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DARWIN'S CONTRIVANCES: ORCHIDS, EVOLUTION AND SCIENTIFIC ETHICS IN THE PHILOSOPHY OF SCIENCE OF XIX CENTURY

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INTRODUCTION

Topic

My research deals with the historical and scientific context that frames the reception of the book *On the Various Contrivances by Which British and Foreign Orchids Are Fertilized by Insects and on the Good Effects of Intercrossing*.[1]

The historical study of this work carried out in this thesis shows the traditions of thought that shaped natural history in the nineteenth century and reconstructs the lines of evolutionary research that converge in Darwin and depart from him, being later synthesised in the works of countless other botanists.

Indeed, in the second half of the nineteenth century, Darwin placed himself at the centre of a group of botanists including Fritz Müller,[2] Federico Delpino,[3] Asa Gray,[4] Friedrich Hildebrand,[5] Joseph Dalton Hooker,[6] the Swedish Severin Axell[7] and later Herman Müller.[8]

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[1] Darwin, 1877.

[2] Johann Friedrich Theodor Müller (1821–1897) studied at universities in Berlin and Greifswald and obtained a doctoral degree in biology. He then started to study medicine, but after the failure of the Prussian Revolution, to avoid dangerous complications for his life and career, he emigrated in 1852 to Brazil, where he dedicated himself to studying life in Atlantic forests and to teaching.

[3] Federico Delpino (1833–1905) was an Italian botanist and assistant professor to Giuseppe Parlatore. In 1871, he became professor of natural sciences and decided to become the naturalist for the battleship Garibaldi in a research voyage around the world. From 1875 to 1884, he was professor at university of Genua, and then he moved to Napoli as headmaster of faculty of sciences.

[4] Asa Gray (1810–1888) was a great American botanist and professor of botany at Harvard university: He graduated in medicine and later became a naturalist. From 1836 to July of 1838, he was involved in United States Exploring Expedition, and then, although the expedtition had been a difficult experience, he continued to travel around Europe to examine American flora in Europe's herbarium, to find books and documents, and to build international relations with other eminent botanists and professors. He received the honorary degree of Master of Arts in 1844 and Doctor of Laws in 1875 from Harvard, as well as Doctor of Laws from Hamilton College at New York in 1860, from McGill University in 1884, and from the University of Michigan in 1887. The most famous of his numerous pubications was the *Manual of the Botany in the Northern United States*, known as "Gray's Manual", a landmark in the botanical taxonomy of North America. As a

professor at Harvard, he devoted himself to building up and looking after plant collections and what is still today called the “Gray Herbarium”. He was one of Charles Darwin’s contemporaries, and they exchanged opinions and information that proved useful for Darwin’s work. After the publication of *The Origin of Species*, Gray became a staunch defender’s of Darwin’s theory of evolution and natural selection, even publishing a collection of essays called *Darwiniana*. In this book, as well as promoting the theories of evolution, he also expressed the hope that there would be reconciliation between these theories and orthodox Christian beliefs, which at that time were considered to be mutually exclusive.

[5] Hildebrand was a German botanist (1835–1915), a teacher at Bonn University (1859), and later a professor in Fribourg from 1868 to 1907. He developed several branches of botany, in particular of flower ecology. One of the most important work was *Die Lebensverhältnisse der Oxalis-Arten* (1884).

[6] Hooker (1817–1911) was an internationally renowned botanist and one of the first British men of science to become a full-time professional. The son of Sir William Jackson Hooker, director of the Royal Kew Gardens in London, he worked with his father from a very young age, collecting plants and taking part in expeditions. Followed his father’s path, he become the director of the Royal Botanical Gardens in Kew, and he was involved in several voyages: to the Antarctic (1839–1843), Himalayas and India (1847–1851), Palestine (1860), Marocco (1871), and in the western United States (1877). He is renowned as the founder of geographical botany. He was made a baronet for the publication of his massive encyclopaedia on plants: in 1865 he was appointed director of Kew Gardens, and from 1873 to 1878, he was president of the Royal Society. He was a close friend and early supporter of Charles Darwin.

[7] Axell (1843–1892), after earning a degree in medicine, studied botanical sciences. To complete his PhD, he wrote the dissertation *De Fanerogama Vaxternas Befruktning*, a pivotal dissertation, being one of the first in Sweden to deal with impollination of flowers in sophisticated detail and, at the same time, a book inspired by Darwin’s work on orchids.

[8] Hermann Müller was professor in the Realschule at Lippstadt in Westphalia, born at Mühlberg in Thuringia on September 23, 1829, died at Prad in the Tyrol on August 25, 1883.

At this point in history, Darwin becomes the centre of an international network concerning pollination ecology: He pays for translations of works of foreign scientists[9] and becomes the conductor of an international network made up of different philosophical and religious orientations underlying the works of the various authors. It was a tradition of international research that dealt with the understanding of the floral morphology and ecological interactions between pollinating insects and plants from an evolutionary point of view.

This tradition of scholars began to publish their work according to an evolutionary perspective after Darwin sent two communications to the Linnean Society[10] and then published his book on orchids.[11]

However, others almost immediately preceded and followed these more illustrious names. By the third decade of the twentieth century, hundreds of botanists around the world based their research methodology directly or indirectly on Darwin's works dedicated to these studies.

More than thirty authors produced works on orchids immediately after the publication of the first edition of the work on orchids, for a total of forty three works on the subject;[12] Hermann Muller's

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[9] For example Fritz Müller, after having published *Für Darwin* in 1864, sent a copy to Darwin. Darwin found German difficult to understand and asked for a translation, probably done by Camilla Ludwig, governess at Down House between 1860–1863: "Fritz Müller sent me his book, but he writes such difficult German that I can hardly read a word of it; but I have employed a person to translate it for me", Letter from Charles Darwin to Ernst Haeckel, 21 November 1864, Darwin Correspondence Project. Darwin then sent to Müller the German translation of *On the Various Contrivances*, A translated in 1862 by Heinrich Georg Bronn: "I do not know whether you care at all about plants but if so I should much like to send you my little work on the Fertilization of Orchids & I think I have a German Copy", Charles Darwin to Fritz Müller, 10 August 1865, Darwin Correspondence Project. Then Darwin sponsored the translation and publication of *Für Darwin* in 1869 in the book of *Facts and Arguments for Darwin*.

