Trémaux on species: A theory of allopatric speciation (and punctuated equilibrium) before Wagner

John S. Wilkins[i] and Gareth J. Nelson[ii]

Abstract

Pierre Trémaux's 1865 ideas on speciation have been unjustly derided following his acceptance by Marx and rejection by Engels, and almost nobody has read his ideas in a charitable light. Here we offer an interpretation based on translating the term *sol* as "habitat", in order to show that Trémaux proposed a theory of allopatric speciation before Wagner and a punctuated equilibrium theory before Gould and Eldredge, and translate the relevant discussion from the French. We believe he may have influenced Darwin's revision to the third edition of the *Origin* on rates of evolution, and suggest that Gould's dismissal of Trémaux is motivated by concern that others might think punctuated equilibrium theory was tainted by a connection with Trémaux.

Introduction

Pierre Trémaux (1818–1895) is not well known. Although he holds a place in the history of photography for his photographs taken during a trip down the Nile to the Sudan in 1847[iii] and he later published one of the first illustrated geographical books, his anthropological and biological work would have received little notice except for the fact that Karl Marx praised him over Darwin. As one of us wrote back in 1989:

> Trémaux's writings were never well known. Perhaps they deserve the oblivion into which they have fallen, but their general theme of earth and life evolving together accords well with the spirit of our modern concerns

[i] Department of Philosophy, University of Queensland, Brisbane 4072, Australia

[ii] School of Botany, University of Melbourne, Melbourne 3010, Australia

[iii] Trémaux was well regarded for a series of anthropological articles based on his journey to the Sudan (Trémaux 1849, 1850, 1855, 1856, 1862a, 1862b).

> with vicariance. For reasons not altogether clear Trémaux's work was of interest for a time to Karl Marx, who felt that it was 'a very important advance' over the state of Darwinism in the late 1860s … . He corresponded with Frederick Engels about it … (Nelson 1989b)

The standard view of Trémaux is given by Bernard Cohen, who says:

> Marx, however, should not be overly credited for special percipience in evaluating the worth and significance of Darwin's theory of evolution. In a letter to Engels on 7 August 1866, one year before the publication of *Das Kapital*, Marx was singing the praises of another "very important work" (Padover 1978, 360–361). The new book, he wrote, constitutes "a *very important* advance over Darwin." He is sending the book to Engels, so that he too may learn its message. "In its historical and political application," he declared, this book "is much more important and copious than Darwin." The book so highly praised by Marx was P. Trémaux's *Origin et transformations de l'homme et des autres étres* (Paris,1865). The judgment of history does not accord with Marx's laudation.For example, Trémaux does not rate an entry in the recently completed16-volume *Dictionary of Scientific Biography*, nor is his name even mentioned in the standard histories of biology and of evolution (as by Bodenheimer, Carter, Eiseley, Fothergill, Mayr, Nordenskiöld, Rádl, Singer). Furthermore, in the international *Critical Bibliography of the History of Science*, compiled and published by George Sarton, by me, and by our successor editors from 1913 to 1975, there is no entry to record a single scholarly article or book on Trémaux's life or contribution to science. As the lawyers say, "res ipsa loquitur." Why did Marx become so beguiled by Trémaux that he considered his book superior to Darwin's? One reason is that, like Herbert Spencer and unlike Darwin, Trémaux evidently believed in progress. As Marx explained to Engels (ibid.), "Progress, which in Darwin is purely accidental, is here a necessity, on the basis of the periods of developments of the earth." (Cohen 1985: 345)

Practically every single reference to Trémaux in the subsequent literature appeals to this correspondence, and nearly all of it dismisses Trémaux in terms of Marx's reading, and Engels' dismissal, and what that means about Marx's and Engels' views on race.[iv] Moreover, Trémaux's views of human races are said to be typical in that

---

[iv] For example, Stebbins (1965), Harris (1968: 236f), Gerratana (1973: 77n), Conry (1974: 220), Poliakov (1974: 244-246), Rogers (1974: 463), Colp (1974: 330), Naccache (1980: 16, 98-104), Lecourt (1983), Carver (1984: 255), Vádee (1992: 243f), Tort (1996), Stack (2000: 702, 2003: 68), and Robert-Devillers (1999: 56). A more extensive analysis is Weikart (1999: 28-36), but repeating the same

they follow the Blumenbach taxonomy with Negroes ranked lowest, closest to apes, and Europeans ranked highest. Marx's affiliation with this view, which Engels did not share, has caused some comment in the literature (Colp 1974; Mikulak 1970; Paul 1981; Stanley and Zimmermann 1984; Weikart 1999). Few apart from Diane Paul (1981) appear to have actually read Trémaux, depending instead upon Engels' evaluation and description. One who actually did check the original is Stephen Jay Gould, who is discussed below.

Nevertheless, Trémaux's discussion on the definitions of species and the nature of species in his 1865 work forms one of the earliest of its kind, and moreover his account of speciation is both a kind of early biological species concept, where mutual fertility acts to equilibrate the species type, and a kind of punctuated equilibrium. The irony is that Gould is one of the originators of a punctuated equilibrium theory of evolution, and thus Trémaux is a precursor to him. Given the difficulties with Trémaux's prose and format, and his reputation amongst historians of science, Gould may have wanted to downplay the resemblances.

Trémaux's theory suffered in the *Académie des Sciences* for reasons that are unclear, but he may have annoyed a senior figure like Pierre Flourens (1794-1867, *Secrétaire perpetuel*, 1833-1867). Apparently the *Académie* was willing to publish the communications from Trémaux for a while, but eventually the contributions were sent to one or another committee and died there. In his 1874 summary volume of his theory, he describes the response to his first book:

> Many other confirmations followed; 70 or 80 journals and reviews took note of my communications to the Academy. Academic reception, a double decoration, etc., nothing lacked; I had demonstrated that our first ancestor had given rise to the whites and to the blacks. My first edition in duodecimo of 490 pages sold out in two months by the Librairie Hachette. But this was only one face of the question.

---

interpretation. Intriguingly, the early science fiction writer Henri de Parville (1865: 184n) did correctly interpret Trémaux's thesis.

> Par. 11. Other reflections. – Afterward that Academy, the philosophy perceived that organisms, adapted to the soil on which they lived, that if, from the first ages of the earth, they have been modified, perfected in consequence of the amelioration of the soil, that is that they transform! Then unthinking tradition fell upon me, everything changed, I was guilty in spite of myself, it proved impossible to achieve a second edition that I wanted to revise. I gave up. It was then that I wanted to know where this terrible science was to lead.
>
> My research became more rewarding and led me to the greatest law that humanity can realize, that is the Universal principle of movement and of life, which results simply from transmission of force. And I was able to confirm that the phenomena of the will and of the intelligence are responses to another principle! ... *This was the dual end desired*: I developed this very important principle; but the Academy did not respond except to try to suppress my work. So, to justify this incomprehensible resistance, it [the Academy] produced its theory of singular equations that promoted the idea that the will does not exist and was only "an appearance."
>
> ....
>
> There was no more hesitation, it was necessary to fight against these miserable ideas, against these blind tendencies of antiquated ignorance that their defenders feared to avow. The transformation of organisms presents notable advantages, such that the geological and paleontological sciences have brought to light facts that were previously unknown. (Trémaux 1874: 68)

Trémaux appears to have the idea that something like thermodynamic principles drive evolution, an idea later proposed also by Boltzmann and elaborated by Lotka (1922, 1925), although it may simply be something like the rather amorphous central idea of Herbert Spencer's philosophy.

