure of Lucas's inheritance classification.<sup>17</sup> Others, such as Gayon and Zalle (1998), Mellon (1996)<sup>18</sup>, Bulmer (1999) and Gayon (2006) have considered his work fundamental in the development of ideas on inheritance. Furthermore, Di Gregorio (1990) in the comments on Darwin's *Marginalia* refers to Darwin's reading of Lucas's *Treatise on Natural Inheritance*.

<sup>13</sup> *Traité Philosophique et Physiologique de L'hérédité Naturelle dans les Etats de Santé et de Maladie du Système Nerveux, avec L'application Méthodique des Lois de la Procréation au Traitement Général des Affections dont elle est le Principe. Ouvrage ou la Question est Considérée dans ses Rapports avec. Les Lois Primordiales, les Théories de la Génération, les Causes Déterminantes de la Sexualité, les Modifications Acquises de la Nature Originelle Des Eêtres, et les Diverses Formes de Névropathie et D'aliénation Mentale*. Lucas' work has not been reedited and can be found in few sites. The two volumes of *De L'Hérédité Naturelle* can be consulted in <http://gallica.bnf.fr/>.

<sup>14</sup> Lucas Prosper, *De la Liberté D'enseignement*, 1831.

<sup>15</sup> *Des Questions Renfermées Sous L'expression Complexe: Magnétisme Animal*, 1837. In: *Recherche dans les Periodiques: Annales D'hygiène Publique et de Médecine Légale. – 1837. – série 1, no. 18*, <http://www.bium.univ-paris5.fr/>.

<sup>16</sup> López-Beltrán (1992) has suggested that Lucas' concepts determined how the idea of biological inheritance would be conceived in France and England (López-Beltrán 1992, p. 169).

<sup>17</sup> Vedder (2005). In Müller-Wille and Rheinberger, 2005, pp. 153–166.

<sup>18</sup> Mellon has translated some pages of the second volume of Lucas' text (pp. 756–798). His intention has been to show the importance of Lucas' work as a key background for ideas on mental illness and inheritance.

### Darwin's First Ideas and Expressions on the Transmission of Characters

Darwin's first expressions on the transmission of traits can be found in his first *Transmutation Notebooks* of 1837.<sup>19</sup> In these notebooks he uses the expression *the hereditary* to refer to inheritance or transmission of peculiarities. However, when he refers to phenomena related to the transmission of characters he employs the terms *atavism*,<sup>20</sup> *hereditary nature* (or *hereditary structure*)<sup>21</sup> and *transmission of contingent modifications*.<sup>22</sup>

During this period of his life he also wrote brief notes on monstrosities and inherited illnesses fixed in human lineages. He considered that these cases result from spontaneous or innate modifications that remain constant in future generations.<sup>23</sup> However, he did not have a clear, useful proposal for understanding character transmission, a proposal constructed for diverse fields: animal crossings,<sup>24</sup> plant hybridization and medical cases. To investigate the rules on how traits are inherited Darwin elaborated a questionnaire<sup>25</sup> and sent it to animal breeders, horticulturists and hybridologists. The survey was distributed between April and May of 1839. Darwin wanted to know how characters behave after a cross: if they are uniform, stable, if offspring look like their father or mother, what happens with characters in future generations, and for how many generations are characters conserved in pure races. In general, Darwin was interested in knowing if rules in the transmission of characters could be established.

During the beginnings of the 1840s he wrote his first *Essays* on variations of plants and animals in a domestic state that would eventually be included in *On the Origin of Species*. In the first part of his *Essay* of 1842 he talks about variation under domestication and in a state of nature as well as selection and variation in instincts and

<sup>19</sup> In his *Transmutation Notebooks* Darwin tried to understand the inheritance of characters that lead to transmutations by analyzing three aspects of how traits are transmitted: similarities between family members, the transmission of inherited illnesses, and patterns of expression of hybrids of different species or varieties. See Barrett et al., 1987, pp. 182, 205, 239–240, 308–309, 333–334, 336, 388, 426, 507, 342, 520, 529–530.

<sup>20</sup> Barret et al., 1987, pp. 58–59.

<sup>21</sup> Barret et al., 1987, p. 225.

<sup>22</sup> Barret et al., 1987, p. 118.

<sup>23</sup> Barret et al., 1987, p. 119.

<sup>24</sup> One of the few works that analyze the history of hybridization in animals is the text of Gienapp (1970).

<sup>25</sup> Darwin, 1839, Questions about the Breeding of Animals.

other mental attributes. Furthermore, he reflects on reversion and the transmission of peculiarities.<sup>26</sup>

Darwin rewrote this manuscript in a more extended version where he delves into the same matters and adds other topics such as the transmission and degree of retention of similarities in hybrids of different species or races.<sup>27</sup> One of the most important sources of his concepts on hybrids and the limits of races and species were Kölreuter's ideas, such as the infertility between species and diverse causes of sterility of hybrids,<sup>28</sup> and the idea that differences in the nature of species result from their constitutional peculiarities.<sup>29</sup>

When Darwin talks about the careful selection of peculiarities and the selection of varieties he refers to the writings of horticulturists and farmers such as James Anderson, Benjamin B. Coke, John Sebright and Thomas A. Knight.<sup>30</sup> From these works he recognized two important points, first that, most breeders of plants and animals are firmly convinced that benefits are derived from an occasional cross, not with another race, but with another family of the same race, and he recognized too, by contrast, the injurious consequences derived from long-continued close interbreeding in the same family.<sup>31</sup>

In the text of 1842 when he analyzes the effect of crossings in characters he did not use the terms *constitutional vigour*, *morbid tendency* or *prepotency*, which he will employ after reading Lucas's work. Furthermore, before 1844 Darwin referred to the transmission of persistent characters not with the terms inheritance or hereditary but with expressions such as "parents beget child like themselves" or "like beget like," common to breeders and cultivators.<sup>32</sup> Due to his experience with

<sup>26</sup> Darwin, 1909, pp. 2–3, 13, 52.

<sup>27</sup> Darwin, 1909, p. 108.

<sup>28</sup> Darwin, 1909, pp. 97, 98, 104, 232.

<sup>29</sup> Darwin, 1909, p. 98.

<sup>30</sup> Darwin, 1909, pp. 65–70.

<sup>31</sup> Darwin, 1909, p. 70.

