Darwinians that aimed at similar goals.

In his later years Charles Darwin's closest professional relationship was with George John Romanes, to whom he entrusted the burden of his life's work. (FORSDYKE, 1999, p. 112)

INTRODUCTION

The early scientific career of George John Romanes (1848-1894) flourished under Charles Darwin's protection. In 1870, while he was a student at Cambridge, Romanes started physiological research under Michael Foster's supervision and soon began to study Darwin's works (LESCH, 1970). In 1873, he discussed an evolutionary issue in a letter to *Nature* that called the attention of Darwin himself (ROMANES, 1873). The old man wrote a kind letter to the young student, starting a correspondence that was to last for two decades. In the next year, Darwin invited Romanes to meet him. There followed a friendship and collaboration between the two men. According to Romanes' wife:

From that time began an unbroken friendship, marked on one side by absolute worship, reverence, and affection, on the other by an almost fatherly kindness and a wonderful interest in the younger man's work and in his career (ROMANES, *The life and letters of George John Romanes*, p. 14).

Of course, their relationship was asymmetric. When they first met, Romanes was 26 years old and had published no relevant scientific contribution. Darwin, who was 65, had published already his main evolutionary works (*Origin of species, Variation of animals and plants under domestication, Descent of man*). Why did Darwin take a special interest on Romanes?

Joel Schwartz has already analyzed some features of the relationship between Darwin and Romanes (SCHWARTZ, 1995). According to him, at the time when Romanes

^{*} Group of History and Theory of Science, DRCC – IFGW – UNICAMP, Universidade Estadual de Campinas, Brazil, rmartins@ifi.unicamp.br, Caixa Postal 6059, 13081-970 Campinas, SP, Brazil

together by personal loyalties and commitment to a particular ideology" (BOWLER, *Charles Darwin: The man and his influence*, p. 150).

Within these principles, the chief Darwinists themselves disagreed considerably over details. Darwin accepted a small element of Lamarckism; T. H. Huxley was a saltationist; while Wallace even advocated divine intervention in the evolution of man. This flexibility helped to disarm the critics, because objections to natural selection could be sidestepped by appealing to the possibility of supplementary mechanisms. At the same time, the Darwinists never fought openly among themselves. They agreed to differ in the hope that future research would solve their problems and thus were able to present a united front to the world, confident that their basic ideas were sound (BOWLER, *Evolution. The history of an idea*, p. 195).

Thomas Huxley always tried to support Darwin's theory, but as a matter of fact Darwin was not altogether happy with Huxley's interpretation of natural selection². It seems that Huxley was not highly committed to the details of Darwin's theory (BOWLER, *Charles Darwin: The man and his influence*, pp. 142-145). Besides all that, in the early 1870's Darwin was fighting new battles.

In 1868 he had published the first edition of *The variation of animals and plants under domestication*, where he proposed his hypothesis of pangenesis to account for hereditary phenomena. Besides explaining many phenomena widely accepted by everyone, the hypothesis of pangenesis provided a theoretical basis for use-inheritance³.

This hypothesis was very dear to Darwin. It has been argued sometimes that Charles Darwin only invented the hypothesis of pangenesis as an answer to Fleming Jenkins

¹ Wallace did not accept Darwin's theory of sexual selection. He held rigidly to the theory of natural selection, without allowing any other causes for organic evolution. Besides that, he claimed that natural causes were unable to explain the origin of human mental endowment (WALLACE 1869).

² "So Huxley had reservations about the role of natural selection even though he praised Darwin and sprang to his defense. Darwin, in his turn, had reservations about Huxley's understanding of natural selection. After hearing Huxley speak on evolution in 1860, he said that 'as an exposition of the doctrine the lecture seems to me an entire failure' and added: 'He gave no just idea of Natural Selection'." (YOUNG, *The discovery of evolution*, p. 151).

³ Darwin always accepted the "Lamarkian" concept of use-disuse and inheritance of acquired characters. This principle is explicitly used in the *Origin of species*, and the *Variation* provided detailed evidence for it.

built for himself a more appropriate profile, with the proposal of a complementary theory ("physiological selection") that, if accepted, would place Romanes in a top position within evolutionary research.

ROMANES' EARLY RESEARCHES: MEDUSAE AND PANGENESIS

Romanes' scientific interests varied widely during his lifetime. Before Darwin's death, his main contributions to evolution theory were:

- 1. A detailed study of the mechanism of motion and of the nervous system of lower invertebrates (jellyfishes, starfishes, sea urchins) and the evolutionary significance of those findings.
- 2. An attempt to provide experimental evidence for Darwin's hypothesis of pangenesis.
- 3. A comparative study of animal and human intelligence, attempting to show that the mental evolution of animals led smoothly to the development of men's mental power.

He also presented minor contributions on other specific points, such as the reduction of useless organs. Moreover, Romanes was a highly successful lecturer, and produced popular but fairly rigorous presentations of Darwin's ideas.

His early researches, which began under Foster's supervision (1873), dealt with the physiology of jellyfishes. He studied the motion of medusae, presenting his first results as a M. A. dissertation (1874). After leaving Cambridge, the 26 years old Romanes moved to London, where he continued his researches on medusae under William Sharpey and John Burdon-Sanderson at University College. His family was wealthy, and he did not need any job – he devoted himself to scientific research just because he enjoyed it. For many years he maintained his own private laboratory in Dunskaith, where he spent the summers studying sea life (ROMANES, *The life and letters of George John Romanes*, p. 14). This was Romanes' profile when he first met Darwin.

It seems that Darwin was strongly impressed by Romanes. They talked about pangenesis, and agreed that Romanes could attempt to find experimental evidence for this hypothesis.

⁴ One relevant piece of evidence that Vorzimmer did not use is Darwin's Diary, where it was clearly recorded that the chapter on pangenesis of *The variation of animals and plants under domestication* was finished on the 21st November 1866 (DARWIN, *The life and letters of Charles Darwin*, vol. 3, p. 42).

⁵ In this paper I will adopt a very broad characterization of 'Darwinians': those who claimed that Darwin's theory was the best available, and who regarded themselves as followers of Darwin.

You will think me very self-sufficient, when I declare that I feel *sure* if Pangenesis is now still born it will, thank God, at some future time reappear, begotten by some other father, and christened by some other name.

Have you ever met with any tangible and clear view of what takes place in generation, whether by seeds or buds, or how a long-lost character can possibly reappear; or how the male element can possibly affect the mother plant, or the mother animal, so that her future progeny are affected? Now all these points and many others are connected together, whether truly or falsely is another question, by Pangenesis. You see I die hard, and stick up for my poor child (DARWIN, *The life and letters of Charles Darwin*, vol. 3, p. 78).

This is an instance of the critique suffered by pangenesis:

Pangenesis has not the advantages of Natural Selection, and cannot therefore hope for so ready an acceptance. It has the disadvantage of not being readily grasped, nor easily brought into confrontation with facts. It has the still greater disadvantage of being hypothetical throughout: not being one supposition put forward to harmonise a series of facts, but a series of suppositions, every one of which needs proof (LEWES, 1868, p. 507).

Two years latter, after the hypothesis had received a lot of criticism, Darwin wrote to Lankester (March 15, 1870): "I was pleased to see you refer to my much despised child, 'Pangenesis', who I think will some day, under some better nurse, turn out a fine stripling" (DARWIN, *The life and letters of Charles Darwin*, vol. 3, p. 120). Was Darwin trying to attract Lankester to help him? If that was his aim, he was not successful.

Taking into account those precedents, it is obvious that Darwin was eager to obtain Romanes' help. The main line of research involved an attempt to produce graft hybrids⁶. In the beginning of 1875, Romanes was already intensively working on experimental pangenesis, as shown by his letters to Darwin (ROMANES, *The life and letters of George John Romanes*, p. 21). All training Romanes had received was in physiology.

⁶ According to the hypothesis of pangenesis, when two plants are grafted together, there should occur an interchange of "gemules" between them. Those gemules should affect the reproductive organs of the plants, and lead to the production of hybrids that could be maintained by sexual reproduction.

was a nice hypothesis. At this time, he was preparing the second edition of *The* variation of animals and plants under domestication (Darwin to Romanes, 12/July/75, in: ROMANES, *The life and letters of George John Romanes*, p. 40), and he would be very glad if he were able to provide positive evidence for pangenesis.

Besides doing botanical experiments, Romanes attempted to graft animal organs and tissues: "Eventually the passing of the Vivisection Act caused me to abandon the whole research as far as animals were concerned" (ROMANES, *Darwin, and after Darwin*, vol. 2, p. 144). Romanes, with the help of E. Schäfer, also repeated Galton's blood transfusion experiments with rabbits, in the hope of obtaining positive results, but no effect was observed (ROMANES, *Darwin, and after Darwin*, vol. 2, pp. 145-146).

In 1875 Darwin decided to propose Romanes for the Linnean Society, with the support of Huxley and Hooker (Darwin to Romanes, 24/Sept./75, in: ROMANES, *The life and letters of George John Romanes*, p. 35). Up to that time, Romanes had published no relevant scientific paper – only small notes in *Nature*. As Romanes himself told Darwin, "I am an M. A. and a fellow of the Philosophical Society of Cambridge, but otherwise I am nothing, nor have I any publication worth alluding to" (Romanes to Darwin, September 29, 1875, in: ROMANES, *The life and letters of George John Romanes*, p. 33). Of course, Darwin thought that Romanes was a promising young researcher, and wanted to please him and to provide him a higher status. Through the influence of Darwin, Romanes soon became personally acquainted with many influent people: Thomas Huxley, Herbert Spencer, Joseph Dalton Hooker, Francis Galton, etc⁸.

Parallel to his involvement with pangenesis, Romanes kept working on medusae. In 1875 Romanes submitted his first paper on this subject to the Royal Society. It was published in the next year (ROMANES, 1876).

⁷ Darwin mentioned more than once the difficulty of convincing physiologists about the value of pangenesis (see Darwin to Romanes, 12/July/1875, in: : ROMANES, *The life and letters of George John Romanes*, p. 40). As Romanes was working in the physiology laboratory of Sharpey and Burdon-Sanderson and was still attached to Foster, it is likely that he suffered some pressure *against* his graft experiments.

⁸ According to Schwartz, "Romanes eagerly grasped Darwin's hand of friendship. He was keenly aware that Darwin could assist his career by providing him with a much wider access to other members of the scientific community and could help him achieve greater recognition with the scientific public (SCHWARTZ, 1995, p. 286).

Dear Romanes,

As you are interested in Pangenesis, and will some day, I hope, convert an 'airy nothing' into a substantial theory, therefore I send by this post an essay by Häckel attacking 'Pan.', and substituting a molecular hypothesis (Darwin to Romanes, undated letter [1876], in: ROMANES, *The life and letters of George John Romanes*, p. 51).

His research on medusae was going on pretty well, and gave him his first scientific papers (ROMANES, 1876, 1877, 1880). At the same time, he continued to work on experimental pangenesis, with no relevant result. Why didn't he give up the unsuccessful work, and devote himself entirely to his physiological research on jellyfishes? It seems that Romanes wanted to collaborate with Darwin, and was very anxious to please him¹².