We believe that with respect to speciation Trémaux has been the victim of both a mistranslation or misunderstanding of the term *sol* to mean "soil" – which we have

here translated as "habitat" to clarify the argument[v] – and of Engels' dismissal of Trémaux's book, which few have subsequently bothered to investigate. We therefore offer the following summary and translation of the relevant chapter, a précis of which was also published in a later work (Trémaux 1874). Because standard history of biology has Moritz Wagner as the originator of the geographical isolation view of species (e.g., Mayr 1982), now called the *allopatric theory*, in 1868, three years after Trémaux's work was published (Wagner 1868; Eng. Wagner 1873), it may be that Trémaux has not been given due credit in the species debate, though Wagner's lecture and book shows no evidence of familiarity with this work. Darwin noted and replied to Wagner, in the fifth edition of the *Origin* (Darwin 1869: 149), but almost nobody mentioned Trémaux. Unlike Wagner, Trémaux did not correspond with Darwin directly, although two copies of the work are in Darwin's library (Rutherford 1908: 84). Hence, he has been unnecessarily relegated to the mists of history. It is our purpose here to revive his reputation.

The argument

At the time Trémaux wrote, there was no "species problem" as such, but rather a "species question". The species *question* has not to do with the definitions of "species", but of the origins of species, the question that Darwin's work addresses. Still, Trémaux manages to raise the species *problem* in a nascent way, for the first time ever, which gradually develops over the course of the nineteenth century into the modern debate, beginning with William Bateson (1894) and Edward Bagnell Poulton

---

[v] We justify this interpretation in part by the principle of charity, but also by Trémaux's later passage in his later summary publication (Trémaux 1874) in which he says:

> Eh bien, tous ces mystères vont tomber comme un château de cartes devant deux grandes lois: d'un coté l'influence de sol et des milieux qui *diversifie* les êtres, de l'autre le produit moyen des croisements qui unifie constamment dans la même espèce tous les êtres qu'une fécondité commune peut atteindre.

See below, note x, for the entire paragraph translated.

(1903), and his treatment, although obscured by his flowery and difficult prose style, raises many of the issues still in play.

In particular, Trémaux's discussion introduces the notion that species are formed by the attainment of a kind of reproductive equilibrium, and that thereafter they do not vary much. In some ways, although we do not overstress the similarity, this is an anticipation of the theory of punctuated equilibrium of Gould and Eldredge (Eldredge et al. 1997; Eldredge and Gould 1972; Gould and Eldredge 1977; Gould 1994). For this reason, Trémaux is not the obvious caricature of a biologist that Cohen makes him out to be, and deserves to be remembered for more than his racist attitudes.

Exactly how racist Trémaux indeed was is arguable. His notion that habitat (*sol*, or "soil") causes organisms to locally adapt, which is a view that has a long history in pre-Mendelian natural history, arguably going back to the classical era, but especially to be found in the writings of Buffon, led him to argue that local conditions *cause* races. He wrote: "Mix and exchange yourselves, oh peoples! And there will always be, if the environment does not change, English people on the Thames, French people in France, Romans on the Tiber, Egyptians in Egypt, Negroes in Sudan and Redskins in America" (Poliakov 1974). In short, Trémaux is an extreme adaptationist, and for him there is no distinction between a locally adapted population and a race. It appears that the canard that Trémaux thought that negroes are a *degeneration* comes directly from Engels' response to Marx. Rather, Trémaux thought that *all* races are locally adapted populations to the conditions in which they find themselves. It is probable that it was *Engels* who was the racist in this respect. In a letter from Engels to Marx, October 2, 1866, he wrote:

> … I have arrived at the conviction that there is nothing to his [Trémaux's] theory if for no other reason than because he neither understands geology nor is capable of the most ordinary literary historical criticism. One could laugh oneself sick about his stories of the nigger Santa Maria and of the transmutations of the whites into Negroes. Especially, that the traditions of the Senegal niggers deserve absolute credulity, *just because the rascals cannot write*! Besides, it is nice to blame the soil formation for the difference between a Basque, a Frenchman, a Breton, and an Alsatian; and of course, it is also its fault that these people speak four different languages. Perhaps this man will prove in the second volume, how he explains the fact, that we Rhinelanders have not long ago turned into

> idiots and niggers on our own Devonian Transition rocks . . . Or perhaps he will maintain that we are real niggers.
>
> This book is not worth anything, a pure fabrication, which defies all facts and would have to give a proof for every proof which it adduces. [Engels to Marx, 2 Oct 1866, *Werke* vol. 31, p256, (quoted in Paul 1981: 123)]

This is a series of strawmen erected only by Engels. So we should beware interpreting Trémaux through these sources. The reasons for Marx's enthusiasm for Trémaux is well discussed by Weikart.

Trémaux's discussion first lists the views that are in wide circulation amongst French readers about the definition of *species* among natural historians. He begins by considering the creationist or fixist view (the term "creationism" being applied to a theological doctrine at the time). The charge that transformism, or the view that species could transform from one into another, was "a hypothesis without proof" was derived from the notorious hostility to hypothesising held by Cuvier. The evidence is that species are fixed, so far as we can tell, according to this view.

A well-known transformist (the term "evolution" being applied to Darwin's ideas later) was Heinrich Bronn. As late as 1857, Bronn had defended the constancy of species, but after translating the *Origin of Species* into German, he fully defended transformism until his death in 1862 (Junker 1991). Here, Trémaux quotes the earlier Bronn, perhaps ironically, asking why species are well defined. Trémaux quotes Darwin and Herschel, and then asserts that the solution is simple, based on the appearance of new characters, which form a unity of type in a following generation. The reason for this is due to interbreeding, or as he calls it, "crossing" (*croisement*). While not exactly a species definition along the lines of Mayr, for Trémaux does not have a particulate, but a blending, notion of heredity (as almost everyone did then, an exception being Lewes 1856), this is a direct and overt conception of species as maintained by interbreeding.

Trémaux appears to think that because variation is averaged out over generations (a fraction of the total difference is averaged in each generation), the entire population will eventually converge on a stable "type". The causes of variation are due to local geography, which we presume includes soil type, but also the geographical landscape,

climate and necessary habits of life. He notes that species have always been defined as individuals that resemble each other and can reproduce together – thus combining Cuvier's definition and Buffon's. Cuvier famously defined a species as "*the individuals who descend from one another or from common parents and those who resemble them as much as they resemble each other*" in his *Règne Animal* [i, 19 (Cuvier 1812)], while Buffon had defined species thus: "We should regard two animals as belong to the same species if, by means of copulation, they can perpetuate themselves and the likeness of the species; and we should regard them as belonging to different species if they are incapable of producing progeny by the same means" in his *Histoire naturelle* [Vol. 2 (1749), 10 (Lovejoy 1959: 93f)].[vi] Both of these definitions were widely known among naturalists both within and without the Francophone communities. Trémaux treats resemblance as the consequence of the interfertility of organisms, and so attacks that issue as sufficient. He then makes the comment for which he has become recently known (Nelson 1989a): "Of definitions of species, there are as many as there are naturalists, and this is the inevitable consequence of ignorance of the principle on which the species is based", a comment echoed by Mayr some eight decades later (Mayr 1942: 115).