<sup>32</sup> Darwin used the terms "inheritance" after 1844. In his *Essay* of 1844 he employs five times the term *inheritance*. See in Darwin, 1909, pp. 60, 80, 114, 116, 247. In the eighteenth century, the term inheritance had been utilized in another sense, for instance: Bligh, Michael (1764) *The Church of God his Peculiar Portion and Inheritance, Opened and Improved: in a Discourse on Deuteronomy XXXII*. 9. London. Benjamin Cracknell (1794), *The Christian's views and Reflections During his Last Illness. With his Anticipations of the Glorious Inheritance and Society in the Heavenly World*. London, and Watkins, Charles (1798), *An Enquiry into the Question, Whether the Brother of the Paternal Grand-mother shall Succeed to the Inheritance of the Son, in Preference to the Brother of the Paternal Great-grand-mother?* London. These books can be seen in <http://galenet.galegroup.com/servlet/ECCO>

breeders and cultivators he knew that they were interested in constant characters that could be modified to some degree; domestic races were the best proof of a dual principle of modification and constancy.

Darwin's preoccupations with the transmission of characters were motivated by his preoccupations with a solid argumentation for his evolutionary explanations; and this was the reason why it turned out to be fundamental to understand the phenomenology regarding the causes of variation and rules for the transmission of characters.

A fundamental point in this analysis is that in this first period Darwin conceived inheritance and variation as inevitable effects of the process of reproduction.<sup>33</sup> This idea was taken to an extreme when he affirmed that interbreeding could be a conspicuous source of new races.<sup>34</sup> The effect of crossing on the characters of descendants was overestimated by Darwin in this period. However, his ideas changed after 1856. This is shown in his analysis of the genealogical relations of pigeons when in *On the Origin of Species*, 1859, he proposed that characters present in distant ancestors tend to reappear in hybrids.<sup>35</sup> In this new consideration, hybridization is interpreted as a process which maintains the constancy of characters in species; thus, the interpretation of the effects of interbreeding is different. The return of characters, apparently a great difficulty, was interpreted by Darwin as evidence of common origin.

### **Prosper Lucas: *Treatise on Natural Inheritance***

After many years of research concerning matters of inheritance Lucas published his *Treatise on Natural Inheritance*. This work is a mixture of philosophy and physiology that has, as a fundamental purpose, to reflect on the primordial laws (general and primary laws) of generation, sexuality, acquired modifications and mental illness in humans. The *Treatise on Natural Inheritance* was published in two volumes, the first one in 1847 and the second one in 1850. It was awarded a prize by the French Academy of Science and became a common reference for psychiatrists.<sup>36</sup>

<sup>33</sup> Darwin, 1909, pp. 1–2, 63.

<sup>34</sup> Darwin, 1909, pp. 63–64.

<sup>35</sup> Darwin, 1872, *The Origin*, pp. 23–27.

<sup>36</sup> In texts of history of psychiatry, criminality or public health references to the *Treatise on Natural Inheritance* are almost obligatory. For example, see Nouzeilles, 1997; Mucchielli, 2000; and Burbridge, 2001.

The first volume of this text proposes diverse laws, which have been established by God, that govern the origin of any new individual. Lucas states that in the transition between creation and procreation two general laws of life operate: the first one, the law of invention brings forth the law of variation (*innéité*),<sup>37</sup> and the second one, the law of imitation (*imitation*) gives way to the law of inheritance (*hérédité*), which represents the memory of life in the natural process of generation. Both intervene simultaneously in the composition of beings.<sup>38</sup> Lucas discussed the nature of the laws of variation and inheritance in the first volume and in the second volume their consequences.

In the first book of the first volume Lucas states that the law of *innéité*<sup>39</sup> generates variability in species, that is, individual differences.<sup>40</sup> He accepts Prichard's concept of an origin of human races all derived from a single original race. Nevertheless, he considers that the law of variation affects only in a slight degree specific characters; those characters that define a species impose limits to variation.<sup>41</sup> Therefore, according to this naturalist this force does not produce modifications that generate new species. Lucas assumes an antitransformist perspective rejecting those ideas defended by Robinet, Lamarck and Geoffroy Saint-Hilaire.<sup>42</sup>

Lucas conceives that the laws of inheritance and variation can explain internal differences, (of constitution), and external ones (of temperament).<sup>43</sup> That is, even though he only studied behavioral characteristics, he sustained that his laws can be extended and are valid for visible and invisible characters. According to this naturalist all characters are ruled by both the law of inheritance and the law of variation.

<sup>37</sup> López-Beltrán (1992, 2004a) translated *innéité* as *variational*, *variation* and as *source of variation* and Mellon as *mutation*. In this essay we use the term as *variation*, because we think that the law of *innéité* generates individual variations.

<sup>38</sup> Lucas, 1847, Vol. 1, p. 96.

<sup>39</sup> Lucas, 1847, Vol. 1, pp. 97–190.

<sup>40</sup> Lucas, 1847, Vol. 1, p. 98.

<sup>41</sup> Lucas, 1847, Vol. 1, p. 132.

<sup>42</sup> Lucas, 1847, Vol. 1, p. 99.

<sup>43</sup> Lucas, 1847, Vol. 1, p. 104. Lucas conceives *constitution* as the group of physiological characteristics that determine a healthy condition (or disease) and *temperament* as the group of behavioural characteristics that determine mental instability, such as criminal conduct or alcoholism. Nowadays, we consider that all the characteristics included by Lucas in the terms *constitution* and *temperament* form part of the phenotype.



For Lucas what occurs during conception and development is a multifactorial compromise of many influences especially two fundamental ones. Resemblance is promoted by inheritance, differences by variation. Even though specific characters can only be mildly modified, all characters can be influenced by inheritance or variation. If inheritance prevails, likeness occurs. If variation triumphs characters adopt a modified condition.<sup>44</sup> Modifications are generated spontaneously during development, that is, not in a predetermined manner. Therefore, the law of variation and the law of inheritance operate as opposite forces.<sup>45</sup>

In the second book of the first volume Lucas deliberates extensively on inheritance.<sup>46</sup> With this law he explains constancy in specific types, which he considers immutable because neither the law of variation, nor plasticity in form, nor dynamism in forms of existence, nor the influence of time, nor various generations, can modify them. He does not admit the influence of the environment in modifications of specific characters. The force of inheritance maintains constant characters that define a species and transmits them to the next generation.<sup>47</sup> This explains similarities between ancestors and descendants. Apart from defining specific characters, according to Lucas, laws of inheritance can explain sensorial characters, as well as affective, mental, vocal and motor traits.<sup>48</sup>

To reinforce his ideas on the laws of inheritance Lucas resorted to available information in the literature on different family cases gathered during centuries, concerning inheritance of a criminal tendency,<sup>49</sup> of an alcoholic tendency and a great list of illnesses, such as blindness and mental disease. Lucas considered that a complete knowledge of human genealogy would help us to understand, not only the nature of our behavioral tendencies, but also how morphological characters appear and, therefore, the laws of inheritance.

In the second volume (1850), Lucas states that three types of modifications can originate individual differences: spontaneous, congenital

<sup>44</sup> See López-Beltrán, 1992, p. 166. However, Lucas' terms *hérédité* and *innéité* cannot be translated as genotype and phenotype as has been stated by this historian. Certainly inheritance is a law of imitation that is somewhat analogous to genotype. Nevertheless, according to Lucas similarities generated by the law of inheritance and differences promoted by the law of variation are included in the phenotype.