Romanes kept Darwin fully informed about the progress (and failures) of his grafting experiments. From time to time, he excused himself for dealing with other research subjects: "As you have heard about the Medusae, I fear you will infer that they must have diverted my attention from Pangenesis; but although it is true that they have consumed a great deal of time and energy, I have done my best to keep Pangenesis in the foreground" (Romanes to Darwin, 14/July/75, in: ROMANES, *The life and letters of George John Romanes*, p. 41). Again, in 1876 Romanes wrote to Darwin:

I have an idea that you are afraid I am neglecting Pangenesis for Medusae. If so, I should like to assure you that such is not the case. Last year I gave more time to the former than to the latter inquiry; and although the results proved very disproportionate, this was only due to the fact that the one line of work was more difficult than the other. [...] I confess, however, that but for personal reasons I

⁹ It seems that Romanes began to investigate starfishes just because sometimes he could not find jellyfishes to study: "On the days when I could get no jelly-fish I took to starfish" (Romanes to Darwin, 11/Aug./77, in: ROMANES, *The life and letters of George John Romanes*, p. 61).

¹⁰ This line of research culminated with the publication, in 1885, of his book *Jelly-fish, star-fish, and sea urchins*.

¹¹ The experiments never succeeded, and no publication resulted from this line of research.

¹² Darwin kept stimulating Romanes to find evidences favorable to pangenesis. See Darwin's letters in: ROMANES, *The life and letters of George John Romanes*, letter of 24/Sept./75, p. 35; letter of 12/July/75, p. 40; undated letter [1876], p. 49; undated letter [1876], p. 51; undated letter [Nov. 1877], p. 69; letter of 26/Mar./81, p. 113.

applicable to a worker in science, Blessed is he that expecteth nothing, for he shall not be disappointed. But I am still more sorry to hear of your feeling knocked up" (Romanes to Darwin 17/Aug./78, in: ROMANES, *The life and letters of George John Romanes*, pp. 75-76).

In the period from 1879 to 1881, Romanes' involvement with pangenesis decreased¹³, but he always returned to the subject. In the beginning of 1881, Darwin was still stimulating Romanes to think about pangenesis, telling him about sugar cane graft-hybrids produced in Brazil (DARWIN, *More letters of Charles Darwin*, vol. 1 p. 389-390). In March 1881 Romanes was consulting Darwin concerning new kinds of experiments he wanted to try (ROMANES, *The life and letters of George John Romanes*, p. 112). Darwin replied: "You are very plucky about Pangenesis, and I much wish that you could have any success" (Darwin to Romanes, 26/Mar./81, in: ROMANES, *The life and letters of George John Romanes*, p. 113).

Many years later, Romanes clearly acknowledged to Edward Poulton, who was his adversary, that the experiments attempting to confirm pangenesis had never succeeded:

Although I spent more time and trouble than I like to acknowledge (even to myself) in trying to prove Pangenesis between '73 and '80, I never obtained any positive results, and did not care to publish negative. Therefore there are no papers of mine on the subject, although I may fairly believe that no other human being has tried so many experiments upon it (Romanes to Poulton, 11/Nov./89, in: ROMANES, *The life and letters of George John Romanes*, p. 228).

During those years, Romanes' researches on medusae were as successful as he could possibly expect. In 1879 the 31 years old physiologist was elected a Fellow of the Royal Society (ROMANES, *The life and letters of George John Romanes*, p. 93). Up to this time, he had published only two relevant physiological investigations on Medusae in the *Philosophical Transactions of the Royal Society*. Of course, Darwin's support was instrumental in Romanes' election¹⁴.

¹³ Probably because of his involvement with graft experiments, Romanes was invited in 1880 to write an article on 'hybridism' for the *Encyclopaedia Britannica*, and asked for Darwin's help (ROMANES, *The life and letters of George John Romanes*, p. 104).

¹⁴ In 1877 Darwin had already recommended Romanes for membership in the Royal Society (SCHWARTZ, 1995, p. 295).

to your subject. By the way, I was pleased at your discussing the selection of varying instincts or mental tendencies, for I have often been disappointed by no one ever having noticed this notion (Darwin to Romanes, 20/Aug./78, in: ROMANES, *The life and letters of George John Romanes*, p. 77).

In the same letter, Darwin suggested that Romanes should keep a monkey at home, to observe and describe its intelligence. Towards the end of 1880 Romanes obtained a monkey (ROMANES, *The life and letters of George John Romanes*, p. 110) and convinced his sister, Charlotte, to keep the monkey for several months. He described his observations in *Animal intelligence*¹⁵.

Romanes began to devote more and more attention to compared psychology, devoting less time to physiological researches (Romanes to Darwin, 29/Aug./78, in: ROMANES, *The life and letters of George John Romanes*, pp. 79-80). In 1880 he was still doing some work on echinodermata with his friend James Cossar Ewart (ROMANES, *The life and letters of George John Romanes*, pp. 104, 109), and his last piece of research on marine zoology was a study concerning the smelling power of anemones (ROMANES, *The life and letters of George John Romanes*, p. 97).

While he was carrying out this important work in physiology [on *medusae*], Romanes was gathering observations and corresponding with Darwin on the subject of animal intelligence. To both Darwin and Romanes it appeared that the theory of evolution required a fundamental continuity in the spectrum of mental life, extending from the lowest organisms up to and including man. Moreover, the ascending stages of mental development should be susceptible of explanation in terms of natural causes. Romanes set himself the task of demonstrating the fact of this continuous development and of giving an account of psychological processes in the light of their probable historical origins (LESCH, 1970, p. 518).

Darwin felt that this was a gap in evolution theory. In the closing paragraphs of *The origin of species*, he had remarked:

¹⁵ See also Romanes' own account of how in 1887 he taught a zoo chimpanzee to recognize numbers from 1 to 5: ROMANES, *The life and letters of George John Romanes*, pp. 253-259.

scale topics that could be illuminated by his particular approach to evolutionism. Far from writing a great survey of the history of life on earth he chose to investigate the origin of particular adaptations in the light of his theory of natural selection (BOWLER, *Charles Darwin: The man and his influence*, p. 137).

Up to 1872 (the year of publication of the 6th edition of *The origin of species*), Darwin was waiting for someone who would take the pain of writing down the evolution of mind. A few years later, he put again his hope in Romanes' hands. It is noteworthy that Darwin handed his unpublished notes on instincts and comparative psychology to Romanes, allowing him to make free use of his manuscript¹⁶.

My dear Romanes

You are quite welcome to have my longer chapter on instinct. It was abstracted for the Origin. I have never had time to work it up in a state fit for publication, and it is so much more interesting to observe than to write. It is very unlikely that I should ever find time to prepare my several long chapters for publication, as the material collected since the publication of the Origin has been so enormous. But I have sometimes thought that when incapacitated for observing, I would look over my manuscripts, and see whether any deserved publication. You are, therefore, heartily welcome to use it, and should you desire to do so at any time, inform me and it shall be sent (Darwin to Romanes, 19/June/78, in: ROMANES, *The life and letters of George John Romanes*, p. 74).

Darwin felt that he would be unable to develop this important complement of evolution theory, and entrusted to Romanes this new burden¹⁷. "G. J. Romanes, who inherited the Darwinian mantle in the area of mental evolution, expounded a development system in which social activity – via the emergence of language – was the real cause of mental progress (1888)" (BOWLER, *Evolution. The history of an idea*, p. 236).

¹⁶ Of course, Romanes acknowledged Darwin's help, and published Darwin's manuscript as an appendix to his book *Animal intelligence*.

¹⁷ Many years before, Darwin had offered Wallace his notes on man, in the hope of motivating him to write on human evolution. Wallace, however, chose to follow a different path (SCHWARTZ, 1995, p. 307).

and letters of George John Romanes, p. 104).

The main result of those researches was a series of books: *Animal intelligence* (1882)¹⁸, *Mental evolution in animals* (1883), and *Mental evolution in man* (1888). Of course, the last book of this series opened a conflict between Romanes and Wallace, who could never accept that the human mind had developed from the animal mind by a continuous transition (SCHWARTZ, 1984).

Peter Bowler criticized Romanes' approach to mental evolution as being more related to Herbert Spencer's views than to Darwin's:

In fact Romanes' account of mental evolution owed more to the philosophy of Herbert Spencer than to Darwin's biological theory. His approach was to trace out a logically plausible sequence by which the mental functions of animals with the simplest nervous system could be developed through to the human level of intelligence. [...] Although recognizing that natural selection could act on instincts, Romanes preferred Spencer's Lamarckian approach in which instincts were produced when learned habits became so deeply ingrained that they became hereditary (BOWLER, *Charles Darwin: The man and his influence*, p. 193).

One should remember, however, that Darwin accepted that use-disuse and inheritance of acquired characters had a relevant role in the origin of instincts¹⁹, and also that he clearly stated that Herbert Spencer's approach in this respect was the best available: "In the future I see open fields for far more important researches. Psychology will be securely based on the foundation already well laid by Mr. Herbert Spencer, that of the necessary acquirement of each mental power and capacity by gradation (DARWIN, *The origin of species*, p. 428).

ROMANES' EARLY THEORETICAL ATTEMPTS

Darwin's death in 1882 was a hard blow upon Romanes and ended the first scientific period of his life. Except for the work on jellyfishes (that had been started and

¹⁸ Animal intelligence is regarded as the first book on comparative psychology ever published. The very phrase "comparative psychology" was framed by Romanes.

¹⁹ There are several points in chapter 8 of the *Origin of species* where Darwin refers to use-inheritance as a source of instincts, and in the Summary of that chapter we can find: "In many cases habit or use and disuse have probably come into play" (DARWIN, *Origin of species*, p. 233).

[...] When my paper was published, and Darwin accepted the idea with enthusiasm, I put it to him in conversation whether this idea might not supersede Lamarckian principles altogether²². (By carefully reading between the lines of the paper itself, you will see how much this question was occupying my mind ad the time, though I did not dare to challenge Lamarck's principles *in toto* without much more full inquiry.) Then it was that Darwin dissuaded me from going on to this point, on the ground that there was abundant evidence of Lamarck's principles apart from use and disuse of structures – *e.g.* instincts – and also on the ground of his theory of Pangenesis. Therefore I abandoned the matter, and still retain what may thus be now a prejudice against exactly the same line of thought as Darwin talked me out of in 1873²³ (Romanes to Poulton, 11/Nov./89, in: ROMANES, *The life and letters of George John Romanes*, p. 229).

Besides being unable to accept Romanes' proposal, a few years later Darwin favored another explanation of the same phenomenon. In 1881, Wilhelm Roux published *Der Kampf der Theile*, where he proposed that there should exist a competition between the inner parts of each organism. The hypothesis was used by Roux to explain the reduction in size of useless organs (such as the eyes of cave animals). Darwin received the book and enjoyed Roux's hypothesis. He urged Romanes to write a review about that work for *Nature* (Darwin to Romanes, 16/April/81, in: ROMANES, *The life and letters of George John Romanes*, p. 115).