For Trémaux, the result of crossing mutually fertile individuals of different traits is that the progeny will be intermediate. This presents him with a problem, as it did Darwin: how do novel traits evolve? At some point, he says, organisms too different will be infertile, so he needs to explain how a distinct population can become different from the parental population or type. He defines a species as *all the organisms which,*

[vi] Note that, for Buffon, a "species" was much more like a Linnean *genus* or an Adansonian *family*. He believed that taxonomic species, as we might call them, were local geographical variants of the *premiere souche* or "first stock", and by back-breeding, the first stock could be regenerated. Buffon held that local variants were the effect of the action of climate and soil (*sol*), or, in modern terms, habitat. Also, note that Linnaeus himself had discussed the effect of *"soil, locality, climate*" in his *Plantae hybridae* (1751, 35, cited in Müller-Wille and Orel 2007: 179) on varieties and whether they should be considered good species or not.

able to procreate together, actually do so and group their descendents together in an intermediate type (p136). And then, he imagines a case scenario.

If a subspecific group of diverse organisms find themselves in a novel habitat (which he calls here a "geological layer") either because they have migrated into it, or because it has recently formed, they will be characterized by interfertility, initially (*ex hypothesi*), maintained by interbreeding (crossing). A natural barrier will prevent the averaging of the local colony with the parental species, and they will adapt over time to the new conditions, forming an equilibrium, but maintaining their cohesiveness as a species despite local geographical races evolving, again through crossing. Interbreeding counters the "modifying effects" of habitat, but over time the "favoured variety", that is, the locally fittest form, will tend to become a distinct species such that, when in contact with the parental population, it would be infertile in cross-breedings. Hence, the new form will now be a good species. And the local adaptations will remain constant by crossing, even if it moves into a new terrain or environment. In short, local adaptation can occur only in isolation from the rest of the population, and so long as populations are contiguous, that will counteract any further transformation. Trémaux also allows that a new species may form by "degeneration" in unfavourable conditions, but that it is likely to become extinct.

The primary claims of punctuated equilibrium, and allopatric speciation, are all here, and also an argument relying on blending inheritance. Evolution will occur rapidly, at the beginning of the new species, and thereafter be maintained with only minor modification by interfertility. Moreover, the geological fossil record will shown species appear suddenly, by migrating from the locale in which they evolved, again, an idea championed by the punctuated equilibrium proponents. The paleontological record is explained by the slowness of deposition, as we would say, and the fact that many species live in unfavourable conditions and are thus rare. Nevertheless, he does mention possible transitional forms, of a bear and a monkey.

Trémaux then lists various instances and facts that support his view, citing Buffon, Flourens and others. He especially relies on the comparative differences between Old World and New World forms, and Australian unique forms. He regards climatic conditions as of small influence on local adaptations, treating the geographical

conditions (such as maritime coastlines) as more significant, and as isolating factors in their own right. The rule of Wallace (1858) that allied species arise adjacent to the range of related species is thereby explained. Trémaux also notes, presciently, that asexual species are more variable, because they lack reproductive compatibility to maintain the forms (cf. Wilkins 2007).

Much of the rest is taken up with reiterating Darwin's arguments for the phylogenetic tree as an explanation of groups within groups, and for accidental dispersal of species to account for biogeographical anomalies. Some species, such as Man, are able to live in a variety of conditions and regions, but usually convergent evolution explains similarities in different regions of relatively unrelated species. And in 1865, before Lyell or Darwin had written on the matter, Trémaux clearly intends this to explain the evolution of humanity, which may explain to a degree his subsequent unpopularity in the Academy.

Trémaux and Darwin, and Gould

Although so far as we can establish, Darwin never cited or referred to Trémaux's work in any of his publications and correspondence, he did have the 1865 work, in French, in his library.[vii] Whether or not Darwin was aware of Trémaux's view of speciation consciously, a year later, in the very next edition of the *Origin*, in 1866 (fourth edition), Darwin added the italicised words to his summary of the arguments of the chapters on geology (chapters IX and X, pp409f):

> … although each species must have *passed through numerous transitional stages, it is probable that the periods, during which each underwent modification, though many and long as measured by years, have been short in comparison with the periods during which each remained in an unchanged condition. These causes, taken conjointly, will to a large extent explain why—though we do find many links between the species of the same group—* we do not find interminable varieties, connecting together all extinct and existing forms by the finest graduated steps. (Darwin 1866: 409f).

[vii] Down House library, pers. comm. to John Wilkins, July 2006.

Now, it is not established that Darwin *did* read Trémaux and revise his ideas accordingly, but it is suspiciously coincident, as Darwin was fluent in French and read French naturalists assiduously. Moreover, this precedes the work of Moritz Wagner, whose geographical theory of speciation is remarkably similar to Trémaux's and who also doesn't cite him, by two years (Wagner 1868). Darwin cites Wagner's work extensively, and they had a famous debate in publication over the cause of speciation, whether it was due directly to selection, as Darwin thought, or indirectly due to local adaptation, as Wagner thought. It is very likely that Darwin was influenced by Trémaux's raising of the issues, if not his formulation.[viii] It is also possible, though we can find no evidence in Wagner's works, that he, too, was influenced by Trémaux.

This passage of the *Origin*, incidentally, is often cited by commentators on the punctuated equilibrium theory of Gould and Eldredge, to show that it is not a novel idea. And this leads us to a curious episode in the history of Trémaux interpretation. Only one post-Engels commentator (apart from Paul) actually has taken the trouble to read Trémaux's work – Stephen Jay Gould, and here is the full extent of what he had to say (apart from a mention of a diagram of Trémaux's in his 1997: 39f):

> I had long been curious about Trémaux and sought a copy of his book for many years. I finally purchased one a few years ago—and I must say that

---

[viii] Gould (2002: 745-749) tries to argue that Darwin was influenced by Falconer, but this appears in an letter dated 1 October, 1862 (available online at <http://www.darwinproject.ac.uk/darwinletters/calendar/entry-3746.html>), which does not indicate any punctuationism in Darwin's thought – although he does indicate that migration may have maintained adaptations in nearly identical conditions – and the publication of the fourth edition was four years later. Although no other edition of the *Origin* occurred between this correspondence and the fourth edition, Trémaux's work would have been fresher in his mind than Falconer's at the time he did revise it, in the spring of 1866 (Browne 2002: 267), although he had meticulously kept the criticisms and reviews to hand for that revision. We think Gould is over-interpreting the importance of that letter. In any case, we are not proposing that *only* Trémaux's book was influential on Darwin in this respect.

> I have never read a more absurd or more poorly documented thesis. Basically, Trémaux argues that the nature of the soil determines national characteristics and that higher civilizations tend to arise on more complex soils formed in later geological periods. If Marx really believed that such unsupported nonsense could exceed the *Origin of Species* in importance, then he could not have properly understood or appreciated the power of Darwin's facts and ideas. (Gould 1999: 90)

But if, as we have suggested, it is the commentators who have not understood Trémaux, it is time to ask why he has received these criticisms. Why, in particular, did Gould treat him so poorly, when Trémaux's view of evolution is so close to the view Gould and Eldredge proposed under the term "punctuated equilibrium theory"? Trémaux even uses the term "equilibrium", and clearly believes that most phenotypic change occurs early in the history of an isolated population leading to speciation. Is it because Gould knew of Trémaux's poor reputation via the Marx–Engels correspondence, and wished to avoid his own theoretical views being hitched to such a nag of a horse? We consider it very likely. But had Gould read Trémaux charitably in the light of prior literary naturalists such as Buffon, whose influence was still strong at the time, he might have seen that *sol* was generally used in French natural history works for what came to be known as "habitat", and that Trémaux was a selectionist, not a "Lamarckian". The claim that Trémaux believed more complex civilisations would form on younger (i.e., later) soils is in fact a gross misinterpretation of Trémaux's actual views, literary merits notwithstanding.