<sup>45</sup> Lucas, 1847, Vol. 1, p. 134.

<sup>46</sup> Lucas, 1847, Vol. 1, pp. 191–606.

<sup>47</sup> Lucas, 1847, Vol. 1, p. 191.

<sup>48</sup> Lucas, 1847, Vol. 1, p. 605.

<sup>49</sup> Lucas, 1847, Vol. 1, p. 480.

and direct modifications. The latter ones are related to environmental influences.<sup>50</sup> He accepts Prichard's idea that considers that the environment can modify the constitution of an individual but he denied that these transformations are transmitted and, for that reason, that they generate new species. Therefore, he reinforces his opposition to Lamarck's idea of inheritance of acquired characteristics.<sup>51</sup>

Lucas also deliberated against various beliefs of his time. For example, he denies *maternal impression*, that is, the acquisition of characteristics in an embryo due to the mother's imagination. He also rejects that mental illnesses are caused by moral failures, that is, sins, or by physical laws.

Lucas examined in the second volume of his treatise how studying genealogical relations can give us information on the laws of inheritance. He considers that the analysis of kinship relations indicates four types of laws of inheritance (*loi d'hérédité*).<sup>52</sup> These laws are of direct inheritance (*l'hérédité directe*), indirect inheritance (*l'hérédité indirecte*), inheritance of regression (*l'hérédité en retour*) and inheritance of influences (*l'hérédité d'influence*).<sup>53</sup>

In the first type, direct inheritance, the paternal or maternal characteristics are expressed in the descendants, in sons or daughters. It indicates a higher influence of the father or mother in inheritance. Likeness between progenitors and offspring take place in their body characters, mental or emotional capacities, health or longevity takes place.<sup>54</sup>

The second type of inheritance, indirect inheritance, occurs when an individual has similar attributes not with his parents but with other family members such as aunts or uncles in their corporal traits, character, mental capacities, monstrosities or illnesses.<sup>55</sup>

In the third manifestation of inheritance, inheritance of regression or atavism and latency, a characteristic disappears and reappears in the same lineage. It indicates the transmission of a predisposition latent in ancestors (parents, grandparents or great-grandparents) that is expressed in a new generation by atavism.<sup>56</sup> Lucas considers that all characters, corporal, moral or morbid, have a predisposition to manifest their

<sup>50</sup> Lucas, 1850, Vol. 2, pp. 455–458.

<sup>51</sup> Lucas, 1850, Vol. 2, pp. 457–458.

<sup>52</sup> Lucas, 1850, Vol. 2, pp. 2–28.

<sup>53</sup> Lucas, 1850, Vol. 2, pp. 1–2.

<sup>54</sup> Lucas, 1850, Vol. 2, pp. 2–29.

<sup>55</sup> Lucas, 1850, Vol. 2, pp. 29–39.

<sup>56</sup> Lucas, 1850, Vol. 2, pp. 39–53.

discontinuity and reappearance. That is, no character escapes the law of atavism.<sup>57</sup>

The last type of inheritance,<sup>58</sup> the inheritance of influences, manifests itself when unusual kinds of fertilizations occur due to strange influences, such as in parthenogenesis and in various forms of crossings between individuals of close or distant lineages, that is, between different species or varieties. Lucas considers that a fabulous example of this type of inheritance takes place in asexual reproduction present in inferior species like greenflies.<sup>59</sup> This researcher conceives that this case can be explained by females that are fertilized in a specific moment but reproduce later on during various events generating organisms that present the same characteristics than those exhibited in the first generation. He recognizes that asexual reproduction does not occur in superior organisms. However, he affirms that “the crossing of different species of animals allows us to verify this curious phenomena,”<sup>60</sup> that is, the inheritance of influences.

These four types of inheritance conceived as different ways of how characters manifest themselves were employed to explain three types of transmission of human mental diseases: direct transmission, crossed transmission, transmission of reversion, and a type of action of inheritance, that is, indirect action.<sup>61</sup>

In the first type of transmission of mental diseases a direct transmission from father to son or mother to daughter occurs. The second one takes place when a father transmits an illness to his daughter or a mother to a son. Both types are considered as cases of direct inheritance.

The best known type of transmission of mental diseases is, according to Lucas, the third one, an inheritance of regression. To sustain it this physician shows various examples of grandchildren that exhibited similar mental diseases than their grandparents not present in their parents. To explain this case he suggests a seminal transmission of these illnesses that manifest themselves only in some individuals. In this type of transmission of mental diseases, an apparent break in the flow of the transmission of characters in lineages occurs, which is explained by Lucas with the ideas of latency and regression.

The indirect action of inheritance is not explained in detail by Lucas. However, he considers it a particular type of regression, as reappearance

<sup>57</sup> Lucas, 1850, Vol. 2, pp. 46–47.

<sup>58</sup> Lucas, 1850, Vol. 2, pp. 53–65.

<sup>59</sup> *ibid.*

<sup>60</sup> Lucas, 1850, Vol. 2, p. 58.

<sup>61</sup> Lucas, 1850, Vol. 2, pp. 760–763.

in collateral relatives of a trait, in this case, a mental illness, present in ancestors. He affirms that in mental diseases that manifest themselves in isolated members of a family it is difficult to differentiate from a *morbid spontaneous heredity* and the indirect action of inheritance.

Lucas employed the term morbid spontaneous heredity to refer to illnesses or morphological alterations (that we identify nowadays as a result of chromosome mutations generated during development). He considered albinism, which appears in diverse groups of animals in isolated cases not present in ancestors, as a case of this type of inheritance.

With the purpose of determining the causes of inheritance Lucas synthesizes and evaluates an immense amount of registered facts and notes elaborated over many decades by physicians and naturalists. He presents a great amount of confusing and contradictory evidence and proposes a rational model that tries to make sense of it. Lucas states that only by conceiving two opposite forces, one conservationist (*hérédité*) and the other one that generates variation (*innéité*), acting in different moments and combinations, can we understand, on the one hand, similarities between relatives, and, on the other, the surprising cases of whimsical reappearances or loss of characteristics between different generations of a family.<sup>62</sup>

Lucas's work was influential not by the answers he gave to problems on hereditary transmission, but due to the paths he indicated to those that followed, including Darwin. In this paper we pay attention to the Lucas – Darwin relationship, but the analysis of Lucas's influence can be extended in the English context, since others authors read Lucas's works under different perspectives, for instance, Lewes (1856), and Galton (1865); others could had received Lucas's influence through Darwin's work.<sup>63</sup> Lucas's ideas had a strong vitalist influence because he considered God as the primary cause of all primordial laws. However, empirical research was of great importance in his studies on the transmission of mental diseases as is shown in his analysis of their patterns of

<sup>62</sup> López-Beltrán (1992, 2004a, b) has considered this way of explaining inheritance as a new theoretical framework. This author shows how during many centuries the transmission of human characteristics from one generation to the other had been conceived only as a metaphor of legal inheritance. Lopez-Beltrán states that this led to the coinment of a substantive, *inheritance*. He names this process as the *reification of inheritance* and states that it originated the creation of a new domain that we now denominate biological inheritance (López-Beltrán, 2004, p. 83).