Of course, Romanes was not very enthusiastic about the proposal, because Roux's ideas conflicted with his own interpretation. A few months later, Darwin insisted: "I received yesterday the enclosed notice, and I send it to you, as I have thought that if you notice Dr. Roux's book in 'Nature' or elsewhere the review might possibly be of use to you" (Darwin to Romanes, 7/Aug./81, in: ROMANES, *The life and letters of George John Romanes*, p. 125). Romanes replied: "Many thanks for the notice of Roux's book. I have not yet looked at the latter, but Preyer, of Jena (who has been our guest during the Congress meeting, and who knows the author), does not think much of it" (Romanes to

²⁰ Romanes sometimes called Darwin 'The Master' (ROMANES, *The life and letters of George John Romanes*, p. 138).

²¹ Romanes' proposal was very similar to Weismann's later ideas on panmixia (ROMANES 1893).

²² Romanes referred here to his paper: ROMANES, 1874.

²³ The conversation must have occurred in 1874, of course.

a single common species²⁰.

Darwin had attempted to explain this possibility in *The origin of species* with the help of natural selection (BOWLER, *Evolution. The history of an idea*, pp. 212-214) and rejected isolation as a *necessary* condition for the rise of divergent evolution. Darwin's answer to Romanes' speculations was not very encouraging (SCHWARTZ, 1995, pp. 299-302). Romanes withdrew his suggestion and never discussed the subject again with Darwin.

It seems that Darwin regarded his own theory as essentially correct and perceived any proposal of new ideas in attempts to solve its difficulties as a challenge to his own ideas. Of course, Romanes' purpose was not to criticize Darwin: he was attempting to improve the theory. He understood, however, that he was treading upon dangerous ground, and chose to move back.

STEPPING OUT OF DARWIN'S SHADOW

When Romanes received the news of Darwin's death, he wrote to Francis Darwin:

Half the interest of my life seems to have gone when I cannot look forward any more to his dear voice of welcome, or to the letters that were my greatest happiness. For now there is no one to venerate, no one to work for, or to think about while working (Romanes to Francis Darwin, 22/April/82, in: ROMANES, *The life and letters of George John Romanes*, pp. 135-136).

Those seem honest words.

It is curious that Romanes always referred to Darwin's death as a crucial date, and usually counted events from that year onward, *e.g.* "[...] four years after Darwin's death [...]" (ROMANES, *Darwin, and after Darwin*, vol. 2, p. 313).

²⁴ Romanes sent his first draft on this subject to Darwin on June 6, 1877 (ROMANES, *The life and letters of George John Romanes*, p. 54).

²⁵ The necessity of geographical isolation for the production of new species had been claimed by Moritz Wagner in 1868 (MAYR, *The growth of biological thought*, p. 563). Darwin could not accept this proposal.

²⁶ Peter Vorzimmer discussed the evolution of Charles Darwin's thought on blending inheritance and how it was possible to conciliate the "swamping effect" of blending inheritance with natural selection (VORZIMMER, 1963).

Romanes work on mental evolution was an outstanding achievement, and won him some prominence²⁷. Had his ambition been modest, he could rest content with this work, which had filled a *desideratum* in Darwin's program. He was regarded as Darwin's worthy disciple. He remained faithful to Darwin's memory, and was occasionally summoned by Francis Darwin to defend Darwinism:

One of these same saints has been behaving outrageously in print, and everybody is full either of jubilation or indignation at what he has been writing about Darwin and Darwinism. F. Darwin asked me to do the replying, and to-day I am returning proof of an article for the 'Contemporary Review'" (Romanes to his sister Charlotte, 18/May/88, in: ROMANES, *The life and letters of George John Romanes*, p. 194).

It seems, however, that Romanes longed for a higher status in the scientific world.

It is difficult, of course, to apprehend what was going on in Romanes' mind. The interpretation that will be presented in this paper is offered as a plausible *reconstruction* of his aims and professional strategy. That is, assuming that Romanes had in view some goals (compatible with the available evidence), it is possible to understand the main steps he took after Darwin's death as ways to attain those goals. However, this reconstruction does not amount to say that Romanes consciously planned those stages as instrumental in attaining that aim.

Romanes took part in several controversies on evolution, especially in the period from 1886 onwards. The main targets of his criticism were Herbert Spencer, Alfred Wallace and August Weismann. He avoided any clashes with Thomas Huxley. Sometimes he referred to Huxley as one of the "highest authorities on the theory of natural selection", on a par with Darwin (ROMANES, *Darwin, and after Darwin*, vol. 2, p. 307). However, as Huxley did once criticize Romanes' views, he did reply, but his answer was of a most respectful kind (ROMANES, *Darwin, and after Darwin*, vol. 2, p. 307-310).

It would be quite absurd to deny that Mr. Romanes liked a fair and free fight, and there was a good deal of scientific controversy, but he was absolutely incapable of anything but fairness, and never imported into private life any

²⁷ Many historians of psychology mention Romanes' work, but they always emphasize that his work was soon superseded.

letters of George John Romanes, p. 203).

In Romanes' biography written by his wife there is scanty information on his scientific undertakings between 1882 and 1886. Most of his time was probably taken by the preparation of the series of books on mental evolution. *Animal intelligence* had already appeared in 1881, before Darwin's passing. In 1883, Romanes published *Mental evolution in animals*, and then he probably kept busy working on *Jelly-fish, star-fish, and sea urchins* (published in 1885) and *Mental evolution in man* (1888). Between the two later books, however, he diverted his attention to something completely new, different from all his former contributions: the theory of physiological selection.

PHYSIOLOGICAL SELECTION

In May 1886 Romanes published a paper presenting what he regarded as his most important contribution to evolutionary thought: the theory of physiological selection. He chose to communicate his ideas at the same place where Darwin and Wallace had presented their first papers on natural selection: the Linnean Society.

Shortly before the presentation of his paper to the Linnean Society, Romanes sent letters to several scientists, inviting them to attend the meeting and announcing the aim of his contribution. This is the content of his letter to Raphael Meldola²⁸:

May 5th '86

My dear Sir,

I hope you may find it convenient to attend the next meeting of the Linnean Society, which takes place tomorrow at 8 o'clock. I am to read a paper on a new theory upon the origin of species, and should like to know what you think of it.

To me it appears a theory of considerable importance, but on this account I want to expose it to the best criticism.

G. J. Romanes

²⁸ Letter from Romanes to Professor Raphael Meldola (from Meldola papers, Newham Museum Service, London), cited by Donald Forsdyke (http://post.queensu.ca/~forsdyke/romanes1.htm). Some years before, there had been a scientific discussion in *Nature* between Romanes and Meldola (ROMANES, *The life and letters of George John Romanes*, p. 93). Meldola was a supporter of Weismann, and had translated one of his main works: WEISMANN, August. *Studies in the Theory of Descent*. Translated by Raphael Meldola. 2 vols. London: Simpson Low, Marston, Searle and Rivington, 1882.

Meldola was not Romanes' friend. They had

The life and letters of George John Romanes, p. 175). Romanes' ideas were not well received²⁹, and produced a lot of criticism and debate: "I spoke for an hour and a half, and the discussion lasted another hour" (Romanes to his sister Charlotte, May 1886, in: ROMANES, *The life and letters of George John Romanes*, p. 175).

When one reads Romanes' paper, it is not difficult to perceive why it should bring about a strong wave of negative reaction. The very first paragraph of the communication read³⁰:

There can be no one to whom I yield in my veneration for the late Mr. Darwin, or in my appreciation of his work. But for this very reason I feel that in now venturing to adopt in some measure an attitude of criticism towards that work, a few words are needed to show that I have not done so hastily, or without due premeditation (ROMANES, 1886, p. 337).

What should any one expect after this introduction? Romanes was clearly begging the public (or the readers) to forgive him, because he was going to criticize Darwin's work. He was unfortunate enough to use the very word "premeditation", so frequently applied to crimes³¹. All evidences suggested that the disciple was going to dishonor Darwin's memory. After listening to (or reading) this first paragraph, every Darwinian would feel an immediate strong prejudice against Romanes' proposal.

The second half of the next paragraph would not help to dismiss this first negative impression:

It is now fifteen years since I became a close student of Darwinism, and during the greater part of that time I have had the privilege of discussing the whole philosophy of Evolution with Mr. Darwin himself. In the result I have found it impossible to entertain a doubt, either upon Evolution as a fact, or upon Natural Selection as a method. But during all these years it has seemed to me

²⁹ However, Romanes wrote to his sister: "The Linnean Society paper went off admirably" (Romanes to Charlotte, May 1886, in: ROMANES, *The life and letters of George John Romanes*, p. 175).

³⁰ The published version of Romanes' paper might be different from the communication he read at the Linnean Society, but it seems that he did not rewrite the original paper: after presentation and discussion, he just added a "Postscript" and sent it for publication.

³¹ "**pre-med-i-ta-tion** n. **1**. The act of speculating, arranging, or plotting in advance. **2**. *Law*. The contemplation and plotting of a crime in advance, showin intent to commit the crime" (MORRIS, *The heritage illustrated dictionary of the English language*, p. 1034).

Romanes' paper must have brought a wave of thoughts like these.

On the whole, the rest of the paper is much milder than the beginning, but Romanes was not careful enough in his choice of words and sentences. There were several shocking remarks that could be interpreted as a complete break with Darwinism. For instance, Romanes stated that the was "drifting into this position of **scepticism** with regard to natural selection as in itself a full explanation of the origin of species" (ROMANES, 1886, p. 337; my emphasis). Other sentences implied that Darwin's theory had been superseded or rejected, and that he was now criticizing the theory of natural selection:

And since Mr. Darwin's death the tide of opinion continues to flow in this direction; so that at the present time it would be impossible to find any working naturalist who supposes that survival of the fittest is competent to explain all the phenomena of species-formation [...] (ROMANES, 1886, p. 337).

Therefore, in now adopting an attitude of criticism towards certain portions of Mr. Darwin's work, I cannot feel that I am turning traitor to the cause of Darwinism (ROMANES, 1886, p. 338).

At other places, Romanes employed a different tone and endeavored to convince his audience that he was not opposing Darwin's theory, but offering a complementary explanation:

On the contrary, I hope thus to remove certain difficulties in the way of Darwinian teaching; and I well know that Mr. Darwin himself would have been the first to welcome my attempt at suggesting another factor in the formation of species, which, although quite independent of natural selection, is in no way opposed to natural selection, and may therefore be regarded as a factor supplementary to natural selection (ROMANES, 1886, p. 338).