Conclusion

We think that Trémaux has been unfairly treated by association with Marx and Engels, and their own misreading of his ideas. It is not clear that Trémaux was unduly racist, and indeed he seemed to think that adaptation was purely to local habitats, and there was no absolute valuation of racial differences. Indeed, he thought that populations could be exchanged and identical results would eventually follow, which is about as adaptationist and plastic a view of human nature as one might find. The reasons for the Marx-Engels misinterpretation is of no consequence for the value of Trémaux's ideas.

His view of speciation was that local demes (colonies) would reach an adaptive equilibrium rapidly, and thereafter remain static by the process of interbreeding

(*croisement*). This is very similar, both in intent and form, to the punctuated equilibrium views of Gould and Eldredge and the allopatric speciation theory that is the common view today. He is perhaps the first person to treat the species problem as being one of definitions of the species concept, and directly or indirectly he probably influenced the subsequent debate, including a likelihood that he affected Darwin's own views around 1865–66.

Contributions

The initial translation of the text and quotations from French language books was done by Prof. Nelson, and the text revised by Wilkins. The contributions to the main article are equal. John Wilkins' work on this paper was supported by Australian Research Council grant FF0457917. Thanks are due to Jon Hodges and Paul Griffiths for helpful suggestions.

The text

Pierre Trémaux, Chapter VIII, "Formation of Species" (Trémaux 1865) translated by Gareth J. Nelson, with revisions by John S. Wilkins.[ix] Pages 127–165. Text in square brackets are editorial comments and notations. Footnotes marked by roman numerals are editorial.

"The word *species* is perhaps the most commonly encountered term in the study of the natural sciences. It is the first word and the last according to a celebrated zoologist[1], and on the day we are totally in control of it, we will be very close to the millennium of science in general."

1. I. Geoffroy Saint-Hilaire, *Histoire naturelle génerale des règnes organiques*, vol. II, p. 349. [(Geoffroy Saint Hilaire 1859)]

[128] The most formidable task of the naturalist, says Candolle, is to deal with *species*.

Species are fixed and of independent creation, says one school. They are variable and related among themselves, responds another. "We show one fact, fixity as far as can be traced," responds the first, "and you, you do nothing but expose an hypothesis without proof and one that encounters the strongest objections."

All schools agree in recognizing the greatest difficulties, and posing the most serious objections, to the transformations of organisms in order to pass from one species to another.

"If all species descend from other species by gradual, continuous transitions," says Bronn, and many others, "how is it that we do not find innumerable [129] transitional

[ix] [*Translators' note:* Whenever Trémaux has used the term "being" (*être*), we have rendered it "organism" for clarity, which was a common English usage in the period and earlier (cf. Whately 1875: 183).]

forms everywhere? How is it that species are so well defined, and that everything is not confusion in nature?"

"These difficulties are so grave," says Mr Darwin[1], "that I have been shaken by them for a long time… What geological research has been unable to reveal to us is the existence of numerous degrees of transition, as close to one another as recent varieties, and relating among themselves all known species. This is the most important of the objections that could be raised against my theory."

"This objection is decisive," cries Mr Flourens[2]. "This eternal distinction between species is both the greatest marvel and the greatest mystery in nature."

"The mystery of mysteries," others have said before him.[x]

---

[x] [John Herschel, in a letter quoted by Charles Babbage in the *Ninth Bridgewater Treatise*, (Babbage 1837) and quoted by Darwin in the opening paragraph of the *Origin*. *Trans.*

In the 1878 summary book (Trémaux 1874), this paragraph is followed by the following:

> So all of the mysteries fall like a house of cards faced with two great laws: one relative to the habitats and the conditions [*milieux*] that *diversifies* organisms, the other to the intermediate, or average, product of interbreeding that constantly unifies in the same species all of the organisms that common fecundity can embrace. And to understand the immense power of unification achieved by interbreeding within the species, it is necessary to observe that each organism has two parents in the initial ascending line, of which it is the average, four in the second (two grandmothers and two grandfathers). And before them, 8 great-grandparents, 16 great-great-grandparents, of which it is the average. Briefly, with continued doubling, each organism is the average of hundreds of thousand of ancestors after 60 generations! Thus, interbreeding groups in the same species all of the organisms it embraces, and thereby

1. *Op. cit.* [*Origin of species*] p241 and p422.

2. Pages 41 and 98 of his book criticizing the origin of species [Marie Jean Pierre Flourens, 1794–1867 (Flourens 1864)].

[130] "The secret that God has reserved to himself," says Mr Duruy.[1]

Faced with such testimony one must acknowledge that the difficulty is great. But really, the solution is simple; so simple that, for not having found it, one could accuse our predecessors and all antiquity of blindness, if we did not keep in mind the view of the most eminent [scientists] of our era, which will help us towards this mystery of mysteries. Here is this point of view:

"The characters of the parent [species] could be *different*. In this case the corresponding characters of the child [species] would be a *consequence* [*résultante*], that is to say, in reality, a new character that did not exist in the father or in the mother.

"The same cause operating in each generation would evidently

1. *Histoire de la formation du sol français* (first part).

[131] produce effects of the same nature. Simple heredity, direct and immediate, is in certain respects a source of new variation of the first type."

> separates distinct species; thus the species is constituted by all of the organisms that, being able to reproduce together, by this fact actually group together their descendants in a type and the extent of the possible and continuous interbreeding makes precisely the difference that separates related species.

Clearly, he here expands on the notion of the causal influences of *sol* and the *milieux* to indicate that this is not simply a matter of adapting to "soil", as the standard misinterpretation has it. This supports the Darwinian selectionist nature of his theory.]

Before going on, dear reader, let me ask a question: does this reasoning seem just, or does it seem false? In other words, the father, the mother, and the child, do they constitute a source of variation so that there are three types instead of two? …

You may respond most probably, yes, and our predecessors, and all of antiquity, would be absolved.

But wait! A hair, an imperceptible thread, has slipped into this reasoning and vitiated it; the defect is this: the father and the mother belong to the current generation that is going to disappear, the child to the generation that succeeds it. Thus, the generation which disappears *unites* as a type in the following generation.

[132] This is quite contrary to the point of view that we have just cited: instead of seeing a source of *variation* of types, we find a cause of their *unification*. And, if we have a large group of individuals, the definitive consequence will be the same after a certain number of generations.

Thus, let us take a highly variable population, where we find the most perfect and most imperfect types, the blackest as well as the whitest tints, in a word everything that is most disparate. At the moment of interbreeding, what will happen: if two similar organisms unite, their offspring will continue the same type; but if one of the progenitors is beautiful, and the other ugly, one black and the other white, the generation that will follow will be a *consequence*, which is to say, an intermediate type. And if, as is probable, different types cross only [133] in part in each generation, a certain number of generations will be sufficient for all of the types to increasingly *unite* and in the end form only one average type, apart from causes of variation that arise from other sources.