<sup>63</sup> See for instance Marianne Sommer, 2005. "How Cultural Is Heritage? Humanity's Black Sheep from Charles Darwin to Jack London." In Müller-Wille and Hans-Jörg Rheinberger, 2005. pp. 233–254.

appearances in individuals of a same lineage. Even though his reflections tend towards philosophical matters, he was convinced that the study of the inheritance of mental illnesses should be confined to medicine.

We can distinguish various concepts of inheritance in Lucas's works, such as latency of transmission, prepotency, and recurrence of atavism. These concepts and the systematization of Lucas influenced Darwin as can be seen in this naturalist's explanation of the transmission and expression of traits based on an analysis of regularities in the appearance during many generations of atavistic characters, mental attributes, inherited illnesses and prepotent traits.

### Lucas's Influence on Darwin's Ideas on Inheritance

In the 1850s Darwin's interest in variation and transmission of characters increased to such a degree that it became a fundamental aspect of his theory. In 1856 Darwin wrote his manuscript known as *Natural Selection*,<sup>64</sup> and in this draft he developed several chapters about variation and inheritance, chapters which show the presence of Lucas's work. Probably Darwin read about Lucas's ideas for the first time in the *Westminster Review* published in July, 1856; the item was sent by Lyell to Hooker by way of Darwin,<sup>65</sup> In it there was an anonymous review: "Hereditary Influence, Animal and Human," whose author was G. Lewes that summarized in a general way the ideas of the *Treatise on Natural Inheritance*, Afterwards, Darwin began to read this *Treatise* on September 5th of 1856.<sup>66</sup>

Darwin had a great interest in the topic of heredity, in causes of variation, and character transmission. His interest was stimulated by the necessity to give more arguments for the transformation of species, and problems related to other discussions like the problem of specific characters and limits of species. In the context of the delimitation of species and transformation, the discussions of Lucas become important because Lucas insists that variation or *innéité* operates weakly on "specific characters," assuming that "specific characters" remain indefinitely stable. Revising Lucas's inheritance ideas and arguing in an opposite sense were fundamental for Darwin, since exactly his proposal of transformation became a problem in taxonomic practice and

<sup>64</sup> Stauffer Ed., 1975.

<sup>65</sup> Burkhardt et al., 1990, Vol. 6, pp. 191–192.

<sup>66</sup> See Vorzimmer, 1977, pp. 107–153.

important for the discussion about the limits of any species concept.<sup>67</sup> This last subject was common between Darwin and Joseph Hooker,<sup>68</sup> who shares with him his first impressions and knowledge upon causes of the variation. On November 23, after completing Lucas's treatise or during his lecture, Darwin sent to Hooker a letter where he stated that he had already developed preliminary matters on the causes of variation. In this letter he affirms: "No doubt the variability is governed by laws, some of which I am endeavouring very obscurely to trace."<sup>69</sup>

In his copy of Lucas's book, Darwin wrote about what was the most important point in this discussion: "The only point that it worries to me is, if new structures are inherited or not."<sup>70</sup> This indicates his interest in understanding how different types of variation are maintained. To fulfill this purpose he employed various important ideas of inheritance from Lucas's work.

Darwin started writing *Natural Selection* in 1856. He began to work on the chapters on variation during the summer.<sup>71</sup> By October he had concluded chapters I and II and in November and December he wrote the chapter on hybridization. Darwin had showed also interest in variation and inheritance in 1855 when he started his studies on pigeons.<sup>72</sup>

A re-elaboration of chapters I and II of the essays of 1842 and 1844 were included in *Natural Selection*. In this re-elaboration he inserted eight quotations of the *Treatise on Natural Inheritance*. Later on, he employed the same information and he added other references in various chapters of *Variation*, 1868. In this text there are 21 references to Lucas.<sup>73</sup> Darwin states that he wrote this book with various purposes in mind being an important one to "learn something on the laws of inheritance."<sup>74</sup>

<sup>67</sup> Bonneuil, 2002.

<sup>68</sup> See for instance Bellon, 2006, pp. 1844–1860.

<sup>69</sup> Letter of November 23. In Burkahardt et al., 1990, Vol. 6, p. 281.

<sup>70</sup> In Di Gregorio, *Marginalia*, p. 515.

<sup>71</sup> His interest in general matters on variation is shown in his correspondence. See, for example, Burkahardt et al., 1990, Vol. 6, pp. 217, 227, 235–236, 236, 238.

<sup>72</sup> See, for example, the letters sent March 19 and 27 of 1855 to his cousin Fox. In Burkahardt et al., 1989, Vol. 5, pp. 288 and 293.

<sup>73</sup> In *On the Origin of Species* (1859, p. 12) and *The Variation of Plants and Animals under Domestication* (1868, Vol. 2, p. 1, 7) Darwin indicates the importance of Lucas' works.

<sup>74</sup> Darwin, 1868, Vol. 1, p. 3.

Darwin's annotations present in the margins of Lucas's text indicate the interest he had in inheritance.<sup>75</sup> No other work on the subject that he read has a similar amount of annotations, with the exception of the text of Kölreuter (*Vorläufige Nachricht von Einigen das Geschlecht der Pflanzen Betreffenden Versuchen und Beobachtungen*, 1961).<sup>76</sup> This shows the importance he gave to Lucas's work.

On the other hand, Darwin's use of the term *inheritance* shows the influence of Lucas. Prior to his lecture of the treatise he rarely used the term *inheritance*. In his Essay of 1844 we find it only a couple of times.<sup>77</sup> Instead of it he employed *hereditary* and *transmission of peculiarities*. After using it in annotations he made in the margins of Lucas's work and in his manuscript of 1856 he will start to employ it in matters related to inheritance, reversion and reproduction in his correspondence.

For example, in a letter sent to Huxley in November of 1857 he exposes his personal opinions on fertilization of aphids and he manifests the interest that he has had in recent times on matters of inheritance and in speculating in relation to this subject.<sup>78</sup> Other examples which suggest the inheritance subject related to change and continuity, causes of variation, reversion as an inheritance kind and importance of heritability can be seen in two letters sent to Hooker on May 3 and 11 of 1859.<sup>79</sup>

We can see the direct influence from Lucas to Darwin through concepts as prepotency and the rules of similarities between ancestors and descendants, in particular prepotency linked to sex (male or female), direct inheritance, the transmission of mental peculiarities and inherited illnesses, and the laws of inheritance and reversion. All of these ideas are present in the manuscript of *Natural Selection*<sup>80</sup> and in *Variation*, 1868.