Whether consciously or not, Romanes used an aggressive language, stating that Darwin had **failed** to explain the mutual sterility of natural species:

Mr. Darwin himself allows that this difference cannot be explained by natural selection; and indeed proves very clearly, as well as very candidly, that it must be due to causes hitherto undetected. As we shall presently find, he treats this

account for useful changes – that is, natural selection was a theory explaining the origin of *adaptations*. However, sometimes species differ from one another by characters that are not conspicuously useful. Besides that, the main distinction of well-marked species is the infertility of the offspring of individuals belonging to different species. Darwin had admitted that this cross-infertility could not be explained by natural selection. The third difficulty was the possibility of divergent evolution that was very difficult to understand in the absence of geographical isolation. For all those reasons, Romanes boldly declared that Darwin's theory could not be regarded as a theory on the origin of species, and that Darwin's main book had been misnamed:

In view of the foregoing considerations it appears to me obvious that **the theory of natural selection has been misnamed; it is not, strictly speaking, a theory of the origin of** *species*: it is a theory of the origin – or rather of the cumulative development – of *adaptations*, whether these be morphological, physiological, or psychological, and whether they occur in species only, or likewise in genera, families, orders, and classes (ROMANES, 1886, p. 345; my emphasis).

Again, it is comparatively seldom that we encounter any difficulty in perceiving the utilitarian significance of generic and family distinctions, while we still more rarely encounter any such difficulty in the case of ordinal and class distinctions. Why, then, should we often encounter this difficulty in the case of specific distinctions? Surely because some cause other than natural selection must have been at work in the differentiation of species, which has operated in a lesser degree in the differentiation of genera, and probably not at all in the differentiation of families, orders, and classes. Such a cause it is the object of the present paper to suggest; and if in the foregoing preamble it appears somewhat presumptuous to have insinuated that Mr. Darwin's great work on the 'Origin of Species' has been misnamed, I will conclude the preamble with a quotation from that work itself, which appears at once to justify the insinuation, and to concede all that I require (ROMANES, 1886, pp. 346-347).

The citation presented by Romanes³² does not, of course, show that Darwin acknowledged that natural selection was not a theory on the origin of species. It shows

³² DARWIN, *The origin of species*, p. 176.

397-398; my emphasis).

Only, if species were always distinguishable in points of utilitarian significance, if natural selection were able fully to explain the fact of their mutual sterility, and if it were a part of the theory to show that in some way the mutual crossing of varieties is prevented; only under these circumstances could it be properly said that a theory of the genesis of adaptive modifications is likewise a theory of the origin of species. But, as matters stand, supplementary theories are required (ROMANES, 1886, p. 398).

Leaving the rhetorical features aside, Romanes did present nice arguments for his idea that natural selection *alone* was unable to explain several features concerning the origin of species. Darwin himself had allowed that besides natural selection there were some supplementary natural causes of organic evolution, such as use and disuse, sexual selection, correlated variability, prolonged exposure to similar conditions of life, prevention of intercrossing by geographical barriers (or by migration). However, Romanes claimed that none of those auxiliary causes was able to explain the above-described problems. That was his excuse for proposing the theory of physiological selection.

According to Romanes, closely allied species can only originate from a common ancestral species if they become isolated from one another, in such a way as to prevent intercrossing. Geographical barriers can sometimes produce this effect. However, geographical barriers do not always separate closely allied species, and Romanes suggested that the initial step in the origin of new species could be a variation that produced a partial or total cross-infertility which prevented intercrossing with the parent form.

The aim of Romanes paper was not to deny that natural selection was the main cause of evolution, but to propose a new, independent factor, that was in no way opposed to natural selection but that could explain facts that presented a difficulty to Darwin's theory.

If one states Romanes' ideas in those terms, his proposal seems acceptable. However, returning to his own way of expounding his own achievement, we find out that he boasted having solved the greatest of all mysteries, the origin of species:

Whatever, therefore, may be thought as to the truth of this theory, or as to the extent of its applicability, it is certainly something very much more than a bare

experiments to check the theory. Toward the end of his paper, he asked for the help of other naturalists: "In view of this consideration, I have deemed it best to publish my theory before undertaking the labour of verification; for, by so doing, I hope to induce other naturalists to cooperate with me in carrying on the research in different parts of the world" (ROMANES, 1886, p. 403).

REACTION AGAINST ROMANES

What reaction did Romanes expect from his speech at the Linnean Society? We have no documented evidence that he anticipated an easy and general acceptance. However, the careless language he used in the paper strongly suggests that he counted on a sympathetic reception, and Romanes' correspondence shows that he did not anticipate such a negative reaction as was witnessed after his talk.

Let us try to reconstruct Romanes' expectations. If he could convince his fellow scientists that Darwin's theory was unable to explain the origin of species, and that he, Romanes, had a nice theory to account for that origin and to solve several difficulties of Darwin's theory, he would be regarded as the most competent evolutionist of his time.

However, Romanes' tactics was not successful. Besides being criticized in the discussion at the Linnean Society, he soon received letters blaming his attitude. The general opinion was against him.

Wallace soon published a criticism of Romanes' paper in the *Fortnightly Review* (WALLACE, 1886) with the title "Romanes *versus* Darwin". The theory of physiological selections was also criticized at the British Association meeting, in August 1886:

Physiological selection seems to have brought a regular nest of hornets about my head. If I had known there was to have been so much talk about it at the British Association I should have gone up to defend the new-born (Romanes to Meldola, 16/Sept./86, in: ROMANES, *The life and letters of George John Romanes*, p. 176).

In the following years, Romanes had to justify and explain himself many times, because his proposal was regarded by several scientists (not unjustly) as an attack

^{*} Romanes' footnote: "Viz. – the problem of the origin of species, which, as shown in the preceding paper, his theory of natural selection serves only in small part to explain".

species. Everywhere throughout the paper, from the title-page to the conclusion, I represent it as an 'additional suggestion', a 'supplementary hypothesis', &c., &c. Sexual selection is in my view (as it is also in Darwin's, Wallace's, and doubtless that of all evolutionists) one of the 'other theories that have been propounded on the origin of species'. So is Lamarck's theory, which was considered by Darwin as *more or less* 'supplementary' to natural selection; and this is all that I meant [...] by speaking of physiological selection as another theory of the origin of species (Romanes to Dyer, 7/Jan./89, in: ROMANES, *The life and letters of George John Romanes*, pp. 218-219).

The reaction against Romanes' work was much stronger in England than in other countries – probably because abroad the emotional factors were much milder.

It is most astonishing to me with what a storm of opposition this idea has been met in England, and how persistent is the misunderstanding. In Germany and America it is being much more fairly treated, but meanwhile I intend to keep it as quiet as possible, till I shall be in a position to publish a large body of experimental observations. As far as time has hitherto allowed, the results are strongly corroborative of the theory (Romanes to Le Conte, 21/Jan./89, in: ROMANES, *The life and letters of George John Romanes*, p. 242).

Several years later (a few months before his death), Romanes still complained that he was not understood in England:

I have, indeed, often wondered how you and <u>and</u> and <u>can have so</u> persistently misunderstood my ideas, seeing that neither on the Continent nor in America has there been any difficulty in making myself intelligible (Romanes to Dyer, 26/Sept./93, in: ROMANES, *The life and letters of George John Romanes*, p. 344).

What was Francis Darwin's reaction? We do not know. It is likely that Romanes had talked to him in advance of the Linnean Society talk, and that he was sympathetic to Romanes' work. However, Romanes' correspondence presents evidence that he was

³³ William Thiselton-Dyer (1843-1928) was the Director (1885-1905) of the Royal Botanic Gardens, Kew.

(Panmixia), this, I am convinced, is the one and only particular wherein I have at all departed from the judgments of Darwin; though, curiously enough, it is the particular on which my critics have laid least stress when accusing me of Darwinian heresy (Romanes to Dyer, 7/Jan./89, in: ROMANES, *The life and letters of George John Romanes*, pp. 221-222).

RELEVANT TESTS OF PHYSIOLOGICAL SELECTION

According to the theory of physiological selection, closely related species in immediate contact (with no geographical barrier) should be at least partially sterile as regards each other, while closely related species isolated by geographical barriers (nearby islands or mountains) needed not be mutually sterile. Romanes thought that confirmation of those predictions would help to win new adepts for his theory. He couldn't find sufficient information on this subject, however. Hence, he tried to obtain the help of other scientists to check his theory of physiological selection:

My object in now writing – over and above that of thanking you for your paper – is to ask whether you yourself, or any other American naturalist whom you may know, would not feel it well worth while to try some experiments on the hybridisation of the peculiar species. [...] And I should expect him to find marked evidence of mutual sterility between closely allied unique species growing on the same island, with possibly unimpaired fertility between allied species growing on different islands. If this anticipation should be realised by experiment, the fact would go far to prove my theory (Romanes to Le Conte, 11/Oct./87, in: ROMANES, *The life and letters of George John Romanes*, p. 238).

He also wrote to his critic, Thiselton Dyer, looking for relevant references:

Would you mind sending me on a postcard the name of the genus of plants the constituent species of which you alluded to in the train as being mutually fertile, and also separated from one another topographically? I want to get as many of such cases as I possibly can, so, if any others occur to you, please mention them likewise.

By reading pages 401 and 404 of my paper, you will see why such cases are of quite as much importance to me as the converse, viz. Where closely allied

course I shall do the hybridising experiments myself, but he will collect the material from the different mountains -i.e. nearly allied species, topographically separated, and therefore, I hope, mutually fertile. The converse experiments of nearly allied species on common areas may be tried in England (Romanes to Francis Darwin, 20/Jan./89, in: ROMANES, *The life and letters of George John Romanes*, p. 216).

There are none so blind as those who will not see. Where can your powers of 'observation' have been when you can still remark that I ignore the facts of hybridisation? I can only repeat that from the first I have regarded them as evidence of the utmost importance as establishing a highly general correlation between *separate* origin of allied species and *absence* of cross-sterility. In fact, for the last five years I have had experiments going on in my Alpine garden, which I helped in founding for the very purpose of inquiring into this matter. And Focke, with whom I have been in correspondence from the first, and who *does* understand the theory, writes that in his opinion it will 'solve the whole mystery' of natural hybridisation in relation to artificial (Romanes to Dyer, 15/Sept./93, in: ROMANES, *The life and letters of George John Romanes*, pp. 340-341).

In the years following the presentation of his paper (1886) Romanes obtained many evidences favorable to his theory, as he put it to Dyer, one year before his death:

In fact, as stated over and over again in my original paper, *this* correlation between geographical isolation and cross-fertility is *one* of my lines of verification, the *other* line being the correlation between identical stations and cross-sterility.

Now, as above state, I have found both these correlations to obtain in a surprisingly general manner.

I wish that, instead of perpetually misunderstanding the theory, you English botanists would help me by pointing out *exceptions* to these two rules, so that I might specially investigate them. It seems to me that the group you name goes to corroborate the first of them, while all Jordan's work, for instance, uniformly bears out the second. And whatever may be thought about him in other respects, I am not aware that anyone has ever refuted his observations and experiments so

my sorrow is that I fear I shall have to leave the verification of phys. sel. to other hands in larger measure than I had hoped. I have little doubt that it will eventually prevail; but more time will probably be needed before it does (Romanes to Dyer, 15/Sept./93, in: ROMANES, *The life and letters of George John Romanes*, pp. 340-341).