Readers, permit me another question: now that this great fact is clear and you see that we are on the road to discovery, do you understand the mystery of the formation of species? … perhaps not yet. So our predecessors can be totally excused for not having recognized it, even though all of modern science is superfluous for its recognition and serves only for its confirmation.

Well then, what is this great mystery?

Two principal notions have served to define species: resemblance between individuals and the ability to reproduce. To the extent that the first of these conditions, which is only a [134] consequence of the second, can be abandoned in order to concentrate on the second, one approaches the solution to the problem.

For Laurent de Jussieu, the species is a succession of individuals that are entirely similar, perpetuated through reproduction.

For Buffon, the species is the constant succession of individuals which reproduce, and the character of the species is continual interfertility [*fécondité*].

Blainville defines species: the individual repeated in time and space.[xi]

According to Lamarck, the species is a collection of similar individuals, which reproduction perpetuates in the same state so long as the circumstances of their situation does not change enough to cause variation in their habits, their character, and their form.

Of definitions of species, there are as many as there are naturalists, and this is the inevitable consequence of ignorance of the [135] principle on which the species is based. Even so, Flourens contributes, with Buffon, Illiger, Koelreuter, Goertner and others, to help us take a step towards the question, by characterising a species only by *continuous fecundity*. At this point, one need only distinguish the effect from the cause.

We understand perfectly what happens when two organisms cross that are as different as possible but are freely interfertile. The product in general is an intermediate type,

[xi] [Henri Marie Ducrotay de Blainville]

or about average between the two extremes.[1] Also, in the sum of many crossings, it is even more exactly the same. We also know that

1. "I give to the product of crossed unions, the name *Mongrel*, because *Mongrel* seems to me to comprise half of each of the two producing species" (Flourens, *op. cit.,* page 109).

Numerous observations have, indeed, noted that the types of the descendants are in general intermediate between those of the generators of different races or species, and if there are some rare exceptions, they could not have a marked influence on the group.

[136] if the organisms are too different, one from the other, they are unable to produce descendants capable of reproduction, or even to procreate at all. The effect of interfertility and the limits of its action, so to speak, two results of experience that are perfectly known, are all that is needed to form and reform species, whenever there occurs a cause of the modification of the established order.

With these facts, so simple, and known by all, the mystery reveals itself. God has delivered to us his secret.

First the definition of species, the essence of the great secret:

The species is composed of all the organisms which, able to procreate together, actually do so and group their descendents together in an intermediate type.

To enter into the details, we will follow step by step the application [137] of the principles we have developed; then we will submit the result to checking [*contrôle*] by all the facts that nature offers.

Imagine now an expanded and mixed group of organisms, diversified, but not to specific level; or instead a moment in which a geological event brings some change to a species, diversifying that part of each species that is in a new habitat [*couche géologique*; *lit.* geological layer] which is discovered or is formed. Whether this geological event is the result of an abrupt movement or a very slow process that gives the effects of crossing time to act, the definitive result would be the same. Admit, for argument's sake, that the range of variation, from the simple to the complex, is

continuous with [138] infinite degrees of transition or of varieties without a clear demarcation.

From the moment when, in this suite of organisms, interfertility extends within a fraction limited by a certain degree of difference, whether very pronounced or slight, it is evident that from then on, this interfertility will group in the same species and type all the organisms that it does, in fact, embrace. And this species will be precisely characterized by interfertility, because it is that which founded and unified, in an average type, all of the organisms affected by it. One understands why interfertility persists among all of them, because it would have constantly united them in a single average type. But if interfertility extended to just fractions, each representing one-hundredth of these organisms, it is clear that after a certain number of generations, these organisms would be grouped in one hundred species, [139] each unified and characterized by the interfertility that formed them.

With respect to the possibility of crossing, it is thought that it is very easy between organisms of adjacent areas, but it is more difficult if the areas are far apart. On this subject, I can make two remarks. First, a single cross between organisms unites them in their offspring in an average type, whereas a long suite of generations, combined with differing conditions of habitat, is needed to produce the divergence that a single crossing might in a given case destroy. It is understood, thereby, that fairly rare crossings or those that take place little by little in adjacent areas are sufficient to return or maintain the unity of the species. But if a natural barrier should prevent such crossing, well then the species would indeed be circumscribed, and this is precisely what nature shows to us.

[140] Another consequence is that if some fractions of a species become separated and widely distant from the rest of that species, they would again establish a condition of equilibrium, because they would not be ordinarily distributed in some areas of diversity or habitat [*sol*], and this variety of habitat would tend to produce various races which would equilibrate through crossing.

Once species are formed and distributed, special conditions are necessary in order to lead to the formation of a new species: not only the isolation of a race from the rest of

its species, but also that it is isolated in a fairly homogeneous terrain, which, moreover, is different from the average terrain of the species, else it would tend to maintain the average type. It would be exceptional if a new species could arise in such a way.

So we see that crossing strongly [141] counteracts the modifying effects of the habitat, and that it always tends to unify in an average type the degenerate varieties that arise in poor habitats with the more perfect races of the recent terrains. Now let us look at what happens to a variety which finds itself in a new habitat.

If the organisms that this habitat tends to transform, so as to perfect them, continue to cross with those of less favourable habitats, they could only attain a difference of variety, even without numerous crossings typically displayed within a species.

Thus, if crossing within the species is impeded by whatever cause, the favoured variety would necessarily become a species, and continue to change up to the point where crossing with the mother species would no longer produce interfertility. By this alone, a [142] certain degree of difference conflicts with continuing interfertility, and one understands that this degree of difference, and its effect, is inevitable if change continues. We will later show (chapter IX) that it happens, in our own epoch and under our own eyes, in humans and plants. Once constituted, the new species can expand into the areas occupied by the mother species without ceasing to be distinct.

Despite this independence of the new species, its progress will not continue, either because it will have reached the normal degree of perfection which is appropriate in its habitat, in respect of its starting point and the conditions in which it is found, or because while multiplying due to the good ground which supports it, it will be obliged to invade various terrains whose contrary tendencies are neutralized by crossing.

[143] Also, a new species would be able to form in a similar way, by degeneration, if a variety is confined to an unfavourable habitat; in which case instead of being able to invade other areas it would be exposed to extinction in the face of other species because of its own inferior qualities.

A new and progressive species would become all the more stable as it extended into a variety of habitats; for then, one part of it in a favourable habitat and another in an unfavourable one, there would be further progress in the one and degeneration in the other, and these would tend to equilibrate and unite through crossing. The species would thus remain in this sort of equilibrium for a long time; for the general amelioration of the habitat is hardly noticeable even over a span of a few thousand years, and would hardly produce any appreciable results. [144] Even so, says Bronn, "species found through several geological horizons show a few variations in their characters." This is explained by the slight general modification of the habitat.

It is not really necessary that the small colony undergoing transformation is absolutely isolated, because if some individuals escape from it before they are sufficiently transformed, they would simply be absorbed within the mother species. The small colony, in contrast, only being able to progress and multiply, would have a greater tendency to expel individuals rather than receive them – a circumstance that would protect it.