[10] Darwin , 1862a; Darwin, 1862b.

[11] Darwin, 1862c.

[12] On The Various Contrivances by Which British and Foreign Orchids Are Fertilised by Insects, and on the Good Effects of Intercrossing, 2nd edition, D. Appleton and Company, New York, USA, Italian translation edited by Giovanni Canestrini e Lamberto Moschen, I diversi apparecchi col

bibliography has 814 works,[13] and finally Knuth,[14] who arrived years later, offers another 3,748 publications plus a hundred zoological works on visits to flowers by animals. These were not complete lists, however: Knuth admitted his inability to enumerate many Italian and French works.

Why orchids?

I decided to analyse this book because I believe its historical role goes beyond that of a simple floral morphology treatise: Darwin wrote and published this work initially driven by his love for plants, but ultimately he decided to use it as a tool to provoke conversion[15] in a scientific community that continued to show distrust and scepticism towards the daring generalisations contained in *The Origin of Species*.

During the first phase of the historical reception of the work on orchids, the strictly technical public realised that Darwinian reflections allowed scientists to

- draw up a phylogeny of the plants and furnish a continuous explanation of the historical development, or evolution, of the flowers belonging to these plants, as well as for so many other facts inexplicable without it (as for example the homologies, analogies, and the conversion of rudiments to new functions);
- try to establish the structure of the common ancestor of orchids;

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mezzo dei quali le orchidee vangono fecondate dagli insetti, Unione Tipografico-Editrice, 1883, p. 7–8.

[13] Müller, H. *The Fertilisation of Flowers*, translated and edited by D'Arcy W. Thompson, with a preface by Charles Darwin, Macmillan and CO., London, England, 1883.

[14] Paul Erich Otto Wilhelm Knuth (20 November 1854 in Greifswald–30 October 1900 in Kiel) was a German botanist and pollination ecologist. He studied chemistry and natural history at the University of Greifswald and obtained his PhD in 1876. His most important contribution is *Handbook of Flower Pollination*, based upon Hermann Müller's work "The Fertilisation of Flowers by Insects," by Dr Paul Knuth formerly professor in the Ober-Realschule in Kiel and corresponding member of the botanical society Dodonaea in Ghent, translated by J. R. Ainsworth Davis, Oxgord Clarendon Press.

[15] The belief that setting up a shared research method could literally convert the scientists involved is expressed to Hooker about Harvey in a letter from Darwin to Hooker, December 4, 1860, Darwin Correspondence Project.

- yield more new experimental data for colleagues faster than was before possible; and[16]
- give to readers the tools to examine whether the application of his theory of descent and natural selection is supported or leads to such contradictions as would falsify it.

What induced Bentham,[17] Müller, Gray and many others to align with Darwin in the debate concerning the theories contained in *The Origin of Species* were not only these results.

Darwin was able to convince English botanists and other naturalists because what they needed most were two tests: first, a test which could provide proof that the bold generalisations of *The Origin of Species* respected the inductive and ethical criteria of the Victorian philosophy of science; second, one which could provide proof that the theory could be applied without forcing to specific areas of the natural sciences and could explain clearly and systemically the seemingly messy process of speciation.

With *On the Various Contrivances*, botanists realised that not only had Darwin worked following the criteria imposed by Whewell and Herschel and been inspired by the behaviour of scientists of the calibre of Cuvier, but also by applying the theory of common descent and natural selection in their areas of research, they could get more benefit than they had obtained with the usual botanical deductions and, above all, that the results of the conclusions that they now reach again could find a mutual agreement between those who adhered to the common and general Darwinian point of view.

The British and international scientific community recognised that *On the Various Contrivances* respected the canons of the Victorian philosophy of science, as well as that it applied the theory of common descent and natural selection to innumerable series of observations and facts obtained in the field, yielding original results and demonstrating that these results could not be achieved except with the methodological aid of these two ideas that came from *The Origin of Species*.

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[16] Fritz Müller to Hermann Müller, 16 December 1862, Briefe:40–1. But also the results about the studies on *Catasetum.*

[17] George Bentham, (1800–1884), eminent systematic botanist, secretary of the London Horticultural Society and grandson of the philosopher of law Jeremy Bentham, became president of the Linnean Society in 1861 and held office until 1874. One of his most important works was *Genera plantarum ad exemplaria imprimis in herbariis kewensibus servata defined* (3 vols., 1862–83), written in collaboration with J.D. Hooker; it comprises the description and classification of all the species then known among phanerogams.

The first point indirectly provided botanists with a defence against the criticism of *The Origin of Species*: If Darwin worked scientifically with orchids, it cannot be said that he was not as methodologically critical and scrupulous with *The Origin of Species*. This idea led botanists to re-evaluate *The Origin of Species* both epistemologically and politically in all major societies and scientific communities.

The second point showed botanists that in order to progress in their studies and in their research, they could no longer ignore the scientific conclusions of *The Origin of Species*, with all the philosophical consequences that they entailed, most of which represented a novelty in the botanical field, where classificatory and systematic interest had hitherto prevailed.

If the thesis is able to demonstrate the series of historical and cultural circumstances that accompanied the two publications of *On the Various Contrivances*, then the conclusion I propose consists in re-evaluating the meaning of "the flank movement",[18] a concept by which Gray has interpreted in philosophical and teleological[19] terms Darwin's choice to publish *On the Various Contrivances*.[20]

It was not just a defence against the criticism of creationists and those who entrusted scientific explanation to the existence of a design capable of implementing all the most sophisticated adaptations directionally: Darwin's intent was much more radical.