<sup>75</sup> Darwin's interest on inheritance can be shown in the following annotation that differentiates between inheriting a characteristic and expressing it: "Good remarks on the little distinction between inheritance of predisposition and disease itself." In Di Gregorio, 1990, pp. 518. By distinguishing the inheritance of illnesses Darwin conceives that inheritance can be an agent of disease.

<sup>76</sup> *Vorläufige Nachricht von einigen das Geschlecht der Pflanzen betreffenden Versuchen und Beobachtungen*, 1961.

<sup>77</sup> See for example Darwin, 1909, p. 82. With 'heredity' and "inheritance" Darwin indicates the importance of the laws of the inheritance, but neither in this text nor in any other written before 1865, he does not describes laws of inheritance, as he will do later in *The variation*, where he writes three chapters on the subject, and suggests a systematization of the laws that regulate the transmission and expression of characters.

<sup>78</sup> Darwin and Seward Eds., 1903, Vol. 1, pp. 102–103.

<sup>79</sup> In Burkhardt et al., 1991, Vol. 7, pp. 291, 296.

<sup>80</sup> See Stauffer Ed., 1975, pp. 105, 106, 430, 453, 454, 455, 456, 457, 458, 480.

Our evidence is firstly based, on Darwin's direct references to the work of Lucas when he reflects on each of the indicated subjects, and, secondly, on the similarities of Darwin's explanations related to the transmission of the characters. As it will be seen later, the clearest similarity lies on what both of them called the laws of inheritance and in their speculations on the rules that determine the resemblance and similarities between ancestors and their descendants; when he makes his reflections, he recognizes Lucas's Treatise's remarkable effort in understanding these problems:

On the whole I entirely agree with Dr. Prosper Lucas, who, after arranging an enormous body of facts with respect to animals, comes to the conclusion, that the laws of resemblance of the child to its parents are the same, whether the two parents differ much or little from each other, namely in the union of individuals of the same variety, or of different varieties, or of distinct species.<sup>81</sup>

The type and order of the following subjects have arbitrarily been drafted by the authors, trying to recover those topics that Darwin approaches in relation to specific problems and that reflect, at the same time, thematic proposals by Lucas. In this sense we began with Inheritance of mental tendencies, we continue with hereditary diseases, later with the prepotency and resemblance between progenitors and descendants, central subjects as much in Lucas as in Darwin when they approached the diverse issues of the inheritance.

We finish this section with the Prepotency and the effect of crossing, a subject on which Darwin reflected from the information of his readings and data obtained during several years of experimentation.

### *Inheritance of Mental Tendencies*

Due to the fact that Lucas was a psychiatrist many of his explanations on the study of inheritance are generalizations that specifically apply to alterations of human behavior. Lucas tried to show that mental illnesses are not necessarily due to environmental conditions but can be inherited. His concepts are relevant if we are aware that in those days it was considered that environmental influences were very important in determining human conduct.

Even though Darwin conceived that variation is generated by the influence of environmental conditions, he accepted Lucas's concept that considered the inheritance of mental diseases. This is shown next:

<sup>81</sup> Darwin, 1859, p. 275.



With respect to the inheritance of all sorts of mental tendencies, peculiarities, consensual movements etc., it is quite superfluous to give examples: they may be found in all *Treatises on Inheritance*.<sup>82</sup>

Darwin refers to the examples of inherited mental illnesses mentioned mainly in the chapter of the treatise *On the laws of inheritance (De la Loi D'hérédité)*. In this section Lucas reflects on diverse subjects related to the transmission of moral matters, such as the inheritance of a tendency towards moral conducts,<sup>83</sup> the inheritance of tendencies, certain qualities or defects of an individual type,<sup>84</sup> the inheritance of a tendency or predisposition towards crime, the origin of predispositions towards crime, and how this predisposition in some families is transmitted through generations.<sup>85</sup>

Darwin recognized the difficulty of analyzing these matters, especially those related to complex mental attributes. Nonetheless, he considered that one shouldn't doubt that many were inherited.<sup>86</sup> However, he also examined the inheritance of other hereditary diseases, as will be exposed next.

### *Hereditary Diseases*

Darwin made the biggest number of references to Lucas's treatise when he discourses on matters related to mental diseases and inherited disorder,<sup>87</sup> which also were considered like constitutional defects, persistent traits in some familiar lineages.<sup>88</sup> The subject of hereditary diseases in the Victorian context of second half of century XIX has extensively

<sup>82</sup> Darwin refers to Lucas, 1847, Vol. 1, pp. 340–598. In Stauffer Ed., 1975, p. 480.

<sup>83</sup> Lucas, 1847, Vol. 1, p. 446.

<sup>84</sup> Lucas, 1847, Vol. 1, p. 461.

<sup>85</sup> Lucas, 1847, Vol. 1, p. 480.

<sup>86</sup> Darwin, 1868, Vol. 2, p. 7.

<sup>87</sup> See Darwin, 1868, Vol. 1, pp. 329, 404; Vol. 2, pp. 7, 9–11, 13, 17, 23, 35, 65, 68, 64, 78–79, 335.

<sup>88</sup> These constitutional defects were denominated by doctors as hereditary diseases or hereditary disorders. During the first half of the nineteenth century it was common to use the idea of constitutional defects or constitutional vigour to refer to conditions of disease or health. In general “constitution” was an idea that included the view of the body as wholly organized and of its constituent characteristics, healthy or diseased, they could be inherited. James C. Prichard was important in the definition of this concept, he also made the distinction between congenital characteristics and inherited characteristics. An excellent essay on this subject and the constitutional defects, heritability, consanguinity and its transformation through to genetic changes is in Olby, 1993. Olby indicates the importance of Lucas' work in history of constitutional disease's concept.

been analyzed and debated, but we think that even greater attention needs to be paid to the influence that Lucas's work had in that context.<sup>89</sup>

Both Darwin and Lucas analyzed similar aspects on inheritance and morbid characteristics of descendants by means of the examination of a group of regularities related to the effects of cross-breeding on females, hereditary diseases, hereditary affections of the eye, inheritance of anomalies in the human eye and in that of the horse,<sup>90</sup> inheritance of polydactylism, morbid uniformity in the same family, inheritance of mutilations, and inheritance of deafness in cats.<sup>91</sup>

In *Variation* Darwin discusses the inheritance of some diseases and refers to Lucas's work.<sup>92</sup> He examines various cases of eye and vision illnesses, among them, a particular case of the inheritance of the congenital absence of the iris present in men of a particular family. On this subject he states that "Lucas emphatically remarks that there is not one single faculty of the eye which is not subject to anomalies; and not one which is not subjected to the principle of inheritance."<sup>93</sup> On the other hand, after consulting many works, he found surprising the unanimity of belief by veterinarians of all nations in the transmission of various morbid tendencies.<sup>94</sup>

Darwin considers that in plants and animals differences in color are related to constitutional dissimilarities,<sup>95</sup> and points out that Lucas seemed to deny this relation. Apparently this physician did not believe in this connection because he considered that individual traits such as color and specifically albinism, are present in all animal species not determined by a specific rule.<sup>96</sup>

<sup>89</sup> See for instance Waller, 2002, who made three tangential references to Darwin; the absence of Darwin's thought in Waller's work is important because he omitted the great interest that Darwin maintained by hereditary diseases, constitutional defects, and transmission of beneficial and morbid constitutional peculiarities.