The most remarkable fact of this transformation is that it would necessarily take place in a very limited area, because it would belong exclusively to a new habitat. The facts already cited show that the [145] transformation would occur rather quickly, relative to the length of the geological epochs, as long as it is not impeded by crossing with other races. Also we see that it could not take a very long time because there are two causes that would tend to terminate it. The manner in which the species forms shows that transitional forms could not persist, because of crossing either with the new species, or with the mother species. So we see why, if a species formed in a small area, and afterwards spreads from area to area, it seems to have appeared all of a sudden, as paleontology generally indicates.

This *all of a sudden* for paleontology involves a really rather large number of generations; for we know how slowly the thinnest geological layers form. And the species newly spread, being better adjusted to [146] the conditions of the time, would necessarily progress quickly, and at the expense of the older species, over which it would prosper in the conditions of the equilibrium of life.

So we understand how it is, as Bronn says, "gradual development is observed only very occasionally."

We begin, however, to discover some of these forms transitional from one species to another: between the cave bear and the brown bear, both very common, there has been found, as to time and to type, a specimen of *Ursus priscus*, of which the head and lower jaw are still united. Between the langur [*semnopithèque*] and macaque there has been found an entire skeleton of an intermediate monkey. And we have seen with our own eyes an analogous effect operating on varieties transported from Europe to America. These need only a few generations to acquire new [147] characters, which persist indefinitely, until there is a new cause of modification.

Thus, the short time period of transformation, few organisms undergoing change, prompt grouping into distinct species, unfavourable conditions for fossilization because of the relatively recently formed habitat or geological elevation – these are among the many causes that make it difficult, if not impossible, to discover organisms intermediate between species.

Paleontology shows us also that species persist mostly less than one geological epoch, but sometimes much longer. We see that thousands, even hundreds of thousands of generations, are produced by the entire species only with variation into races, comparatively a feeble fraction, or one only, which transforms in isolation during a small number of [148] generations. From this it is no surprise that transitional organisms are so rare, especially when one considers that they generally live during times unfavourable to their preservation. Besides, if these rare organisms actually come to hand, they risk being taken for anomalies, or for a variety of a related species. And in effect they are not otherwise.

The degree of separation of species thus becomes the confirmation of the manner in which the species originate.

Organisms that interbreed promptly give to their offspring an average type, while the habitat can cause their differentiation only very slowly, thus by this principle the manner by which species arise and become distinct becomes evident.

Besides, many facts in nature, which we will mention in part, [149] confirm this principle. We cite below a chain of facts that are the consequence, of which the clarification is also the solution searched for in vain by more than one naturalist.

Buffon has pointed out as a law the following fact that is only the consequence of the law of interbreeding that we have exposed: “no animal of the tropics of one of the two grand continents [Old World and New] is found in the other.”[1]

Mr Flourens has confirmed this distribution of organisms, in recognizing like Buffon that before the conquest no species of the Old World existed in America. Mr de Quatrefages has also developed this fact in relation to the following circumstances in order to contest the doctrine of centers of creation: Mammals of Australia, or New Holland, and the small neighboring islands are clearly distinct from those that

1. Clearly, man is an exception here.

[150] are seen elsewhere in the world. With respect to insects, this area relates to New Zealand and to New Caledonia. The facts become even more striking when one compares the animals living in air and those in water, or even these among themselves, when different oceans are separated by a small extent of dry land. At the Isthmus of Suez the aerial faunas are nearly identical on the coasts of the Red Sea and the Mediterranean; the marine faunas in contrast are extremely unlike on the opposing coasts. Mr Edwards among others has not found a single crustacean common to both. And it is the same at the Isthmus of Panama.

Australia[xii] is essentially the home of marsupials, America the home of edentates. Between these two areas there are few if any genera in common, and fewer species in [151] common, and *these characteristic differences become accentuated as one considers higher groups*. For example, in comparing the Old World and the New, one has the most extensive regions that it is possible to compare.

The two regions have in common only five or six genera of bats, and only one species of these; not a single genus, nor a single species, of monkeys. Australia forms with these two regions a contrast still more marked. South and North America could form two distinct regions; and North America merges in part with Europe and Asia, South America is completely separated from one and the other.

Also, the long maritime coastlines, separated either by the large [152] continents or by the deep ocean basins, offer the same distributions of species, of genera, etc. Thus the east coast of America has a fauna very different from the west coast; and this fauna is likewise very different from that of coast of the West Pacific.

Each of these coasts extends very far from south to north; this shows the small influence of climatic conditions, which have always been considered as the principal modifying agent. But from the region of the West Pacific to the Indian Ocean, and even to the coast of Africa, where numerous islands and the continents offer many places that facilitate communications, the fauna is much more uniform.

Mr Wallace had called attention to the remarkable fact that the birth of a species coincides, in time and in space, with [153] another pre-existing species that is closely allied to it.

So there are many facts that seem inexplicable in ignorance of their cause. The origin through interbreeding, having separately formed each species, easily explains this distribution so far as it concerns species. If the interbreeding is found in the Red Sea,

---

[xii] New Holland [*La Nouvelle-Hollande*]

it is evident that it cannot propagate itself in the Mediterranean. But why does this assemblage conserve the same linkage with respect to families, genera, if these had not previously formed by the same filiation as the species? Why are genera that have a greater than average number of species found in the same areas as their species that have a greater than average number of varieties, if these genera were not formed by the same descent as the varieties? The area [154] we will see is not the cause of this linkage.

The transformation of organisms by action of the habitat, and their grouping in species by interbreeding, fully explain all of these facts. It is certain that the grouping in species by interbreeding acts independently in the Mediterranean and the Red Sea, in the Old World and in the New, also in Australia; that the species of marsupials, or those of edentates, in dividing into new species, give birth to species in the same genus and in the same continent where they are found; that the mammals of Australia have less possibility to disperse to surrounding islands, relative to insects that may be transported by various means, even a branch that also carries its seed; that the terrestrial or aerial fauna of the Mediterranean and the Red Sea freely interbreed [155] together, while the marine faunas cannot do so; that in North America, the fauna can have some resemblance with that of Asia and Europe, from which it is only incompletely separated, etc., etc.

Following from the manner of species formation, one understands why unisexual organisms, or those that interbreed only rarely, are also the most variable; because to that extent they lose the ability to unite themselves through interbreeding.

If creations had taken place by species, or separately, one would not understand why cave animals would not have a special form, and the same one in Europe and America; why they have rudiments of eyes that are non-functional, why despite the special conditions to which they must conform those of America belong to the fauna of that region, as those of [156] European caves belong to the European fauna.

This explains why animals of the same genus that live in different caves are also different species, because interbreeding with inhabitants of another cave could no longer occur since their introduction into those cavities.

In a word, the moment when animals of one continent, one ocean or one region can not longer, or only a little, communicate with those of another, it is certain that from the beginning of the barrier the species form in isolation in each continent, ocean or region, without being able to unite by interbreeding, even when for such there is enough similarity in constitution.