[...] although I have now recovered to the extent of being able to crawl about a little, I am but a wreck of my former self. Moreover the doctors prohibit work of every kind, so that my misery is absolute, all my experiments have come to an untimely end, and it is improbable that any of my half-written books can ever be published.

I am most of all disappointed about my theory of 'Physiological Selection', for which I have accumulated a large mass of evidence during the last seven years, and which I had hoped would satisfy most people as an explanation of the contrast between natural species and artificial varieties in respect of cross-sterility (Romanes to Huxley, 26/Sept./93, in: ROMANES, *The life and letters of George John Romanes*, p. 343).

So, Romanes regarded this theory – and its foundation – as the summit of his scientific work. Had he been able to provide a firm basis for physiological selection, and to convince the scientific community to accept it, he would regard his scientific work as complete. However, after proposing the theory of physiological selection, Romanes devoted himself to other enterprises. It is necessary to analyze those other lines of work in order to understand fully Romanes' professional strategy.

DARWIN, AND AFTER DARWIN, PART 1

Presenting popular courses and writing popular accounts of Darwin's theory should be a relevant part of the strategy of anyone attempting to become the spokesman of Darwinism. It seems that Romanes was a successful lecturer, but as he was not attached to any university³⁴ he had scanty opportunity of presenting himself in public: a few invited talks, and presentations at meetings of scientific societies³⁵. His more technical

³⁴ Only towards the end of his life, in 1890, he accepted an invitation to join the Oxford University.

³⁵ For instance, he lectured in the Royal Institution in January 1883 (ROMANES, *The life and letters of George John Romanes*, p. 155).

hundred very steadily (usually one hundred and fifty), and is in part made up of outsiders (Romanes to his sister Charlotte, 18/May/88, in: ROMANES, *The life and letters of George John Romanes*, p. 195).

Lecturing gave him much pleasure. Besides that, the lectures gave him the stimulus for reviewing most evolutionary works published before and after Darwin. He soon decided to write a series of books where he was to present his own view on the theory of descent in a general and systematic way. And so he settled his plan to publish what was to become his last work: *Darwin, and after Darwin: an exposition of the Darwinian theory and a discussion of post-Darwinian questions.*

Why did Romanes feel that it was necessary to discuss the theories that had arisen after Darwin's death? According to Romanes, there were "several divergent schools of thought which have arisen since Darwin's death", regarding different opinions on this point: "whether natural selection has been the sole, or but the main, cause of organic evolution" (ROMANES, *Darwin, and after Darwin*, vol. 2, p. 1). However, different views existed already before Darwin's death. Wallace only accepted natural selection; Spencer (and Häckel) strongly emphasized use-inheritance. What was really new after Darwin's death was that evolutionists declared war to one another, attempting to take hold of the Master's mantle³⁸. Darwinians were fighting among themselves, and not against anti-evolutionists or against those who clearly criticized Darwin and suggested that natural selection was of no significance.

In the second volume of *Darwin, and after Darwin*, Romanes does not discuss antievolutionists. He does not address, either, other evolutionary views of the time, such as discontinuous "jumps" and the hypothesis of an internal drive toward perfection. He refers to neo-Lamarckians, but they do not seem to disturb him, and he does not criticize their views. Indeed, his whole concern is with other Darwinians.

Neo-Darwinism,³⁹ the school associated to Weismann's name, was the strongest Darwinian view after Darwin's death. It was natural that Romanes attempted to criticize

³⁶ Romanes never tried to publish this part of his lectures: "Of these the first – of that which deals with the purely historical side of biological science – may be allowed to stand over for an indefinite time" (ROMANES, *Darwin, and after Darwin*, vol. 1, p. vi).

³⁷ The lectures given in the Royal Institution from 1888 to 1890 had the title "Before and after Darwin" (ROMANES, *Darwin, and after Darwin*, vol. 1, p. v).

³⁸ Romanes sometimes referred to Darwin as "the Master".

³⁹ The phrase "Neo-Darwinism" was coined by Romanes in 1889.

regarded as a compendium, or hand-book, adapted to the requirements of a general reader, or biological student, as distinguished from those of a professed naturalist (ROMANES, *Darwin, and after Darwin*, vol. 1, p. 10).

However, the book was not a mere popularization of Darwin's thought: it was to present the *correct* view of Darwinism.

As the present volume is thus intended to be merely a systematic exposition of what may be termed the Darwinism of Darwin, and as on this account it is likely to prove of more service to general readers than to professed naturalists, I have been everywhere careful to avoid assuming even the most elementary knowledge of natural science on the part of those to whom the exposition is addressed (ROMANES, *Darwin, and after Darwin*, vol. 1, p. vi).

It is very easy to ascertain what Romanes had in view when he wrote that he was going to present "the Darwinism of Darwin". In 1889 Wallace had published a book called *Darwinism: an exposition of the theory of natural selection, with some of its applications*, which Romanes immediately criticized (ROMANES, 1889).

Romanes also intended to use *Darwin, and after Darwin* to work as an introduction for his own theory, and he justified his approach as a denial of dogmatism:

For while not a few naturalists have since erred on the side of insufficiently distinguishing between fully verified principles of evolution and merely speculative deductions therefrom, a still larger number have formed for themselves a Darwinian creed, and regard any further theorizing on the subject of evolution as *ipso facto* unorthodox.

 $^{^{40}}$ "But the struggle will almost invariably be most severe between individuals of the same species, for they frequent the same districts, require the same food, and are exposed to the same dangers"; "As the species of the same genus usually have, though by no means invariably, much similarity in habits and constitution, and always in structure, the struggle will generally be more severe between them, if they come into competition with each other, than between the species of distinct genera" (DARWIN, *The origin of species*, pp. 58, 59).

⁴¹ In 1892, Romanes published a popular, illustrated book on Darwin's theory of evolution: *Darwinism illustrated; wood-engravings explanatory of the theory of evolution*. The biography written by Romanes' wife nowhere mentions this book.

I believe that it will eventually stand (ROMANES, *Darwin, and after Darwin,* vol. 1, p. 9; my emphasis).

Romanes wanted to reach not only the general public, but also younger naturalists, attempting to persuade them to abandon what he regarded as the wrong Darwinian creed:

Now the only difference between such naturalists [those of Darwin's time] and their successors of the present day is, that the latter have grown up in a Darwinian environment, and so, as already remarked, have more or less thoughtlessly adopted some form of Darwinism creed. But this scientific creed is not a whit less dogmatic and intolerant than was the more theological one which it has supplanted; and while it usually incorporates the main elements of Darwin's teaching, it still more usually comprises gross perversions of their consequences (ROMANES, *Darwin, and after Darwin*, vol. 1, pp. 11-12).

In *Darwin, and after Darwin* Romanes also attempted to undermine the standing of some well-known authors. One of his targets was Herbert Spencer.

Herbert Spencer had been arguing for evolutionary ideas since 1851, when he published an essay calling the attention to and defending Lamarck's work (BOWLER, *Charles Darwin: The man and his influence*, p. 169). After the publication of the *Origin of species* he had also accepted natural selection, but he still believed that use-disuse and inheritance of acquired characters was the main cause of evolutionary change (BOWLER, *Evolution. The history of an idea*, pp. 238-241). When Weismann began to argue for a kind of Darwinism without use-inheritance, Spencer wrote against Weismann (BOWLER, *Charles Darwin: The man and his influence*, p. 171).

Spencer was a highly influential author. He was one of the few British candidates to the leadership of evolutionary thought. In order to undermine his status, Romanes put Herbert Spencer in the same group as Erasmus Darwin and Lamarck as a supporter of the pre-Darwinian theory of use-inheritance (ROMANES, *Darwin, and after Darwin,* vol. 1, p. 253). Romanes then clearly stated that the Lamarckian theory "even if it be supposed to present any truth at all, is clearly insufficient as a full or complete theory of organic evolution" (ROMANES, *Darwin, and after Darwin,* vol. 1, p. 256). After that, Romanes mentioned the principle of natural selection, and again referred to Herbert Spencer: "Still more remarkable is the fact that Mr. Herbert Spencer – notwithstanding

most frequently met with - especially among supporters of the theory - is that of employing the theory to explain all cases of phyletic modification (or inherited change of type) indiscriminately, without waiting to consider whether in particular cases its application is so much as logically possible. The term "natural selection" thus becomes a magic work, or Sesame, at the utterance of which every closed door is supposed to be immediately opened. Be it observed, I am not here alluding to that merely blind faith in natural selection, which of late years has begun dogmatically to force this principle as the sole cause of organic evolution in every case it is *logically possible* that the principle can come into play. Such a blind faith, indeed, I hold to be highly inimical, not only to the progress of biological science, but even to the true interests of the natural selection theory itself. As to this I shall have a good deal to say in the next volume. Here, however, the point is, that the theory in question is often invoked in cases where it is not even logically possible that it can apply, and therefore in cases where its application betokens, not merely an error of judgment or extravagance of dogmatism, but a fallacy of reasoning in the nature of a logical contradiction. Almost any number of examples might be given; but one will suffice to illustrate what is meant. And I choose it from the writings of one of the authors of the selection theory itself, in order to show how easy it is to be cheated by this mere juggling with a phrase – for of course I do not doubt that a moment's thought would have shown the writer the untenability of his statement (ROMANES, Darwin, and after Darwin, vol. 1, p. 271).

Why did Romanes stress that one should not adhere in a dogmatic way to natural selection? He had two main motives for that emphasis. First, because his own proposal of physiological selection was a complement to Darwin's theory, and could only be accepted if one interpreted natural selection as the main, but not the exclusive, cause of organic change. Secondly, Romanes used this interpretation of Darwin's theory to undermine Wallace's views, which amounted to say that the only factor of organic evolution was natural selection. Accordingly, immediately after the above quoted text, Romanes presented a detailed criticism of Wallace.

Romanes pointed out many misconceptions of Darwin's theory presented by the *critics* of natural selection (see, for instance, ROMANES, *Darwin, and after Darwin,* vol. 1, chapter 9). However, he dealt at greater length with faulty interpretations by those who *defended* Darwinism. Why did he do that? It is likely that his main intent was to establish himself as the only Darwinian who was faithful to Darwin, and therefore it

The three objections to which I allude are, (1) that a large proportional number of specific, as well as of higher taxonomic characters, are seemingly useless characters, and therefore do not send themselves to explanation by the Darwinian theory; (2) that the most general of all specific characters – viz. Cross-infertility between allied species – cannot possibly be due to natural selection, as is demonstrated by Darwin himself; (3) that the swamping effects of free intercrossing must always render impossible by natural selection alone any evolution of species in divergent (as distinguished from serial) lines of change (ROMANES, *Darwin, and after Darwin*, vol. 1, p. 374).

These three objections have been urged from time to time by not a few of the most eminent botanists and zoologists of our century; and from one point of view I cannot myself have the smallest doubt that the objections thus advanced are not only valid in themselves, but also by far the most formidable objections which the theory of natural selection has encountered. From another point of view, however, I am equally convinced that they all admit of absolute annihilation (ROMANES, *Darwin, and after Darwin*, vol. 1, p. 374).