<sup>90</sup> Darwin obtained data on blindness of horses from the *Treatise on Natural Inheritance*. Many of the pages of Lucas' treatise quoted by Darwin contain information on the transmission of blindness. Darwin, 1868, Vol. 2, p. 455. Darwin refers to Volume 1, p. 399, of Lucas' treatise.

<sup>91</sup> On the inheritance of deafness in cats, see Darwin, 1868, Vol. 2, pp. 329; and Lucas, 1847, Vol. 1, p. 428.

<sup>92</sup> Darwin, 1868, Vol. 2, p. 453 where he refers to Lucas, 1847, Vol. 1, pp. 391–408.

<sup>93</sup> Darwin, 1868, Vol. 2, p. 10.

<sup>94</sup> *Ibid.*

<sup>95</sup> See Darwin, 1868, Vol. 2, pp. 329–335.

<sup>96</sup> Lucas, 1850, Vol. 2, pp. 88–94.

*Prepotency*

Darwin understands prepotency as the persistence of a character that occurs primarily in crosses of different races or varieties.<sup>97</sup> It can be considered the capacity an individual has of transmitting his characters expressed by means of likeness with his descendants. He examines prepotency many times in the manuscript of *Natural Selection* (1856) when he refers to the work of Gärtner (*Beiträge zur Kenntniss o Bastaderzeugung*, 1849),<sup>98</sup> however, in *Variation* he states that this subject had been amply discussed by Prosper Lucas.<sup>99</sup>

Darwin considered that “the truth of the principle of prepotency comes out more clearly when certain races are crossed.”<sup>100</sup> During many years he had been interested in knowing how characters behave after a cross. He thought that the answer could be established by analyzing the rules of transmission. Therefore, he examined various types of transmission of characters and elaborated different ideas about each one. For example, he attributed sexual limitations to transmission and he considered that in some crosses no blending of certain characters occurred.<sup>101</sup>

As has been shown, Lucas also analyzed rules of transmission such as why some varieties predominate over other. Both Lucas and Darwin referred to the works of Kölreuter and Gärtner when they examined these rules.<sup>102</sup>

Gärtner’s ideas on the expression of characters in *Nicotiana* were used by Lucas and Darwin to elaborate a general principle or law on exclusive inheritance of one sex that explains likeness between progenitors and descendants and the transmission of morbid characters.

*Prepotency and Resemblance between Progenitors and Descendants*

Darwin had great interest in understanding the degree of similarities between parents and offspring. He considered that the key to understand this subject and other matters such as the rules of transmission of different types of characters was to know the effects that crosses had in them, as well as the effects of some principles of prepotency. In the manuscript of *Natural Selection* on this matter he wrote:

<sup>97</sup> Darwin, 1868, Vol. 2, p. 64.

<sup>98</sup> *Beiträge zur Kenntniss o Bastaderzeugung*, Gärtner, 1849.

<sup>99</sup> Darwin quoted to Lucas, 1850, Vol. 2, pp. 112–120.

<sup>100</sup> Darwin, 1868, Vol. 2, p. 65.

<sup>101</sup> See Darwin, 1868, Vol. 2, pp. 68, 72–73, 88, 92, and 116.

<sup>102</sup> For example, in one reference Darwin alludes to the *Treatise on Natural Inheritance* (Lucas, 1850, Vol. 2, p. 308), where Lucas analyzes Gärtner results on *Nicotiana*.

With respect to the rules of resemblance of hybrids & mongrels to their parents, it deserves notice that very many attempts have been made to give laws such as that the father gives external characters & the mother internal or vital organs... None of these rules, if widely extended to all animals seem to hold good, as has been ably shown by Dr. P. Lucas & Gaertner.<sup>103</sup>

To explain these rules, Darwin uses the “prepotency.” He understood it as the ability of one parent to transmit his characteristics with certain strength, as is shown in the following affirmation: “the fixedness of characters or the strength of inheritance has often been by the preponderance of certain characters.”<sup>104</sup>

He was convinced that the principle of prepotency was clearly expressed when different races were crossed “as the cattlemen that possessed Shorthorn cattle knew well.” He thought that when two well differentiated races or species were crossed, the common result was that the descendants in the first generation was intermediate with respect to the characters of its parents, or a part was similar to one of the progenitors and the other part resembled the other parent. However, this was not an invariable rule. He stated that: “...in many cases it is found that certain individuals, races, and species are prepotent in transmitting their likeness.”<sup>105</sup>

Darwin affirmed that Lucas had analyzed this condition, but considered that much was needed to be understood on this matter, especially because prepotency was not exclusive of one of the sexes and because sometimes it was stronger in one of the two parents.<sup>106</sup>

### *Prepotency and the Effect of Crossing*

After the publication of *Variation* Darwin continued his research on inheritance, the transmission of characters and prepotency. The results of his investigations were published in *The Effects of Cross and Self Fertilization in the Vegetable Kingdom* published in 1872. His ideas acquired more importance because in the English context, ‘inheritance’, had been converted in a battlefield of methodological, scientific and ideological proposals, in which the influence of Lucas in different authors seems to have a great importance; for instance, Galton indicates

<sup>103</sup> In Stauffer Ed., 1975, p. 455.

<sup>104</sup> Darwin, 1868, Vol. 2, pp. 64–67.

<sup>105</sup> Darwin, 1868, Vol. 2, p. 65.