But once species are formed, one understands that it can, even must, happen *exceptionally* some cases of accidental dispersal beyond these natural [157] barriers, because only rarely can they be absolute. And this is precisely what happens: it is sufficient that transport be possible in the course of the ages for it also to happen *exceptionally*. One notices in effect that the most numerous exceptions involve organisms for which accidental dispersal is the easiest, such as a branch or a trunk floating on the ocean, at the mercy of wind and current, transporting from coast to coast seeds and even insects. Also herbaceous plants, being more easily dispersed and more adaptable to soil than trees, are also more widely distributed; while certain species of mammals can communicate only with greater difficulty, more rarely or not at all, except a few cases: as for example that when an isthmus connects islands to a continent; as seems to have occurred among the Sunda Islands, or even also [158] by floating ice. If one notices that the frequency of these exceptions exists precisely in relation to the ease of transport of the species, this circumstance becomes a confirmation of the law. In any case we will point out in the second part of this work, with respect to the distribution of simple organisms, a large source of error that should not be confounded with the cases of dispersal.

With respect to the variations, or to the absence of variations, shown by these emigrants in their new habitats, and for which one has vainly sought the cause, they depend principally on the physical environment [*sol*], which be either similar or not, the other factors being only accessory.

Also it is worth remarking that the variations could have occurred a long time ago. Diverse circumstances could have led to divergence of characters, transformation of species, [159] then by new transformations, and convergence of characters, if the conditions once more become similar. So it is with the plants that, more than with

animals, are subject to climatic action. One sees that alpine floras differ from others, and, by the same reason, present certain analogies in areas widely separated.

For the freshwater fauna distributed in separate lakes and rivers, the same causes would have been able to lead to analogous results. The same species in the ocean could transform itself in the same way in encountering the same conditions; but the eggs could very well be transported from one river to another by aquatic birds that frequent them one by one, accomplishing for this fauna a work analogous to that for the plants by insects and birds. [160]

Mr Darwin cites many facts that illuminate this distribution, among others the following: "Two times I have seen," says he, "a duck emerging from a pond, covered with duckweed, with some of these plants still adhering to the feathers of its back. I have suspended a duck's foot in an aquarium where many shellfish eggs were in process of hatching and I soon found it covered by a large number of shellfish just recently hatched; they adhered so firmly that I was unable to detach them in taking the foot from the water. Even emerged, these shellfish lived from twelve to twenty-four hours."[xiii]

A grand fact that confirms the distribution of species in terms of their ease of dispersal is that among the species of the same country or the same region many of them are common and widespread, but when it concerns regions widely separated the species are very different regardless of the [161] similarity of climatic and other conditions

Consider another order of facts, reptiles, whose means of dispersal are the most restrictive, have the most restrictive habitats among the particular faunas. Birds, in contrast, have the greatest facility for dispersal, and exhibit the least restricted distributions.

[xiii] [(cf. Darwin 1859: 385)]

We restrict ourselves to these few details concerning accidental dispersals of species, which can be produced by a great diversity of circumstances.

This distribution corresponds then in an evident manner not with certain *influences of regions* but rather with *natural barriers*, which have led to the relationships between species, genera, families, etc., because one sees that it is not regions that determine this ensemble, but rather the barriers, and this to the point that the obstacle that is a barrier for one [162] species and not another acts precisely in reason of this condition.

Besides one cannot say that one of these regions cannot support species from the other because if they are transported there, they propagate themselves very well.

So we recognize therefore: the formation of species in the localities where they are confined; then their dispersal in the proportion presented by their ease of dispersal and their modifications according to the habitat.

All of this state of affairs is thus the most exact consequence of the laws that we have exposed. As for man, who occurs in all continents, we know that his superiority has enabled him to cross oceans and to survive inclemencies. This exceptional condition is the consequence of his superior faculties.

But, adds Mr Flourens, "If the species are different, then they are *parallel*, and [163] the law of parallelism among living species is found among fossil species. Living species, fossil species," says he, "species of one continent, those of the other, there is always the same return, the same source of the type, a same design. The animal kingdom is one."

The animal kingdom certainly is one, but that fact is far from favoring the presumed eternal distinction between species.

There are many facts, many affirmations of the laws that we expose. Organisms being governed by the habitat, and the habitat of one continent perfecting itself progressively as that of the other, an analogous cause has produced an analogous

effect; the progressive development of the habitat, that of the organisms, the same law, and same linkage.

One might cite many examples that show how species originate; but the principle of their formation, that we have posed, appears so evident [164] by itself that further insistence seems useless.

One now understands the true extent of the terms that we accept. Thus, one understands that by genus, species or race we do not mean organisms that are essentially different, but in general many ages or many stages of development of the same organisms.

With respect to the extinction of species, a few words are sufficient to explain it. It is a necessary condition of vital equilibrium among organisms. The productive potential of a habitat having a limit, the species that are the least adapted to the time and to the conditions of life, must naturally be extinguished in face of those better adapted. And the new species must often prevail over those with a less advanced organization or are particularly suited to an older epoch.

To establish the transformation of species in [165] response to modifications of the habitat, from the first ages, is to pass gradually from the most simple organisms to the most complete; it is to unveil the creation of man! Psychological faculties, or instinctive and mental, are modified in relation to the degree of physiological perfection, and this unveils also the origin of all the instincts, and also the highest intelligence.

References

Babbage, Charles. 1837. *The Ninth Bridgewater Treatise: A fragment*. London: John Murray.

Bateson, William. 1894. *Material for the study of variation treated with especial regard to discontinuity in the origin of species*. London: Macmillan.

Browne, Janet. 2002. *Charles Darwin: A biography*. Vol. 2: The power of place. New York: Knopf.

Carver, Terrell. 1984. Marx, Engels and scholarship. *Political Studies* 32 (2): 249-256.

Cohen, Bernard I. 1985. *Revolution in Science*. Cambridge MA: Harvard University Press.

Colp, Ralph, Jr. 1974. The Contacts Between Karl Marx and Charles Darwin. *Journal of the History of Ideas* 35 (2): 329-338.

Conry, Yvette. 1974. *L'Introduction du Darwinisme en France au XIXe Siècle*. Edited by Paris, *Librairie Philosophique*: J. Vrin.

Cuvier, Georges. 1812. *Discours sur les révolutions du globe (Discourse on the Revolutionary Upheavals on the Surface of the Earth)*. Translated by I. Johnston. Paris.

Darwin, Charles. 1859. *On the origin of species by means of natural selection, or The preservation of favoured races in the struggle for life*. London: John Murray.

———. 1866. *On the origin of species by means of natural selection: or the preservation of favoured races in the struggle for life*. 4th ed. London,: John Murray.

Darwin, Charles R. 1869. *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. 5th ed. London: John Murray.

Eldredge, Niles, and Stephen J. Gould. 1972. Punctuated equilibria: an alternative to phyletic gradualism. In *Models In Paleobiology*, edited by T. J. M. Schopf. San Francisco: Freeman Cooper: 82-115.

Eldredge, Niles, Stephen Jay Gould, Jerry A. Coyne, and Brian Charlesworth. 1997. On punctuated equilibria. *Science* 276 (April 18): 337c–341c.

Flourens, Marie Jean Pierre. 1864. *Examen du livre de M. Darwin sur l'origine des espèces*. Paris: Garnier Frères.

Geoffroy Saint Hilaire, Isidore. 1859. *Histoire naturelle générale des règnes organiques, principalement étudiée chez l' homme et les animaux*. Vol. II. Paris: Victor Masson.

Gerratana, Valentino. 1973. Marx and Darwin. *New Left Review* I/82: 60-82.

Gould, Stephen Jay. 1994. Tempo and mode in the macroevolutionary reconstruction of Darwinism. *Proc Natl Acad Sci U S A* 91 (15): 6764-71.