The flank movement started from the author's awareness that most nineteenth-century scientists rejected common descent and natural selection first of all because *The Origin of Species*' content did not match the methodology envisaged by the Victorian philosophy of science. What begins as a passion for flowers tended in the garden of his home in Kent results in Darwin's definitive attempt to convince scientists and philosophers of science that his method is authentically correct and scrupulous, because in this way if scientists accept *On the Various Contrivances,* recognising fully its epistemic validity, then they would be forced to admit that the theoretical content of *The Origin of Species* could no longer be conceived as methodologically fallacious.

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[18] From Asa Gray to Darwin, 2–3 July 1862, Darwin Correspondence Project.

[19] According to Ghiselin (1969, 131–159) teleology was the enemy of this flank movement, but James Lennox (2003, 2004) disagrees: since Darwin was a teleologist, the enemy is not teleology, but creationism of species. So the matter remains controversial.

[20] Gray to Darwin, 2 July 1862 and Darwin to Gray, 23 July 1862, Darwin Correspondence Project.

Richard Bellon interpreted the flank movement in this way, claiming that, thanks to his botanical works, Darwin was able to associate his theory with a moral and political reform of the philosophy of inductive sciences established in the Victorian age.

This thesis is sympathetic to Bellon's conclusions, but focuses specifically on the book dedicated to orchids, broadening the meaning of the flank movement: the book provided the theoretical and practical tools to guide classification, realize observational predictions, explain what Creationism and the Teleology left unresolved,[21] execute drawings that represented how internal and external anatomy of flowers had evolved by natural selection, clarify the role of the beauty of nature, set the figurative didactics of botanical treatises, address the techniques and practices of cultivation, exploit the role social of flowers. The last chapter will highlight how Darwinian botanists accepted and developed one or more of these aspects, nurturing this discipline born thanks to Sprengler and Darwin.

Structure of the work

The thesis is divided into three parts.

The first part deals with the Darwinian theory presented in *The Origin of Species* and the botanical production that follows, trying to delineate the historical and scientific context that precedes the landmark book and within which the Darwinian production develops.

The second part examines *On the Various Contrivances*, along with the most important and revolutionary aspects of that work.

The third part connects the first two: reactions to *The Origin of Species* are presented before *On the Various Contrivances* and afterwards, meaning to show how and why scientists changed their minds thanks to the Darwinian contribution to orchids.

In chapter 1 (which begins the first part), Darwinian contributions on the origin of species are historically introduced.

Chapter 2 shows the most recent developments in botanical sciences in Europe to furnish a historical and scientific framework within which to introduce Darwin's production.

Chapter 3 centres on the motivations and contents of Darwin's botanical treatises.

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[21] The thesis that the flank movement can be interpreted as a direct action against teleology and creationism is by Beatty (2006): there is truth, but even this attempt is partial and forgets a synthesis with the other aspects that will be highlighted in this thesis.

Chapter 4 (which begins the second part) describes the historical and social role of orchids in Victorian England, introducing analysis dedicated to the publications of Darwin.
Chapter 5 shows the needs on the basis of which Darwin published his treatise on orchids, while chapter 6 studies the Darwinian contributions to the botanical classification of these species.
Chapter 7 is dedicated to the concept of coevolution, which represents the ecological and explanatory framework of the studies on floral morphology of the time as of today, while chapter 8 deals with the debate concerning of teleology within the Darwinian explanation.
Chapter 9 assesses the epistemic groundwork that Darwin inherited from those who had preceded him and which prompted him to search for the adaptive meaning of the marvellous contrivances of orchid flowers.
Chapter 10 presents the methods of managing scientific teaching through the use of images and the reactions it provoked within the English aesthetic culture: this chapter closes the second part of this study.
In the third part, and for the many examples of misunderstanding of the Darwinian metaphors presented throughout the paper, chapter 11 records initial reactions to his most important work, showing how bold and unusual his ideas were for the public of the time. This discussion is necessarily complex due to the synthesis it requires, but the analysis of the doubts, of the oscillations, and of the ambiguity of *The Origin of Species*' content will turn into an act of accusation as powerful and acute as Darwin's spirit of observation, and finally chapter 12 demonstrates the impact and influence of the flank movement orchestrated by Darwin to convince the scientific community of the credibility of the findings of *The Origin of Species*.

1 THE DARWINIAN THEORY

Abstract

The dissertation starts with a survey of evolutionary theory, which summarizes the basic principles developed by Charles Darwin at different points during his life.

Thanks to works like *Origin*, the theory of descent with modification has become the foundation of modern biology, and the evolutionary perspective has also been extended to diverse scientific disciplines that deal with objects in progress, from cosmology to anthropology and psychology to ethology, and above all, as far as this dissertation is concerned, botany.

Like Darwin and Hooker, many other prominent botanists and scientists undertook what can be called a “training journey”. Experiences like these contribute to dissolving the old concept according to which every organism is adapted to its environment in a unique, perfect and definitive way. Indeed, Darwin was still a "fixist" when he first boarded the Beagle. However, during his journey, he developed an opposing idea, with theoretical consequences that could only involve the philosophy, influenced by Platonic-Aristotelian thinking, which in 1859 still dominated the basic vision of the life sciences and was deeply rooted in common sense.

Nineteenth-century botany, as far as biodiversity studies are concerned, found in Darwin's work the first and most important thread: a theory par excellence, which provided a rational method and a unifying framework, without ever pretending to interpret everything with certainty.

Retracing the steps that led Darwin to write *Origin* is important not only to understand the roots of his botanical thinking. Rather, following him on his journey and in his observations means understanding more deeply the doubts and questions that haunted other botanists and scientists as well. they found studying orchids around the world.

Furthermore, dwelling on the content of *Origin* will help to understand the role of the *Orchid* book within the fierce debate that opposed *Origin* to an enormous number of hostile reactions and reviews that can still be heard today.