<sup>106</sup> Darwin, 1868, Vol. 2, pp. 63–65.

that he uses the Lucas's ideas in the same sense in which Lewes does<sup>107</sup> with the purpose to defend from his own viewpoint persistence of hereditary diseases as behavior characteristics.<sup>108</sup>

In *The Effects*, 1872, Darwin provides experimental data with the purpose of explaining coherently the transmission of constant characters in successive generations and the appearance and fixation of inherited deviations denominated constitutional peculiarities. Darwin employed values of height of plants, germination capacity of seeds and number of seeds per plant to sustain his statements. Data were elaborated and ordered in "statistical tables" by his cousin Galton. High values were interpreted as superior in constitution and low ones as inferior in vigor. Darwin considers that the greater height, weight, and fertility of the crossed plants may be attributed to possessing greater innate constitutional vigour<sup>109</sup>; this constitutional vigour is related by Darwin with prepotency and morbid tendency.<sup>110</sup> At the same time he stated that this same force of inheritance associated to these phenomena can also explain the continuity of constitution: "The force of inheritance is strong with plants (of which abundant evidence could be given), it is almost certain that seedling from the same capsule or from the same plant would tend to inherit nearly the same constitution."<sup>111</sup>

Darwin thought that prepotency could be deduced by the comparative analysis of two groups of plants of the same variety,<sup>112</sup> one group that only permitted self-fertilization and the other one that only allowed cross-fertilization. These experiments had the purpose of determining if the mode of reproduction had an effect in the transmission and expression of characters.

<sup>107</sup> In July, 1856, G. H. Lewes, published an essay about hereditary influence, one of the works that he analyzes is the Lucas's Treatise.

<sup>108</sup> Galton, 1865, See also Carlson, 2001.

<sup>109</sup> Darwin, 1876, p. 285.

<sup>110</sup> Even though Darwin did not define with precision the term morbid tendency, it can be found in his works associated with an element of harmful nature directly related to the reduction of constitutional vigor reflected fundamentally in the lack of fertility that recurrently appears in some lineages. He stated that this property could be a consequence of consanguineous crosses during two, three or four successive generations, exposure to particular environmental conditions or the inheritance of a latent or visible morbid tendency present in one or two parents of an offspring. Darwin considered that when a morbid condition was found in two organisms that were crossed the impairment of their descendants augmented considerably. See, Darwin, 1868, Vol. 2, pp. 10, 115–117, 175; 1876, pp. 436, 445.

<sup>111</sup> Darwin, 1876, p. 305.

<sup>112</sup> Darwin used 57 species for these experiments such as *Phaseolus vulgaris*, *Papaverum vagum*, *Lupinus luteus*, *Pisum sativum* and *Zea mays*.

The more important conclusion he inferred from these experiments in plants was that cross-fertilization is beneficial and self-fertilization sometimes is injurious.<sup>113</sup> However, Darwin considered that the advantages of crossed fertilization are not due to the process of reproduction, but to the differentiation of the sexual elements that harmonize perfectly with a slight modification in the conditions of life.<sup>114</sup>

### **How Similar was Lucas's and Darwin's Ideas on the Laws of Inheritance?**

Based on his analysis of diverse phenomena related to inheritance of mental tendencies, hereditary diseases, prepotency, resemblance between progenitors and descendants, and after read Lucas's *Treatise*, Darwin elaborated a group of ideas that he denominated *laws of inheritance*, which was similar to Lucas's law of inheritance. In *Variation* Darwin resumes upon inheritance:

Finally, though many remains obscure with respect to Inheritance, we may look at the following laws as fairly well established. Firstly, a tendency in every character, new and old, to be transmitted by seminal and bud generation, though often counteracted by various known and unknown causes. Secondly, reversion or atavism, which depends on transmission and development being distinct powers. It acts in various degrees and manners through both seminal and bud generation. Thirdly, prepotency of transmission, which may be confined to one sex, or be common to both sexes of the prepotent form. Fourthly, transmission, limited by sex, generally to the same sex in which the inherited character first appeared. Fifthly, inheritance at corresponding periods of life, with some tendency to the earlier development of the inherited character.<sup>115</sup>

Darwin concludes that in these laws of inheritance, we can see an ample provision for the production of new specific forms, through of variability and natural selection.<sup>116</sup>

<sup>113</sup> Darwin, 1876, p. 436.

<sup>114</sup> See Darwin, 1876, pp. 443, 458–459. For example, damages can determine in some cases the impossibility of crosses between individuals of a same variety. For these conclusions Darwin refers to the works of Sir J. Sebright, Andrew Knight, and Prosper Lucas, as well as: “the distinguished German agriculturist Hermann von Nathusius”, Darwin, 1868, Vol. 2, p. 116.

<sup>115</sup> Darwin, 1868, Vol. 2, p. 84.

<sup>116</sup> Ibid.

If we compare these laws of inheritance with Lucas's types of inherited transmission of mental diseases we find similarities in the ideas of reversion or atavism, seminal transmission (through sexual reproduction), prepotency of transmission confined to one sex, and inheritance of a character that develops at a same age.

The similarities between Lucas's and Darwin's ideas are shown next by analyzing the five laws proposed by Darwin.

(a) First Law: transmission. Both Lucas and Darwin consider that all characters can be transmitted. Lucas indicates that all traits are ruled by the law of reversion. And Darwin considers that there is a tendency of all character, new or old, to be transmitted which implies that he accepted that the law of reversion affects all characters.

(b) Second Law: atavism, reversion or latency. On this matter, Darwin states that:

From these several facts it must be admitted that certain characters, capacities, and instincts, may lie latent in an individual, and even in a succession of individuals, without our being able to detect the least signs of their presence.<sup>117</sup>

With the second law of reversion Darwin tried to determine the phylogeny of pigeons<sup>118</sup> by means of controlled crosses and morphometric measurements. He chose pigeons because it was the group that he knew the best and was sure of collecting proof of the origin of all races from a single form. These experiments led to the conclusion, as a result of the principle or law of reversion, that *Columba livia* is the ancestor of all races of pigeons.<sup>119</sup>

Darwin thought that the causes that determine characters lie beyond what happens in the process of reproduction and development due to reversion as is shown in his following statement<sup>120</sup> and believed that the male and female sexual elements should retain characters, during several generations in the case of pure breeds, 'written as it were in invisible ink,' and should be evolved under the requisite conditions.<sup>121</sup>

<sup>117</sup> Darwin, 1868, Vol. 2, p. 54.

<sup>118</sup> See Darwin, 1868, Vol. 1, pp. 131–224.

<sup>119</sup> April of 1856, Darwin had received a letter from Edward Blyth, in which this latter indicates to him that in his opinion all the doves descend from the *C. Livia*. In Burkahardt et al. 1990, Vol. 6, p. 67.

<sup>120</sup> He communicated his interest on the relation between reversion and inheritance to Hooker on May 3, 1859. See Burkahardt et al. 1991, Vol. 7, p. 291.

<sup>121</sup> Darwin, 1868, Vol. 2, p. 83.

(c) Third Law: prepotency. We have already indicated that Darwin recognized the existence of this process as the ability of one parent to transmit his characteristics with certain strength. Transmission could be direct from father to son or mother to daughter or crossed from father to daughter or mother to son.

Darwin considered that diverse characters presented this condition such as secondary sexual characters, non sexual traits, characters that can develop in specific stages of life and various human illnesses.

(d) Fourth Law: limitations by sex. This is an extension of the third law applied to secondary sexual characters<sup>122</sup> and to the appearance of some inherited diseases, especially some human illnesses that only manifest themselves in men.