———. 1997. Redrafting the Tree of Life. *Proceedings of the American Philosophical Society* 141 (1): 30-54.

———. 1999. A Darwinian gentleman at Marx's funeral. *Natural History* 108 (7): 32-41.

———. 2002. *The Structure of Evolutionary Theory*: Belknap Press.

Gould, Stephen Jay, and Niles Eldredge. 1977. Punctuated equilibria: the tempo and mode of evolution reconsidered. *Paleobiology* 3: 115-151.

Harris, Marvin. 1968. *The rise of anthropological theory: a history of theories of culture*. New York: Crowell.

Junker, T. 1991. Heinrich Georg Bronn und die Entstehung der Arten [Heinrich Georg Bronn and Origin of Species]. *Sudhoffs Arch* 75 (2): 180-208.

Lecourt, Dominique. 1983. Marx au crible de Darwin. In *De Darwin au Darwinisme: Science et Idéologie. Congrès International pour le Centaire de la Mort de Darwin, Paris-Chantilly 13-16 Septembre 1982. Centre d'Histoire et d'Epistémologie de l'Université de Picardie*, edited by Y. Conry. Paris: J. Vrin: 227-249.

Lewes, George Henry, [Anon.]. 1856. Hereditary Influence, Animal and Human. *Westminster Review* 66 (July): 135-162.

Lotka, Alfred J. 1922. Contribution to the energetics of evolution. *Proc Nat Acad Sci USA* 8 (6): 147-151.

———. 1925. *Elements of physical biology*. Baltimore,: Williams & Wilkins company.

Lovejoy, Arthur O. 1959. Buffon and the problem of species. In *Forerunners of Darwin 1745–1859*, edited by B. Glass, O. Temkin and W. L. Straus. Baltimore, MD: Johns Hopkins Press: 84-113.

Mayr, Ernst. 1942. *Systematics and the origin of species from the viewpoint of a zoologist*. New York: Columbia University Press.

———. 1982. *The growth of biological thought: diversity, evolution, and inheritance*. Cambridge, Mass.: Belknap Press.

Mikulak, M. W. 1970. Darwinism, Soviet genetics, and Marxism-Leninism. *J Hist Ideas* 31 (3): 359-76.

Müller-Wille, Staffan, and Vitezslav Orel. 2007. From Linnaean Species to Mendelian Factors: Elements of Hybridism, 1751-1870. *Annals of Science* 64 (2): 171-215.

Naccache, Bernard. 1980. *Marx critique de Darwin*. Paris: J. Vrin.

Nelson, Gareth J. 1989a. Cladistics and evolutionary models. *Cladistics* 5: 275-289.

———. 1989b. Species and taxa: speciation and evolution. In *Speciation and its consequences*, edited by D. Otte and J. Endler. Sunderland, Mass.: Sinauer.

Parville, Henri de. 1865. *Un habitant de la planète Mars*. Paris: J. Hetzel.

Paul, Diane. 1981. "In the Interests of Civilization": Marxist Views of Race and Culture in the Nineteenth Century. *Journal of the History of Ideas* 42 (1): 115-138.

Poliakov, Leon. 1974. *The Aryan myth: a history of racist and nationalist ideas in Europe*. Translated by E. Howard, *Columbus Centre series. Studies in the dynamics of persecution and extermination*. London: Chatto & Windus Heinemann for Sussex University Press.

Poulton, Edward Bagnall. 1903. What is a species? *Proceedings of the Entomological Society of London*: reprinted in Poulton 1908: 46-94.

Robert-Devillers, Flavien. 1999. Étude sur les critiques que Marx adresse à la théorie darwinienne, en tant qu'elle serait le reflet des catégories de la théorie économique de l'époque, Université de PARIS X.

Rogers, J. A. 1974. Russian opposition to Darwinism in the Nineteenth Century. *Isis* 65 (229): 487-505.

Rutherford, H. W., ed. 1908. *Catalogue of the library of Charles Darwin now in the Botany School, Cambridge*. Cambridge: Cambridge University Press.

Stack, David A. 2000. The first Darwinian left: Radical and socialist responses to Darwin, 1859-1914. *History of Political Thought* 21 (4): 682-710.

———. 2003. *The first Darwinian Left: Socialism and Darwinism 1859-1914*. Gretton, Cheltenham: New Clarion Press.

Stanley, John L., and Ernest Zimmermann. 1984. On the Alleged Differences Between Marx and Engels. *Political Studies* 32 (2): 226-248.

Stebbins, Robert E. 1965. French reactions to Darwin (1859-1880), University of Minnesota.

Tort, Patrick. 1996. *Dictionnaire du Darwinisme et de l'evolution: Livres*. Paris: Presses Universitaires de France.

Trémaux, Pierre. 1849. Notice d'un voyage sur le cours du Nil et dans des parties inconnues du Soudan, chez les nègres Bertha, du Darfok et du Dar-Gourum. *Bulletin de la Société de Géographie* 3 sèr., 12 (67-72): 250-278.

———. 1850. Notes sur la localitè ou sont situèes les principales mines d'or du Soudan oriental, et observations critiques sur le rècit du Colonel Kovalevski relatif à cette même contrée. *Bulletin de la Société de Géographie* 3e sér., 13 (73-78): 201-232.

———. 1855. Quelques détails sur les prétendus hommes à queue. *Bulletin de la Société de Géographie* 4e sér., 9 (49-54): 139-148.

———. 1856. Épisode d'un voyage au Soudan oriental et rémarques sur l'esclavage. *Bulletin de la Société de Géographie* 4e sér., 11 (61-66): 153-164.

———. 1862a. Remarques sur l'Afrique centrale et orientale. *Bulletin de la Société de Géographie* 5e sér., 3 (13-18): 69-86.

———. 1862b. Remarques sur l'Afrique centrale et orientale (fin,). *Bulletin de la Société de Géographie* 5e sér., 3 (13-18): 147-165.

———. 1865. *Origin et transformations de l'homme et des autres étres*. Paris: L. Hachette.

———. 1874. *Origine des Espèces et de l'Homme, avec les causes de Fixité et de Transformation, et Principe Universel du Mouvement et de la Vie ou loi des Transmissions de Force*. 4th 1878 ed. Bale, Switzerland; Paris: Librairie Française; Sagnier.

Vadée, Michel. 1992. *Marx: Penseur du possible*. Paris: Meridiens Klincksieck.

Wagner, Moritz. 1868. *Die Darwin'sche Theorie und das Migrationsgesetz der Organismen*. Leipzig: Duncker & Humbolt.

———. 1873. *The Darwinian Theory and the Law of the Migration of Organisms*. Translated by J. L. Laird. London: Edward Stanford.

Wallace, Alfred Russel. 1858. Note on the theory of permanent and geographical varieties. *The zoologist* 16: 5887-5888.

Weikart, Richard. 1999. *Socialist Darwinism: evolution in German socialist thought from Marx to Bernstein*. San Francisco: International Scholars Publications.

Whately, Richard. 1875. *Elements of logic*. Ninth (octavo) ed. London: Longmans, Green & Co. Original edition, 1826.

Wilkins, John S. 2007. The Concept and Causes of Microbial Species. *Studies in History and Philosophy of the Life Sciences* 28 (3): 389-408.