1.1 The origin of *the origin of species*

Charles Darwin (1809–1882) conceived his theory of evolution by natural selection in 1837. He synthesised it in two manuscripts in 1842 and 1844, respectively:[22] the first one is best known as

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[22] Desmond and Moore 2009.

Sketch,[23] which represents a systematic synthesis of all the conclusions and observations that in *Notebooks* supported the hypothesis of a transmutation. The second, in the form of an essay[24] then kept secret, was to be published only in case of sudden death.[25] Only after twenty years of intense work, in 1858, did he make public a communication to the Linnean Society of London, to which was attached an important essay by Alfred Russel Wallace entitled *On the Tendency of Varieties to Depart Indefinitely from the Original Type*, written in the same year.[26] The decision was devised by Charles Lyell, to resolve the question of priority in the publication of the theory and on June 30, once the subject was inserted by Hooker and Lyell[27] on the agenda, in front of an audience without the authors but with 30 scientists present, the Darwin–Wallace communication containing their findings was read.

The reasons for this waiting are many: prudence advised by Lyell, the danger of a possible deduction of kinship between animals and the human race implied by an analysis of the common

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[23] Darwin, 1842, in *The Foundations of the Origin of Species*, *Two Essays written in 1842 and 1844*, Cambridge University Press, Cambridge, 1909, ed. by Francis Darwin.

[24] Darwin, 1844, Essay in The Foundations of the Origin of Species, Two Essays written in 1842 and 1844, Cambridge University Press, Cambridge, 1909, ed. by Francis Darwin.

[25] Pievani, 2013.

[26] Russel Wallace, 1858, paper presented along with Darwin's "Abstract" on natural selection (actually the first edition of *The Origin of Species* at the meeting of the Linnaean Society, which established Darwin's primacy regarding the theory of natural selection). http://rpdata.caltech.edu/courses/Evolution_GIST_2013/files_2013/articles/Ternate_1858_Wallace.pdf

[27] Lyell (1797–1875) was a Scottish geologist. He studied European geology in great detail, examining the palaentology of England and amassing an important collection of fossils. It is to Lyell that we owe several geological terms. Between 1830 and 1833, he published his *Principles of Geology,* in which he applied and developed uniformitarianism, a theory that did not go along with that of the Bible and which was therefore accused of being anti-religious. It was attacked to the same degree as Darwin's theory of evolution; Lyell was a teacher and one of the prime sources of inspiration for Darwin. Lyell also worked on paleoanthropology and, following Darwin, published *The Geological Evidence of the Antiquity of Man with Remarks on Theories of Origin of Species by Variation*.

descent in terms of secondary causes, the fear of political and metaphysical interpretation, the danger of a marginalisation imposed by a scientific community that had acclaimed Darwin after his work on barnacles, the violence with which the conservative component of the British academy had welcomed *Vestiges*,[28] and so on.[29] [30]

However, the publications of the 1850s reflect certain worries, interests, and results surrounding the fact that young Darwin was laboriously, but not casually, elaborating to explain satisfactorily every problematic node capable of illuminating the complex and controversial nature of the phenomenon of the origin of the species.

Until that time, most naturalists had not concerned themselves to inquire how species originated, either regarding the question as too mysterious to be solved by science or being content to assume that there was a particular effort of creative providence engaged in each case.

1.2 The first concept of species

In the early nineteenth century, fixity and distinction of species were considered strictly mutually inclusive: it was not possible to affirm one without presupposing the other. The finding that no individual of a species could give birth to fertile offspring by coupling with an individual of another species cemented the underlying logic of this link, and the resulting philosophical consequences could not be questioned: if the species are distinct, then they are real, as are the individuals who are part of them; if the species are created once and for all in a definitive way and are real, then they cannot change and consequently they remain constant.[31] Thus, speaking of species meant speaking of something both real and permanent, something created by God and which remained distinct through sterility and aversion towards interbreeding among the species.[32]

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[28] Chambers, R. 1844, but the work appeared anonymously and profoundly disturbed the literate portion of the British public.

[29] Richards, 1987.

[30] The private letters show that he chose Hooker as a privileged confidant with whom to discuss his heresies, From Darwin to Hooker, 11 January 1844, Darwin Correspondence Project.

[31] Lamarck was one of the first transmutazionism thinkers to believe that the logic of these two consequences was wrong, just starting from the existence of hybrid and fertile cases.

[32] Kottler 1978, p. 280.

All the eminent naturalists (e.g., Cuvier, Owen, Agassiz, Barrande, Falconer, and E. Forbes) and geologists (e.g., Lyell, Murchison, and Sedgwick) affirmed the immutability of species.[33]

Lyell developed such a concept of species in Principles of Geology trying to contain the transmutationist proposals of Lamarck contained in his zoological philosophy.

While traveling on the Beagle, Darwin started from a creationist position about the species and read Lyell carefully, accepting that the principles to distinguish species were mutual aversion and cross sterility: if interbreeding between two forms of life was almost impossible, then these forms of life were to be considered specifically distinct and mutually exclusive; hence, two different species' characteristics could be analysed for an effective classification, because they were constant.

This observation led him to write in *Notebooks*,

"Definition of species: one that remains at large with constant characters, together with other beings of very near structure"[34]

However, it was almost impossible to establish how many morphological differences were necessary to create an inability to cross different species: it was more a matter of instinct or physiology.[35]

"My definition of species has nothing to do with hybridity, is, simply, an instinctive impulse to keep separate, which no doubt be overcome, but until it is these animals are distinct species".[36]

"It[37] does not bear any precise relation to structure"[38]

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[33] However, Darwin will recognize that Lyell, based on further observations, will develop numerous doubts about species fixity.

[34] Darwin 1860, Notebook B p. 213

[35] "Get a good many examples of animals and plants very close (take European birds Mr. Gould's case of willow wren […] to show that we don't know what amount of difference prevents breeding […])"Darwin 1860, Notebook B. p. 215.

[36] Darwin 1860, Notebook C p. 161.

[37] The subject is the cross-fertility.

[38] Darwin 1860, Notebook B p. 212.