Darwin and Lucas conceived regularities in inheritance as limitations determined by sex, as is shown next:

Dr. P. Lucas, who has collected many facts on this subject, shows that when a peculiarity, in no manner connected with the reproductive organs, appears in either parent, it is often transmitted exclusively to the offspring of the same sex, or to a much greater number of them than of the opposite sex.<sup>123</sup>

Darwin discussed diverse matters on the transmission of characters and its relation with likeness, diseases and prepotency. He emphasized the particularities of the latency of characters. He exposed this condition by explaining the most obvious example of latent characters, masculine secondary sexual characters in females and feminine secondary sexual characters in males.

According to Darwin, males and females present all secondary sexual characters, both masculine and feminine. However, in males feminine characters generally do not express themselves and in females masculine characters are latent. Only in peculiar circumstances these latent characters manifest themselves.<sup>124</sup> Therefore, females can transmit their characters by their male descendants and males inherit their qualities through their female offspring, even though these characters are dormant.

(e) Fifth Law: inheritance at corresponding periods of life, a regularity referred by Lucas as the *law of inheritance at a corresponding age* (*la loi d'hérédité de l'âge*).<sup>125</sup> Darwin presents various examples, many

<sup>122</sup> Darwin, 1868, Vol. 2, p. 52.

<sup>123</sup> Darwin, 1868, Vol. 2, p. 72, see Lucas, 1850, Vol. II, pp. 137–165.

<sup>124</sup> Darwin, 1868, Vol. 2, pp. 51–52.

<sup>125</sup> Lucas, 1850, Vol. 2, pp. 459–461.



taken from Lucas, for example, cases of gout that appears at a same age in sons, fathers and grandfathers.

Both Lucas and Darwin consider that variation is an antagonistic force of inheritance. However, they have opposite concepts of the effects of variation and its relation with the conditions of existence. While Darwin conceives that variation is the fundamental force for the transformation of species, for Lucas it is a limited force that only generates individual differences and not new species. While Darwin considers that variation is generated by environment conditions, for Lucas it appears independently from external influences.<sup>126</sup>

For Lucas, variation and inheritance are *aboriginal* laws, that is, natural laws. And they are antagonistic principles. Darwin's reflections on the causes of variation are related with Lucas' *loi d'inneite*, which led us to consider it a law of variation.<sup>127</sup>

The differences in the concepts on variation, conditions of existence and the transformation of species do not deny Lucas's influence on Darwin, even though inheritance explained, according to Lucas, continuity of natural forms, and, from Darwin's perspective, the continuous transformation of living beings.

## Conclusion

Inheritance was a fundamental subject in Darwin's reflections, his interest with it beginning with his reflections and preoccupations by the transformation of species. His ideas upon the subject, as many other ideas, had been changing in a continual way; a substantial change was the transition from an idea considered to be like an innovation as a result of the processes of generation and development to an idea considered as a character transmission process. We can appreciate this change better,

<sup>126</sup> In May 11 of 1859 he will tell Hooker that he doesn't agree that variability is contingent (Burkahardt et al., 1991, Vol. 7, p. 296). In March 11 of 1862 he will comment similar ideas to Hooker, mentioning Lucas as a defender of modifications inherent to the process of development. In Burkahardt et al., 1997, Vol. 10, p. 122. Also about this difference can see In Stauffer Ed., 1975, pp. 1856, 105; Darwin, 1868, Vol. 2, pp. 250, 271; and 1868, Vol. 2, p. 250.

<sup>127</sup> For Darwin variation was a product of environmental conditions or the constitution of an organism and not a contingency in development as Lucas stated. Also, as has been stated by Churchill (1987), unlike Lucas, Darwin refrains from formulating a fundamental opposition between variation and inheritance. Darwin proposed that inherited variation wasn't limited by a necessary constancy in a racial or specific type, as Lucas considered, because inheritance had to explain the transformation of species.

when we see that his transition was from his weak perception, in which he considered inheritance as an important subject for his explanation of transformation to his consideration in which the history of organic diversity on the planet is a theory of inheritance with modification. Inheritance in fact was considered by Darwin as a set of phenomena (transmission, reversion, prepotency, among other), which was articulated under the dynamic scheme of continuity and change of characters.

A fundamental element in Darwin's change about his ideas on inheritance was the Lucas's *Treatise*, in which Darwin found a consistent proposal in relation to inheritance, his reading in 1856 coincidence with important changes in several ideas in regards to the transmission and expression of the characters. Lucas had worked out a proposal that gave an account of a set of regularities that he called Laws of heredity (loi d'hérédité). In *Variation*, Darwin took up again Lucas proposal, accepting some principles and rejected others, and following Lucas he systematized in a similar way, "The Laws of Inheritance." We have showed that Darwin's systematization reflects, from our own perspective, an evident influence of Lucas's thoughts. He accepted the general proposal, but he rejected Lucas's affirmation that the effects of variation lacked any meaning in the evaluation of specific characters, in contrast he considered that small changes generated by variation and interacting with other natural causes (as natural selection) would consequently have deep effect in specific characters and consequently in the transformation of species. The problem of transmutation is intersected by diverse problems, which can be explained under the same dynamic scheme of continuity and change. For example, the limits of species and the taxonomic practice, which is connected to the effects of variation in specific characters; other important problems were related to hybridization and return of ancestral characters, a problem which in Darwin's laws of inheritance is articulated to reversion and prepotency of characters, a fact that was commonly interpreted as evidence of the impossibility of transformation of species. Darwin, nevertheless, interpreted it as evidence of common origin. Another set of problems was related to persistence of characters that seem to be unalterable by environmental conditions, for instance 'hereditary diseases' and 'morbid tendencies.' Some authors considered this problem as a direct consequence of consanguineous relations. To try to clarify this problem Darwin dedicated several years of investigations upon cross-fertilization and self-fertilization in plants. In all these controversial points, Lucas's proposal of vertical transmission, was modified by Darwin in a mixture of horizontal and vertical characters transmission, and he suggested a proposal

that had the aim to explain simultaneously transmission of ‘new’ and old characters. For Darwin, the search of answers on inheritance was a search for solid argumentation of principles, on which operates the selection, either being artificial as he argues in *The variation*, or being natural as he argues in *The origin* and *The descent* (1871).

As the subject of inheritance of variation has been analysed from diverse historiography aims, nevertheless, we considered that in the historical reconstruction of these ideas, that there are important for biology, we cannot leave to consider Lucas’s proposal and his influence in Darwin (and in other authors like Galton) neither we cannot leave to consider the dynamic knowledge generated upon variation and inheritance before genetics arrival. As occur in biological heredity, in some place of his structure the Darwinian inheritance could be conserved indelible traits of Lucas’s *Treatise*.

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