Romanes then goes on to explain that, if natural selection is regarded as the *sole* cause of organic change, then the three difficulties are insurmountable; but that they can be answered if one regards natural selection as the main but not the only factor of organic evolution (ROMANES, *Darwin, and after Darwin*, vol. 1, p. 375). He promised to discuss those objections in the following volume of his work⁴².

At this point, Romanes emphasized that those difficulties would be insuperable for Wallace, but not for Darwin:

[...] no one of these facts is entitled to rank as an objection against the theory of natural selection, unless we understand this theory to claim an exclusive prerogative in the field of organic evolution. This, as we have previously seen, is what Mr. Wallace does claim for it; while on the other hand, Mr. Darwin

⁴² Of course, the solution of those difficulties was, according to Romanes, physiological selection. He first intended to include that theory in the second volume of *Darwin, and after Darwin*. Afterwards, he decided to devote a third volume to physiological selection.

p. 376), and ne was sufficiently clever to divert all criticism from Darwin and concentrate his weapons against Wallace.

After discussing natural selection, Romanes turned to sexual selection (ROMANES, *Darwin, and after Darwin*, vol. 1, chapter 10). He described the main lines of the theory, and then he called the attention of the readers to the circumstance that sexual selection was an *additional theory*, attempting to explain a class of facts that Darwin could not ascribe to natural selection, and therefore "wholly and completely distinct from the theory of natural selection" (ROMANES, *Darwin, and after Darwin*, vol. 1, p. 384). And Romanes criticized Wallace again:

We may next proceed to consider the objections which have been brought against the theory of sexual selection. And this is virtually the same thing as saying that we may now consider Mr. Wallace's views upon the subject (ROMANES, *Darwin, and after Darwin*, vol. 1, p. 391).

Romanes discussed the objections brought by Wallace against sexual selection in his work *Tropical nature and other essays* (1878), and remarked:

Unfortunately the work in which they [Wallace's objections] are mainly presented was published several years after the second edition of the *Descent of man*, so that Mr. Darwin never had a suitable opportunity of replying. But, if he had had such an opportunity, as far as I can judge it seems that his reply would have been more or less as follows (ROMANES, *Darwin, and after Darwin*, vol. 1, p. 393).

I have now briefly answered all Mr. Wallace's objections to this supplementary theory, and, as previously remarked, I feel pretty confident that, at all events in the main, the answer is such as Mr. Darwin would himself have supplied, had there been a third edition of his work upon the subject. [...] for his very last words to science – read only a few hours before his death at a meeting of the Zoological Society – were:

⁴³ A few pages ahead, Romanes quoted Darwin's famous sentence: "I am convinced that natural selection has been the main, but not the exclusive, means of modification" (ROMANES, *Darwin, and after Darwin*, vol. 1, p. 378).

- 3. A way to present his interpretation of Darwinism, opening the way to the acceptance of his own theory of physiological selection;
- 4. A way to criticize other evolutionists, in an attempt to become the topmost Darwinist.

AN EXAMINATION OF WEISMANNISM

August Weismann was not one of the topmost evolutionists in the period preceding Darwin's death. However, in 1883 he rejected use-inheritance (Mayr preferred the phrase "soft inheritance") and claimed that natural selection was the sole cause of evolutionary change (MAYR, *The growth of biological thought*, p. 538).

The evolutionists presented a rather solid front as long as they still had to convince the world of the fact of evolution. This was largely true until about 1882, the year of Darwin's death. In the next twenty years, however, more and more events took place which sowed seeds of dissension among them. The first of these was Weismann's uncompromising rejection of any inheritance of acquired characters. The reaction which this provoked was a hardening of the claims of the neo-Lamarckians (MAYR, *The growth of biological thought*, p. 540).

That was a major move, and he soon obtained several British supporters. Before Darwin's death, only Wallace and, to a lesser extend, Bates and Hooker, argued that natural selections was sufficient to explain organic evolution. After Weismann's change of opinion, Edward Poulton, Raphael Meldola, Ray Lankester and other young scientists also accepted the all-sufficiency of natural selection (MAYR, *The growth of biological thought*, p. 535).

It seems that Romanes regarded the rise of Weismannism as a serious threat to the Darwinian tradition and to his own ambitions. He started his campaign against Weismann in his Edinburgh lectures, and in 1890 his lectures at the Royal Institution were also on Weismann's theory.

Edward B. Poulton was one of the main supporters of Weismann's ideas in England. He was one of the translators of the *Essays upon heredity and kindred biological problems* and defended Weismann's ideas in press and in public presentations. A clash between Romanes and Poulton occurred in 1889: structure, and expressly discarding the Darwinian recognition of use and disuse, I think they are doing harm to natural selection theory itself. Moreover, because I do not see any sufficient reason as yet to budge from the real Darwinian standpoint (Weismann has added nothing to the facts which were known to Charles Darwin), the post-Darwinians accuse me of moving away from Darwinian principles. But it is they who are moving, and, because they see a change in our relative positions, affirm that it is I (Romanes to Francis Darwin, 20/Jan./89, in: ROMANES, *The life and letters of George John Romanes*, p. 215).

In his correspondence, Romanes also attempted to convince other scientists to abandon Weismann's theory, by arguing that Darwin would not agree with those ideas, if he were still alive:

If there be no difference between Panmixia and Cessation of Selection, from what I have briefly sketched about it, it follows that, had Darwin lived till now, he would almost certainly have been opposed to Weismann. This is not a thing I should like to say in public, but one that I should like to feel practically assured about in my own mind (Romanes to Poulton, 11/Nov./89, in: ROMANES, *The life and letters of George John Romanes*, p. 230).

The discussion of Weismann's ideas was to be part of the second volume of *Darwin*, *and after Darwin*. However, Romanes found two problems. One of them was the Weismann kept changing and improving his theory in successive works, and therefore it was difficult to publish an up-to-date criticism. In 1891 Weismann published his essay on *Amphimixis*, and soon afterwards *The germ-plasm* (1893)⁴⁴, where he presented new views on heredity and evolution.

In 1892 a large part of the second volume of *Darwin and after Darwin* was almost ready for press, when Romanes had serious health problems. At that time he decided to publish a separate book on Weismann's work, including all the chapters he had already prepared for the second volume of *Darwin and after Darwin*, but adding new chapters discussing some of Weismann's later ideas. So was born the book *An examination of Weismannism* (1892).

⁴⁴ The German edition of the book was published in 1892.

It must be understood, however, that under the term 'Weismannism" I do not include any reference to the important question with which the name of Weismann has been mainly associated – i.e., the inheritance or non-inheritance of acquired characters. This is a question of fact, which stands to be answered by the inductive methods of observation and experiment⁴⁵: not by the deductive methods of general reasoning (ROMANES, *An examination of Weismannism*, p. vii).

Romanes' *Examination of Weismannism* is a masterpiece of scientific controversy. The author explored every weak feature of Weismann's work – difficulties in applying the concept of the germplasm to plants, the successive changes of Weismann's ideas, contradictions, etc. Romanes cleverly summoned Darwin's spirit to take part of the battle. He pictured Weismann's theory of the germplasm and Darwin's pangenesis as "the logical extremes of explanatory thought" (ROMANES, *An examination of Weismannism*, p. 1), calling the attention of his readers to the incompatibility of Weismann's work with some of Darwin's dearest assumptions.

Weismann's theory of the germplasm directly conflicted with Darwin's hypothesis of pangenesis. Romanes presented in his book a clear account of pangenesis, using it against Weismann. However, one could doubt that Romanes still believes that pangenesis was a correct hypothesis, even after his unsuccessful attempts to prove it.

There is some evidence that even after Darwin's death, Romanes continued to believe that pangenesis was a sound hypothesis. In 1888 he was attempting to repeat some relevant graft experiments, intended to support pangenesis and, at the same time, to undermine Weismann's theory (Romanes to Dyer, 27/Dec./88, in: ROMANES, *The life and letters of George John Romanes*, p. 213; see also Romanes to Francis Darwin, 20/Jan./89, in: ROMANES, *The life and letters of George John Romanes*, pp. 216-217).

Toward the end of the 19th century, the emphasis of use-inheritance was associated with the so-called "Neo-Lamarckian" school. Did Romanes include himself among Neo-Lamarckians? No, because "by Neo-Lamarckian school we understand all those naturalists who assign any higher importance to the Lamarckian factors than was

⁴⁵ Romanes referred to his old experiments on pangenesis: "As far back as 1874 I had long conversations with Darwin himself upon the matter [transmission of acquired characters], and under his guidance performed what I suppose are the only systematic experiments which have ever been undertaken with regard to it. These occupied more than five years of almost exclusive devotion; but, as they all proved failures, they were never published" (ROMANES, *An examination of Weismannism*, p. viii).

examination of Weismannism, pp. 170-171).

At another place, Romanes wrote: "[...] I was myself one of the first evolutionists who called in question the Lamarckian factors; and ever since the publication of Galton's theory of heredity at about the same time, I have felt that in regard to its main principles – or those in which it agrees with Weismann's – it is probably the true one" (ROMANES, *An examination of Weismannism*, p. 108).

Notice that by calling the attention of the readers to the similarity between some parts of the theory of germplasm and Galton's stirp theory, Romanes was also undermining any claims for Weismann's originality. However, instead of contrasting Galton and Darwin, Romanes chose to use both together against Weismann:

Hence my object throughout has been to display, a sharply as possible, the contrast that is presented between the brass and the clay in the colossal figure which Weismann has constructed. Hence, also, my emphatic dissent from his theory of evolution does not prevent me from sincerely appreciating the great value which attaches to his theory of heredity. And although I have not hesitated to say that this theory is, in my opinion, incomplete; that it presents not a few manifest inconsistencies, and even logical contradictions; that the facts on which it is founded have always been facts of general knowledge; that in all its main features it was present to the mind of Darwin, and distinctly formulated by Galton; that in so far as it has been constituted the basis of a more general theory of organic evolution, it has clearly proved a failure: – such considerations in no wise diminish my cordial recognition of the services which its distinguished author has rendered to science by his speculations upon these topics (ROMANES, *An examination of Weismannism*, p. 115).

As shown above, Darwin's hypothesis of pangenesis had been severely criticized for being highly speculative. Romanes used the same charge against Weismann's theory of germplasm:

[...] I confess to a serious doubt whether it [Weismann's theory] has not been permitted to enjoy an undue amount of liberty. If only they can be laced together by a thread of logical connection, hypotheses are added to hypotheses in such profusion as we are acquainted with in the works of metaphysicians, but which has rarely been approached in those of naturalists. The whole mechanism of amphimixis, in order to give us a theory of heredity which is at once logically intact and biologically probable.