The morphology of the species was certainly important to the extent that the constancy of the characteristics was maintained as a regulatory principle, but the criterion of the impossibility of crossing among different species was the subject on which Darwin focused more intently:

“Instinct goes before structure…hence aversion to generation, before great difficulty in propagation”[39]

1.3 The renouncement of immutability and the problem of classification

Darwin believed in the immutability of species until he deeply evaluated the observations conducted in Galapagos archipelago, and some months after his return to England, he started to deal with the origin of species from a transmutationist perspective.

It was studying the geographical distribution and the speciation of the species of finches, all belonging to the archipelago but some of them confined to single islands, that he became convinced that species, when geographically isolated, varied, potentially forming new species.

He remained convinced when, in 1837, John Gould[40] declared that the varieties of mockingbirds discovered by Darwin on three different islands of the archipelago were actually three different species.[41]

Influenced by the concept of species quoted above, he concluded that geographic isolation could contribute to the acquisition of reproductive isolation, which was the main reason to transmute a variety into a distinguished species: a species isolated from its original habitat and under different external conditions tends to produce new varieties that, once reproductively isolated from the parental form, becomes new species.[42]

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[39] Darwin 1860, Notebook C p. 51.

[40] John Gould (1804–1881) one of the most important ornitologist in Victorian Britain and Darwin’s consultant.

[41] Mayr 1992, p. 346.

[42] “When from being put on and fresh species made parents do not cross” (Darwin 1860, Notebook B p. 189).

This kind of geographic isolation requires a physical barrier to produce the geographic speciation. In the case of the archipelago, a large land mass was subdivided into a series of islands, creating the natural conditions for the formation of new species:

“ –not distance makes species but barrier”.[43]

The criteria of non-interbreeding developed in *Notebooks* makes Darwin’s species concept very close to the modern biological concept or, we could say, a kind of biological concept of species. The consequences of these criteria are that the species are considered real, the acquisition of reproductive isolation is the end point that enshrines the status of species at the end of the process of transmutation starting from a variety, the geographical isolation of Galapagos archipelago added to reproductive isolation formed the causes of geographical speciation, and the creationist perspective about species is not sufficient to explain all these facts.

In *The Origin of Species* the reproductive isolation, as other biological criteria, were opposed to a kind of classification based on purely morphological criteria, and these latter were considered insufficient to definitively help naturalists in their classification work:

“The importance of an aggregate of characters, even when none are important, alone explains the aphorism enunciated by Linnæus, namely, that the characters do not give the genus, but the genus gives the characters; for this seems founded on the appreciation of many trifling points of resemblance, too slight to be defined. Certain plants, belonging to the Malpighiaceæ, bear perfect[44] and degraded flowers; in the latter, as A. de Jussieu has remarked, "the greater number of the characters proper to the species, to the genus, to the family, to the class, disappear, and thus laugh at our classification." When Aspicarpa produced in France, during several years, only these degraded flowers, departing so wonderfully in a number of the most important points of structure from the proper type of the order, yet M. Richard sagaciously saw, as Jussieu observes, that this genus

[43] Darwin 1860, Notebook C p. 21.

[44] Hermaphrodite flowers.

should still be retained amongst the Malpighiaceæ. This case well illustrates the spirit of our classifications."[45] [46]

In other words, the study of degrees of differences for classifying was not sufficient to avoid the differences of opinion among the authors: a form known as a species by some could be recognised as a variety by others, and vice versa.

In *The Origin of* Species, Darwin underlines how the consideration of the characteristics of life forms lacked a unifying principle: some naturalists limited themselves to registering them without wondering what their story was, simply evaluating the importance of the characteristics based on the number of shapes that possessed them; if common and uniform to many individuals they were decisive, if common to a few they became of secondary importance. The criticism of Darwin takes place against the classification made on the basis of mere similarities, without some detailed and historical analysis of the meaning of characteristics that often appeared in combination.

This standard view model was considered insufficient by the author of *The Origin of Species*, as it was believed that there were characteristics that were more important for definition: Milne Edwards[47] and Agassiz[48] believed that the embryonic characteristics were the most important of all; Darwin, while recognising the value of an analysis based on the embryonic characteristics of animals and above all of plants,[49] never wanted to overestimate their importance with respect to that of others.

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[45] We will see as the same problem will appear in Orchid bok with Catasetum tridentatum, Monachantus viridis and Myanthus barbatum and how Darwin will try to solve it in an original way.

[46] Darwin 1859, p. 367.

[47] Henry Milne Edwards (1800–1885) Belgian zoologist and physiologist.

[48] Jean Louis Rodolphe Agassiz (1807–1873) American systematist and paleontologist, a renowned teacher and tireless promoter of science and, after the first publication of *The Origin of Species*, a strong opponent of Darwin's theory of evolution.

[49] As we will see, the similarities in ontogenesis will be an important aspect of the doctrine of homology in Darwin.

Even the use of affinities does not seem to help in the case of crustaceans, and geographical distribution, so often evoked, has further remained trapped in applications that are too often arbitrary and personal, denounced by botanists and by Bentham.

Not a simple resemblance, therefore, but something more and of fundamental importance: something that justifies the partial resemblance of the forms of life and that remains hidden in the various forms of modification and adaptation, which at the same time can be revealed by a classification guided by the study of homologies:

"All the foregoing rules and aids and difficulties in classification may be explained, if I do not greatly deceive myself, on the view that the Natural System is founded on descent with modification;—that the characters which naturalists consider as showing true affinity between any two or more species, are those which have been inherited from a common parent, all true classification being genealogical;—that community of descent is the hidden bond which naturalists have been unconsciously seeking, and not some unknown plan of creation, or the enunciation of general propositions, and the mere putting together and separating objects more or less alike."[50]

Hence, the indication of a strictly genealogical classification to reflect the natural order. The sum of the differences becomes the historical measure of the modifications that the various groups of organisms have undergone by moving away from the common ancestor.

Most historians focused on quotations from *The Origin of Species* where it seemed that Darwin was opting for a nominalistic species concept, however, replacing the reality of species with their artificial and arbitrary use:

"From these remarks it will be seen that I look at the term species as one arbitrarily given, for the sake of convenience, to a set of individuals closely resembling each other, and that it does not essentially differ from the term variety, which is given to less distinct and more fluctuating forms. The term variety, again, in comparison with mere individual differences, is also applied arbitrarily, for convenience sake."[51]

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[50] Darwin 1859, p. 369.

[51] Darwin 1859, p. 42.

It seemed then the lack of a clear dividing line between species and variety was a direct consequence of the evolutionist interpretation: if the change is gradual and if each variety is an incipient species, unlike the fixist thought that postulated a separate and definitive creation for each of them, each species to evolve must have passed through a transition stage in which the passage from variety to species had slowly occurred. Forcing such forms to adapt to the categories of classification could result in the denial of the possibility of a transmutation, as follows:

"In short, we shall have to treat species in the same manner as those naturalists treat genera, who admit that genera are merely artificial combinations made for convenience. This may not be a cheering prospect; but we shall at least be freed from the vain search for the undiscovered and undiscoverable essence of the term species."[52]

The image obtained is that of a Darwin who believed in the reality of lineages that evolve over time, but when he describes species and varieties as names conventionally assigned to certain groups of organisms, he proves not to be such a realistic about the category of species.

According to Mayr, after 1855 Darwin decided to come close to a nominalistic-typological concept of species, seeming to emerge from the notions expressed above, and it was this kind of concept to enable him to give principles to scientist for demarcating between species and varieties.[53]

As Michael Ghiselin highlighted,[54] some of the passages regarding Darwinian nominalism have to be interpreted as attempts to convince the reader of Darwin's understanding of the arbitrary use of the term "species" by those naturalists who believed in special creation and who clearly distinguished species and variety.

In this sense, the paradox inherent in Darwin's title and work should also be addressed: a work that concerns the origin of species and at the same time proposes a popolational reading key without any essentialist pretence can lead to a conventional definition of the term "species".[55] The argument remains controversial, though.

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[52] Darwin 1859, p.426.

[53] Mayr 1992, p. 346.

[54] Ghiselin 1869.

[55] Pievani, 2013.

However, as we will see also in *On the Various Contrivances*, it is difficult to accept that, according to Darwin, the concept of species was only a nominalistic convention: there are criteria by which to distinguish between species and variety, in particular to determine whether two forms are two species or two varieties of a single species, as well as to establish whether one faces three genera or three forms of the same species.[56] In other words, it is possible to clearly demarcate species and varieties without relying upon essentialism or creationism, and it is possible to establish the number of differences considered necessary to give to two forms the rank of species.

Indeed, analysis contained in *On the Various Contrivances*, as well as Darwin's taxonomic practice, suggests that he left aside the biological criteria, including reproductive isolation, and reconciled morphological criteria with what he wrote in *The Origin of Species* about common descent and the role of genealogy in classification.

Likewise, in *The Origin of Species*, although the concept of species is dissolved,[57] the biological reality of the single species does not disappear:[58] Darwin refers to, describes, and explains the history and behaviour of populations belonging to real species.

1.4 Variation

According to Darwin, the enormous variability of organisms makes widely available aspirants to range of species: he contemplates a variety, in botany and zoology, as species in the process of formation or incipient species. This implies that the apparent fixity of the idea of species would give way if we had the objects under our attention for a sufficient time to enable us to observe so large a transition.

It is in the variation that the role of chance in Darwinian theory develops. When Darwin talks about chance or accidental variation he does not mean that organisms respond adaptively to the environment; rather, the variation can be caused by the environment.[59] Above all, Darwin believed that the causal relations between ecological structure and variations were so complex that they could not be predicted.[60] Finally, Darwin seems to assume that random variation has a probabilistic

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[56] See Catasetum.

[57] Sober, 2011.

[58] Sloan, 2009.

[59] Gigerenzer et al., 1989, 132–141.

[60] Lennox, 2004.

behaviour, and this position has philosophical consequences: in the random variation lies the contingency of evolution, and the divergence of varieties from the mother species cannot be predetermined. In this way, the species lose their privileged theological position as constant entities emerging from divine will, in front of which varieties would be only inferior and transitory: each variety, however, if favoured by the circumstances, can access the rank of species, thanks to a fundamental characteristic of organisms, namely the tendency to increase in number in geometric progression.[61]

Instead of repeating the general formula that organisms arise from each other on a scale of increasing complexity or perfection, rather than looking for new facts to show the evidence of such filiation, he prefers to breed pigeons in his personal farming and cultivation and to work for eight years on barnacles, to visit zootechnical and agricultural exhibitions, to attend meetings of the clubs of passionate breeders, to send questionnaires to breeders, to carry out personal experiments and increase international correspondences regarding the variation to the domestic state, and then to re-elaborate all the direct and indirect observational results in theoretical summaries which could explain the phenomena that followed expected patterns, but also the exceptions.[62] An explanatory model starts from the study of domestic animals and cultivated plants to understand variation and coadaptation: in the works of breeders, it was possible to observe the simultaneous selection of two lines of animal descendants that, starting from the same progenitor, continued to be modified in opposite directions in relation to the dimensions and to other physical or behavioural characteristics. Breeders and horticulturists, but also pet owners, showed that differential survival and artificially guided reproduction, even given some exceptions of unintended or unconscious will, made the organism a plastic element that, thanks to a random spontaneous variability, could be directed to a systematic change of the average form in a desired direction.

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[61] Mayr, 1963.

[62] "I have continued steadily reading and collecting facts on variation of domestic animals and plants and on the question of what are species; I have a grand body of facts and I think I can draw some sound conclusions. The general conclusion at which I have slowly been driven from a directly opposite conviction is that species are mutable and that allied species are co-descendants of common stocks. I know how much I open myself, to reproach, for such a conclusion, but I have at least honestly and deliberately come to it." Darwin Correspondence Project, From Charles Darwin to Leonard Jenyns, 12 October 1844.