6. The theory of germ-plasm would then resemble that of stirp in all points of fundamental importance, save that while the latter leaves the question open as to whether acquired characters are ever inherited in any degree, the former would dogmatically close it, chiefly on the grounds which I have considered in Appendix II. It seems to me that in the present state of our knowledge it is more prudent to follow Galton in suspending our judgement with regard to this question, until time shall have been allowed for answering it by the inductive methods of observation and experiment (ROMANES, *An examination of Weismannism*, p. 170).

So, according to Romanes, Galton had proposed everything that was acceptable in Weismann's theory many years before. Other aspects of Weismann's theory were either wrong or unfounded.

INHERITANCE OF ACQUIRED CHARACTERS

In 1890 Romanes delivered his last course of lectures in Edinburgh. In that same year he accepted John Burton-Sanderson's invitation to work at Oxford (ROMANES, *The life and letters of George John Romanes*, pp. 260, 271). He moved from London to Oxford in May 1890, becoming a member of the University and a fellow of Christ Church College.

Romanes was now 42 years old. For the first time in his life he had at his disposal well equipped laboratories and assistants, providing full facilities for scientific research.

Romanes planned two main lines of experimental investigation. The first, that had already been started a few years before, was an attempt to provide an empirical foundation for physiological selection. The second path was searching for confirmation of inheritance of acquired characters.

The question of reality or otherwise of the inheritance of acquired characters had no bearing on physiological selection. It was of the utmost relevance, however, because Wallace and Weismann denied that such a phenomenon could exist. If Romanes could provide a sound experimental foundation for the inheritance of acquired characters, he could completely overthrow the theories of the Neo-Darwinians. In a letter to his brother, Romanes told him about the relevance of those experiments: very day of his death (ROMANES, *The life and letters of George John Romanes*, p. 243).

The inheritance of acquired characters was one of the main subjects of the second volume of *Darwin, and after Darwin*. It had the sub-title: "Post-Darwinian questions – heredity and utility". The Preface clearly shows that in this volume Romanes intended to direct his weapons toward two main targets: Weismann's and Wallace's ideas. In the whole volume, one can find a remarkably large number of references to Wallace and Weismann. Their names appear in the book many times more often than that of any other author – except Darwin, of course (see the Index of ROMANES, *Darwin, and after Darwin*, vol. 2, pp. 339-344).

As regards Heredity, I have restricted the discussion almost exclusively to Professor Weismann's views, partly because he is at present by far the most important writer upon this subject, and partly because his views with regard to it raise with most distinctness the issue which lies at the base of all Post-Darwinian speculation touching this subject – the issue as to the inheritance or non-inheritance of acquired characters (ROMANES, *Darwin, and after Darwin*, vol. 2, p. v).

The primary aim of the second volume of *Darwin, and after Darwin* was to discuss the "doubtful or erroneous" views of "the most eminent of Post-Darwinian writers".

One more remark. It is a misfortune attending the aim and scope of Part II that they bring me into frequent discord with one or other of the most eminent of Post-Darwinian writers – especially with Mr. Wallace. But such is the case only because the subject-matter of this volume is avowedly restricted to debatable topics, and because I choose those naturalists who are deservedly held in most esteem to act spokesmen on behalf of such Post-Darwinian views as appear to me doubtful or erroneous (ROMANES, *Darwin, and after Darwin*, vol. 2, p. vi).

The second volume was not intended to be read by general readers: "On the contrary, I have had in view a special class of readers; and, although I have tried not altogether to sacrifice the more general class, I shall desire it to be understood that I am there

Romanes also recalled that the inheritance of acquired characters was an essential part of the hypothesis of pangenesis.

Finally, it must not be forgotten that Darwin's acceptance of the theory of useinheritance was vitally essential to his theory of Pangenesis – that "beloved child" over which he had "thought so much as to have lost all power of judging it" (ROMANES, *Darwin, and after Darwin*, vol. 2, p. 11).

Romanes fully reproduced the famous paragraph of the 'Conclusion' of the *Origin of species*, where Darwin clearly stated that he regarded natural selection as "the main, but not the exclusive means of modification". Romanes remarked: "In the whole range of Darwin's writing there cannot be found a passage so strongly worded as this" (ROMANES, *Darwin, and after Darwin*, vol. 2, p. 5).

[...] and seeing that since the death of Darwin a large number of naturalists have gone over to the side of Wallace, it seems desirable here to state categorically what these other or sequent points of difference are (ROMANES, *Darwin, and after Darwin*, vol. 2, p. 5).

Romanes contrasted Wallace's to Darwin's view in the following table (ROMANES, *Darwin, and after Darwin*, vol. 2, p. 6):

The theory of Natural Selection according to Darwin

Natural Selection has been the main means of modification, not excepting the case of Man.

(a) Therefore it is a question of evidence whether the Lamarckian factors have co-operated. The theory of Natural Selection according to Wallace

Natural Selection has been the sole means of modification, excepting in the case of Man.

(a) Therefore it is antecedently impossible that the Lamarckian factors can have co-operated.

evidence whether, or how far, they have co-operated.

(e) No detriment arises to the theory of natural selection as a theory of the origin of species by entertaining the possibility, or the probability, of supplementary factors.

(f) Cross-sterility in species cannot possibly be due to natural selection.

operation deemed impossible.

(e) The possibility – and, *a fortiori*, the probability – of any supplementary factors cannot be entertained without serious detriment to the theory of natural selection, as a theory of the origin of species.

(f) Cross-sterility in species is probably due to natural selection.

Romanes admitted that sometimes Wallace had not been that explicit concerning his points of disagreement with Darwin, but remarked: "[...] I am here taking Mr. Wallace as representative of the Neo-Darwinian school, one or other prominent member of which has given emphatic expression to each of the above propositions" (ROMANES, *Darwin, and after Darwin*, vol. 2, p. 7).

It may now be added, that the longer he [Darwin] lived, and the more he pondered these points, the less exclusive was the *rôle* which he assigned to natural selection, and the more importance did he attribute to the supplementary factors above named. This admits of being easily demonstrated by comparing successive editions of his works; a method adopted by Mr. Herbert Spencer in his essay on the *Factors of Organic Evolution* (ROMANES, *Darwin, and after Darwin*, vol. 2, p. 8).

Notice that although Romanes did not agree with Herbert Spencer (and criticized him in the first volume of *Darwin, and after Darwin*), he used his help, whenever that was useful to him.

Why was it necessary to contrast Darwin's to Wallace's views? According to Romanes, the main reason was not because they were different views, but because Wallace and his followers called themselves Darwinians:

hold these or any other opinions to which his own independent study of natural science may lead him; but it appears to me that there is the very strongest reason why any one who deviates from the carefully formed opinions of such a man as Darwin, should above all things be careful to be absolutely fair in his representation of them; he should be scrupulously jealous, so to speak, of not letting it appear that he is unjustifiably throwing over his own opinions the authority of Darwin's name (ROMANES, *Darwin, and after Darwin*, vol. 2, pp. 9-10).

So, Romanes argued that the Neo-Darwinians had no right to call themselves followers of Darwin. Besides that, he accused them of denying to others, who closely followed Darwin, the name of Darwinians:

But in the present case, as we have seen, not only do the Neo-Darwinians strain the teachings of Darwin; they positively reverse those teachings – representing as anti-Darwinians the whole of one side of Darwin's system, and calling those who continue to accept that system in its entirety by the name "Lamarckians" (ROMANES, *Darwin, and after Darwin*, vol. 2, p. 10).

Those biologists who of late years have been led by Weismann to adopt the opinions of Wallace, represent as anti-Darwinian the opinions of other biologists who still adhere to the unadulterated doctrines of Darwin (ROMANES, *Darwin, and after Darwin*, vol. 2, p. 12).

Yet so greatly have some of the Neo-Darwinians misunderstood the teachings of Darwin that they represent as "Darwinian heresy" any suggestion in the way of factors "supplementary to" or "co-operative with" natural selection. Of course, if these naturalists were to avow themselves followers of Wallace, instead of followers of Darwin, they would be perfectly justified in repudiating any such suggestion as, *ipso facto*, heretical. But, as we have now seen, through all his life Darwin differed from Wallace with regard to this very point [...] (ROMANES, *Darwin, and after Darwin*, vol. 2, p. 11).

Weismann's *Essay on Heredity* (which argue that natural selection is the only possible cause of adaptive modification) and Wallace's work on *Darwinism* (which in all the respects where any charge of "heresy" is concerned directly

Darwinism, in the same way that the neo-classicism of the 17th and 18th centuries was not equivalent to the Classical spirit, and as Neo-Platonism was not faithful to Plato.

Wallace and Weismann did not agree in all respects. Wallace did not accept sexual selection, while Weismann did. Weismann developed a complex theory of heredity, while Wallace did not. Wallace could not accept that man had developed from lower animals by natural causes, while Weismann did. There were several other points of disagreement. Romanes, however, chose to emphasize their points of similarity, and to stress their joint opposition to his own view of Darwin's theory, in order to kill two birds with a single shot.

Looking, then, to these serious differences between his own doctrine of evolution – both organic and mental – and that of Darwin, I cannot think that Mr. Wallace has chosen a suitable title for his book; because, in view of the points just mentioned, it is unquestionable that *Darwinism* differs more widely from the *Origin of Species* than does the *Origin of Species* from the writings of the Neo-Lamarckians (ROMANES, *Darwin, and after Darwin*, vol. 2, p. 22).

According to Wallace, both the body⁴⁶ and the mind of man cannot be explained by natural selection or by any other natural cause, requiring therefore the intervention of some supernatural entity. Romanes discussed at great length those features of Wallace's theory (ROMANES, *Darwin, and after Darwin*, vol. 2, pp. 22-33), contrasting them to Darwin's views and arguing for the continuity between animals and man, and for a gradual development of man's peculiar capacities.

It can scarcely be said that any one of these questions has arisen altogether *de novo* during this period; for glimmerings, more of less conspicuous, of all are to be met with in the writings of Darwin himself. Nevertheless it is no less true that only after his death have they been lighted up to the full blaze of active discussion (ROMANES, *Darwin, and after Darwin*, vol. 2, pp. 35-36).

⁴⁶ Wallace stressed the feet, hands, the brain, the voice and the naked skin of man as impossible to explain by natural selection.

the possibility of an occasional inheritance of acquired characters in faint though cumulative degrees (ROMANES, *Darwin, and after Darwin*, vol. 2, p. 42).

Romanes regarded both the evidence presented by Weismann against inheritance of acquired characters, and all evidence presented in support of that phenomenon, as far from demonstrative: "Therefore at present the question must remain for the most part a matter or opinion, based upon general reasoning as distinguished from special facts or crucial experiments. The evidence available on either side is presumptive, not demonstrative" (ROMANES, *Darwin, and after Darwin*, vol. 2, p. 57).

In this book, Romanes referred to his trials of producing graft-hybrids as experiments attempting to test the inheritance of acquired characters (ROMANES, *Darwin, and after Darwin*, vol. 2, pp. 142-144). That was not really their original aim: they were attempts to check the hypothesis of pangenesis.