All this was made possible thanks to the hereditary nature of this variation without intrinsic limits: the results obtained in the greenhouses and on the farms were based on an artificially selected cumulative variation, without which each breeder or horticulturist would have had to start all over again.

Consequently, natural selection is inferred from artificial selection: both start from small individual differences, but the first, which constitutes a model of initial observation, is realised in the limited observation time of breeders or civilisations and can't produce new species but only varieties. An analogous mechanism operating in the times and spaces of natural history, on the other hand, is capable of transformations that influence the philosophical distinction between varieties and species.[63]

However, we have also the example of those men who, by selecting individuals for breeding of the domestic animals, "unconsciously" produce varieties in these species, and Darwin sees a natural process of selection constantly going on with like effects.[64]

In *The Origin of Species*, artificial selection takes on the role of an analogy: in nature, in the immensity of time, a selection process similar to that practiced by breeders and horticulturists acts through dynamic organic and inorganic living conditions that have always produced variations in individual organisms. At the same, time the term "natural selection" metaphorically describes that process of slow accumulation of slight, gradual and favourable variations, and the corresponding elimination of harmful variations, that opens space for environmentally suitable forms in the struggle for existence:

"This preservation of favourable variations and the rejection of injurious variations, I call Natural Selection. Variations neither useful nor injurious would not be affected by natural selection, and would be left a fluctuating element, as perhaps we see in the species called polymorphic."[65] [66]

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[63] Coyne, Orr, 2004.

[64] Browne, 2006.

[65] Darwin, 1859, p. 81.

[66] But in the sixth and final edition, the second sentence presents an addition concerning neutral changes: "This preservation of favourable individual differences and variations, and the destruction of those which are injurious, I have called Natural Selection, or the Survival of the Fittest. Variations neither useful nor injurious would not be affected by natural selection, and would be left

Among the individuals of any species of animals or plants, whatever variations are in any way advantageous in the struggle for existence will give to those individuals an advantage over their fellows, which will be inherited by their offspring until the modified variety supplants the parent species. This process—natural selection—is incessantly at work, and all organised beings are undergoing its operation. By steady accumulation of slight differences over long spans of time, each in some way beneficial to the individual, arise the various modifications of structure by which the countless forms of animal and vegetable life are distinguished from each other.

1.5 The ecological context and the tree of life

Despite that the investigation of the mechanisms of evolution was the focus of his work, Darwin had to demonstrate the context within which this transmutation could happen. In October 1838, his reading of "Essay on Population Principle" by Malthus and his study of a larger body of observed phenomena about the struggle of life convinces Darwin, and years later he will also convince Wallace, that in nature there is not a place for everyone. Adaptations play a fundamental role for survival and reproduction. The sophisticated contrivances that organisms develop in nature are achieved at the price of life and their continuous change or implementation, underlines another Darwinian principle: in nature to be adapted is not enough; an organism must be more adapted than others, because only the fittest survive, take the numerical gain, and give rise to varieties that can be consolidated into new species.

If no species is eternal by birth right and if more individuals are born than can survive, then individuals must survive a struggle for existence and reproduce to pass on to their offspring those variations that have favoured in their environments, given that each variety wants to obtain for itself and its lucky descendants the rank of species.

The force of demographic pressure, already identified, for example, by Linnaeus and Buffon, is a constant threat to the order of nature: this force determines the ecological context within which the variability in the state of nature develops. If resources are neither sufficient nor inexhaustible, and if

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either a fluctuating element, as perhaps we see in certain polymorphic species, or would ultimately become fixed, owing to the nature of the organism and the nature of the conditions." (Darwin, 1872, p.63) natural fruitfulness would push the population to saturate natural spaces, there are Malthusian brakes that will lead organisms to diverge in kind: some thrive while others are destroyed, and some displace their parent species and spread in turn, even if between one branch and another, and so between one species and another, the voids opened by extinctions widen. The natural processes that cut off groups of organisms and establish interspecific differences considered ordered by God are as follows: predation, the presence or lack of resources, the succession of extraordinarily hot or cold seasons, the competition between antagonistic species and epidemics:

"Thus, from the war of nature, from famine and death, the most exalted object which we are capable of conceiving, namely, the production of the higher animals, directly follows. There is grandeur in this view of life, with its several powers, having been originally breathed by the Creator[67] into a few forms or into one; and that, whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being evolved."[68]

In this way, Darwin reaches another fundamental concept of his theory: common descent.

In other words All existing animals have descended from at most only four or five progenitors, and plants from an equal or lesser number.[69] If each group of organisms had descended from a common ancestral species, then the theory of common descent with modification would consist in the proposal of a branched phylogenetic tree, which went against the still-dominant idea of *scala naturae*.[70]

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[67] The words "by the Creator" are not present in the first edition of *The Origin of Species*.

[68] Darwin, C.1872, p. 429.

[69] Quotation.

[70] Aristotle of Stagira (384–322 BC) made it clear that the natural world can be hierarchically ordered: in *De Anima* he imagined organisms as a continuum where the qualities of the soul fade into one another. This is the concept of *scala naturae* which, through the Arab Aristotelians, penetrated strongly into Western biological culture; thanks to the German Domenican Alberto di Böllstad (1193–1280), the Doctor subtilis sant'Alberto Magno, the concept of *scala naturae* was taken up and understood as an ascent to perfection that in the Platonism of the Catalan Franciscan Ramón di Lull (1232–1316) takes on mystical characteristics and aspects of natural magic. The *scala naturae* places at the base of the realization of a perfectibility scale an intrinsic tendency to

1.6 New way of observing nature

Because Darwin came forward with an attempt to solve the question on purely scientific grounds, his approach led to a totally different result than did previous philosophies of nature.

The publication of *The Origin of Species*, its success, and the controversies that accompanied it mark a new "Copernican revolution": the problem of the transformation of organisms has its roots in a new way of seeing nature.