In this book, as in other of his works, Romanes directly attacked several authors, while Darwin never did so – one can only find very mild and passing criticism of any author given by name, although, of course, he does criticize many *ideas*. However, Romanes wrote about Darwin's opinions as if he had himself directly criticized Wallace: "Mr. Darwin repudiated Mr. Wallace's doctrine touching the *necessary* utility of *all* specific characters" (ROMANES, *Darwin, and after Darwin*, vol. 2, p. 314).

The third and final volume of *Darwin, and after Darwin*, was published in 1897, three years after Romanes' death. This volume, as edited by Lloyd Morgan, was not a polemical book⁴⁸. It presented his theory of physiological selection in a much clearer way than in the original 1886 paper. In this volume, contrasting to the former one, Wallace and Weismann were mentioned (and criticized) only a few times. Also, Romanes was wise enough to leave out of those pages anything that could be interpreted as an attack against Darwin. Given the aim of the present paper, it will not be required to provide further information on this volume.

⁴⁷ Romanes is here referring to his 1874 papers, published in *Nature* (ROMANES, *Darwin, and after Darwin*, vol. 2, p. 98).

⁴⁸ Lloyd Morgan, the editor of volumes 2 and 3 of *Darwin, and after Darwin*, omitted "two long controversial Appendices" (ROMANES, *Darwin, and after Darwin*, vol. 3, p. v).

Romanes, p. 302).

Romanes was greatly concerned that because of his illness it would be impossible to continue his experiments on the inheritance of acquired characters:

My eye trouble prevents me from carrying on my experiments in heredity, except by deputy; this to me is most provoking, as they have been yielding very interesting results; and having now trained my hands for the performance of the more delicate among them, I am doubtful where I can find the deputy which I need. I mention this in case you should happen to know of any young physiologist who, possessing some operative skill, would care to join in the research. I am ordered six months' rest from any kind of intellectual work [...] (Romanes to Huxley, 18/June/92, in: ROMANES, *The life and letters of George John Romanes*, p. 297).

After a few days, a second blind spot appeared. Romanes had a hypertension crisis and doctors thought that his life was threatened (ROMANES, *The life and letters of George John Romanes*, p. 303). For two years, his health was precarious.

The one difficulty was to persuade him not to work, and this was almost impossible. He was almost feverishly anxious to finish his book, to work out experiments he had been planning [...] (ROMANES, *The life and letters of George John Romanes*, p. 303).

Romanes' health improved in the following months, and he returned to work. He was trying to finish volumes 2 and 3 of *Darwin, and after Darwin*, and to continue his experimental researches. On the 11th July 1893, however, he has taken by a partial paralysis (hemiplegia). Romanes' wife wrote that "from that time the Shadow of Death was ever on him, and he knew it; from that July day he regarded himself as doomed" (ROMANES, *The life and letters of George John Romanes*, p. 335)

Sometimes the longing to finish his work was too great to be borne, but generally he was calm, and always, even when he was most sad, he was gentle and patient, and willing to be amused (ROMANES, *The life and letters of George John Romanes*, p. 336).

Romanes' greatest worry was that he regarded his work as incomplete. The theory of physiological selection had not been established, and he had not been able to win his battle against the Neo-Darwinians. He thought that he would succeed if he could continue his work for one more decade:

Looking all the facts in the face, I do not expect to see another birthday, and therefore, like Job, am disposed to curse my first one. For I know that all my best work was to have been published in the next ten or fifteen years; and it is wretched to think of how much labour in the past will thus be wasted (Romanes to Dyer, 18/Sept./93, in: ROMANES, *The life and letters of George John Romanes*, p. 342).

Even in his last months of life (October 1893 to April 1894), Romanes was able to keep a detailed discussion with George Henslow, who was proposing the concept of "self-adaptation" to account for evolution (ROMANES, *The life and letters of George John Romanes*, pp. 356-371). His main concern in this period was, however, Weismann's theory. In the beginning of 1893 Romanes was very ill and had been sent to Madeira island by his doctors, but kept in touch with the development of Weismann's theory:

I have got Weismann's new book, 'The Germ-Plasm'. It is a much more finished performance than the 'Essays'. In fact, he has evidently been consulting botanists, reading up English literature on the subject, so he has anticipated nearly all the points of my long criticisms. This is a nuisance.

Per contra, since coming here I have heard of no less than three additional cases of cats which have lost their tails afterwards having tailless kittens. I wish to goodness I had been more energetic in getting on with my experiments about this, so I have written to John to get me twelve kittens to meet me on my return. It would be a grand thing to knock down W.'s whole edifice with a cat's tail (Romanes to his wife Ethel, 19/March/93, in: ROMANES, *The life and letters of George John Romanes*, p. 323).

⁴⁹ The second and third volumes of *Darwin and after Darwin* were published posthumously (1895 and 1897) under the editorship of Romanes' friend Lloyd Morgan.

Ethel, 22/March/93, in: ROMANES, *The life and letters of George John Romanes*, p. 324).

Although Romanes had strongly attacked Weismann's work, he was convinced that the theory of the germplasm was a worthy scientific contribution, and he decided to invite Weismann to present a lecture to the Oxford University:

I have asked W. if he will give the Romanes Lecture⁵¹ some year (Romanes to his wife Ethel, 22/March/93, in: ROMANES, *The life and letters of George John Romanes*, p. 324).

In April 1894 – a few weeks before his death – Romanes received a letter from Weismann accepting the invitation to deliver the Romanes Lecture (ROMANES, *The life and letters of George John Romanes*, p. 377).

On May 3 came the third Romanes Lecture. It was given by Professor Weismann, and was a worthy successor to the two which had preceded it.

Mr. Romanes was glad to meet Professor Weismann, and enjoyed the pleasant talk he and his distinguished opponent had in his house after the lecture (ROMANES, *The life and letters of George John Romanes*, p. 378).

Although Romanes' sight was seriously impaired and he had locomotion difficulties, he kept trying to work up to the end: "He was often at the Museum, and he wrote frequently of the experiments he was devising, all bearing on Professor Weismann's theory; in these he was assisted by Dr. Leonard Hill" (ROMANES, *The life and letters of George John Romanes*, p. 378).

George John Romanes expired on the 23rd May 1894, when he was only 46 years old.

⁵⁰ In 1893 and 1894, there was a famous debate in the pages of the *Contemporary Review* between Weismann and Spencer on the possibility of use-inheritance and on the role of natural selection in evolution (ROBINSON, 1970, p. 237).

⁵¹ In 1891 Romanes offered the Oxford University to found an annual lectureship. The University accepted his offer, and they were called "Romanes Lectures". During his life, Romanes himself invited the speakers. The two first were Gladstone and Huxley. Weismann accepted Romanes' request, and gave the third Romanes Lecture.

reading of his life. Whether consciously or not, he made use of several strategies that could contribute to that aim:

- 1. He always wrote about Darwin in a most respectful way, and defended the Master against criticism, as was required from anyone who expected to be recognized as Darwin's scientific successor.
- 2. He attempted to show that his own interpretation of Darwinism was faithful to Darwin's ideas.
- 3. He criticized the interpretation of Darwinism proposed by other Darwinians (especially Wallace and Weismann) and attempted to show that Neo-Darwinism was incompatible with Darwin's original thought.
- 4. He attempted to complement the theory of natural selection, proposing a new theory that could answer to serious difficulties of Darwin's theory.
- 5. He tried to provide a solid empirical foundation for physiological selection and to obtain acceptance for his theory.
- 6. He made an effort to keep himself in evidence, by publications, lectures, and public controversies.
- 7. He endeavored to undermine the scientific work of the strongest contestants who were fighting for Darwin's mantle (the Neo-Darwinians) presenting arguments and trying to present empirical evidence against their views (especially as regards inheritance of acquired characters).
- 8. He tried to obtain support from key persons, whom he supported and did not criticize, in turn.

If this reconstruction of Romanes' strategy is correct, he had a strong professional program and had a good chance of being successful. Had his experimental studies been victorious and had he lived enough to continue his campaign, it is likely that Romanes could attain the leadership of the Darwinian group in the turn of the century.

ACKNOWLEDGEMENT

The author is grateful to the Brazilian National Council for Scientific and Technological Development (CNPq) and to the São Paulo State Research Foundation (FAPESP) for supporting this research.

- 1905.
- FORSDYKE, Donald R. The origin of species, revisited. *Queen's Quarterly* **106** (1): 112-134, 1999.⁵²
- GALTON, Francis. Experiments in Pangenesis. *Proceedings of the Royal Society of London* **19**: 1393-1411, 1871.
- LESCH, John E. The role of isolation in evolution: George J. Romanes and John T. Gulick. *Isis* **66**: 483-503, 1975.
- LEWES, George Henry. Mr. Darwin's hypotheses. *The Fortnightly Review* **3**: 353-373, 611-628, 1868; **4**: 61-80, 492-509, 1868.
- MAYR, Ernst. *The growth of biological thought: diversity, evolution, and inheritance.* Cambridge, Harvard University Press, 1982.
- MORRIS, William (ed.). *The heritage illustrated dictionary of the English language*. Boston: American Heritage, 1975.
- ROBINSON, Gloria. Weismann, August Freidrich Leopold. Vol. 14, pp. 232-239, in: GILLIESPIE, Charles Coulston (ed.). *Dictionary of Scientific Biography*. 16 vols. New York: Charles Scribner's Sons, 1970.
- ROMANES, Ethel. *Life and letters of George John Romanes*. London: Longmans, Green, and Co., 1896.
- ROMANES, George John. Permanent variation of colour in fish. Nature 8: 101, 1873.

⁵² There is an electronic version of this paper available online at the following Internet address: http://post.queensu.ca/~forsdyke/evolutio.htm

- . Mr. A. R. Wallace on physiological selection. *Monist* 1: 1-20, 1890-1891.

. Darwin, and after Darwin. 3 vols. Chicago: Open Court, 1896-1897.

ROMANES, George John & EWART, James Cossar. Observations on the locomotor system of echinodermata. *Philosophical Transactions of the Royal Society* **172**: 829-885, 1881.

SCHWARTZ, Joel S. George John Romanes's defense of Darwinism: the correspondence of Charles Darwin and his chief disciple. *Journal of the History of Biology* **28**: 281-316, 1995.

. Darwin, Wallace, and the *Descent of man. Journal of the History of Biology* **17**: 271-289, 1984.

SPENCER, Herbert. The inadequacy of 'natural selection'. New York: D. Appleton, 1893.

. *The facts of organic evolution*. New York: D. Appleton, 1887.

———. The inadequacy of natural selection. *Contemporary Review* **63**: 153-166, 439-456, 1893.

VORZIMMER, Peter. Charles Darwin and blending inheritance. *Isis* 54: 371-390, 1963.

WALLACE, Alfred Russel. Review of 'Principles of Geology' by C. Lyell. *Quarterly Review* **126**: 187-205, 1869.

WEISMANN, August. *The germ-plasm. A theory of heredity.* Trans. Newton W. Parker, Harriet Rönnfeldt. New York: Charles Scribner's Sons, 1893.