Even if the vision of nature is not for Darwin the object of general philosophical thought or the consequence of the preliminary assumption of a new philosophy of nature, his theory carried on new conceptual assumptions that inform concrete scientific inquiry, direct it, and manifest themselves in certain theoretical results.

The philosophical consequences were many: Darwin removed man from the centre of an immutable world, to give him his place within the complexity of a nature in perennial transformation, devoid of the principle of order understood by naturalists as a gift from God to maintain a numerical balance among all life forms. Nature itself showed that there was no economy of the beings that populated it, but an immense waste of life forms.

This account led Darwin's naturalists and contemporaries to recognise that there was no established and finalistic plan; nature did not represent the ideal place where the interweaving of divine interventions developed to maintain harmony. If God had acted, God could have placed general principles, but could not operate outside the so-called secondary causes, a term to which Darwin will often refer to in *The Origin of Species*, observing that the concatenations of the phenomena of natural history were to be explained through natural causes and according to the lucid scientific reasoning that appealed to established general laws which did not allow for exceptions of metaphysical origin.

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perfection on the part of nature as a whole, and of the single organisms in particular (see also Charles Bonnet [1720–1793] Contemplation of Nature, Lazzaro Spallanzani, Modena at Giovanni Montanari, 1769).

2 FORERUNNERS OF DARWIN IN THE BOTANICAL FIELD

Abstract

During the nineteenth century there was certainly a revolution that changed people's thinking from a fixed world view with respect to organisms, to a dynamic, evolutionary one. Of this revolution, Darwin was a very important actor, arguably even the most important. He was not the only person who played a role, however. Long before Darwin, people (especially in France, Germany, Italy, etc.) started to tackle the important issue of the structure and history of life. Hence, a revolution did occur in that period, but whether it was a Darwinian Revolution may be questioned.[71] In other words, and almost trivially, what happened after 1859 had much to do with theoretical concerns and choices elaborated well before the publication of *The Origin of Species*.

The characteristics of contemporary botanical science from which Darwin first inherited some philosophical-scientific achievements appeared during the Enlightenment: a naturalistic foundation of ethics based on continuous compromises between the deist and creationist interpretation of the living world, the criticism of the anthropomorphic conception of nature, atheism, the critique of finalism, the diffusion of materialistic themes, and the weakening of the hierarchical conception of nature as a catalogue of ever more perfected and perfectible forms.

We cannot forget, in fact, that 19th century represents the beginning of mass science, taught in schools and universities for technological and industrial purposes: the construction of laboratories, the scientific bases of medicine and agriculture, the combustion spread motorised and steam-powered machines, cable communications, and the pervasive use of chemistry that will continue to the present. Applied scientific research was born, and botanical science remained linked to this birth, but becoming an autonomous and experimental discipline during the second scientific

[71] As Pietro Corsi argued, a multi-faceted European debate on the transformation of life forms had already occurred in Europe around 1800. Of this debate, contrary to long cherished views, Lamarck's was only one voice among many. Naturalists active in different national contexts elaborated solutions and proposed doctrines that shared several viewpoints, yet clearly stemmed from a variety of disciplinary traditions and problematic contexts (Corsi, P. *Before Darwin: Transformist Concepts in European Natural History*, Journal of the History of Biology, 38: 67–83, Springer, 2005).

revolution of the twentieth century, with the origin of “biologists”, a term coined in the same years and independently by Gottfried Reinhold Treviranus (1776–1837) and Jean-Baptiste-Pierre-Antoine Monet and Chevalier de Lamarck (1744–1829), who identified in the study of living beings an autonomous science, with a specific object.

The microscope, invented at the beginning of the seventeenth century, unveiled new dimensions of nature, and van Leeuwenhoek showed the life of protozoa, unicellular algae, rotifers, small crustaceans, infusoria, and bacteria.

The purpose of this chapter is to provide a historical overview of the tools and concepts that formed the basis of Darwinian plant speculations and were personally reworked by Darwinian botanists in a synthesis compatible with the various philosophical orientations that underlay their scientific conclusions. It’s a brief and historical balanced overview that provides several examples of intellectual framework in the light of which Darwinian botanists and *Origin's* opponents interpreted the natural reality.

At the same time, it is a premise that will allow us to grasp how the author of the *Orchid* book put himself into play with the same type of instruments and theories when he found himself performing experiments on the characteristics of orchids.

2.1 Cell and transmutation

Cell life and the molecular mechanisms of reproduction began to be studied, and detailed descriptions of the stages of ontogenetic development of organisms introduced new classification practices[72] into the realm of microscopic life.

However, Italian studies served as eighteenth-century precursors: Gallini, Comparetti, Fontana and Corti paved the way for the discovery of the basic component for the organisation of life: the cell.

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[72] In his *Theoria Generationis* (1759) C. F. Wolff claimed that each new creature developed step by step from a less differentiated microscopic substance. This conclusion did not at all reach a wide audience, and yet the growth of ideas that accepted a development, a gradual emergence, in the case of the individual makes it possible to accept with greater serenity the conception according to which even a species could be born through a protracted process in the time of phylogenetic change. Thus, indirectly, epigenesis—that is, the theory of embryonic development—adapted analogically to the theory of evolution, just as the earlier preformationist doctrine (the homunculus fully formed by microscope) conformed better to the idea of a special creation.

In England, Robert Brown[73] showed that the nucleus covered a stable component of the living cell and described the endosperms and the physical motion of particles in vegetable cells.[74]

France's natural philosophers also offered fundamental contributions: René Joachim Henri Dutrochet[75] became the discoverer of osmosis in plant cells, and Charles-François Brisseau de Mirbel studied and described cytological contents:[76] they contributed to the development of vitalist theses, in contrast with the prevailing mechanicism, which originated with Descartes.

At the same time, in Germany the Zellforschung developed as an important current of research concerning the physiology of cellular life, and with Mathias Jakob Schleiden research emerged a cell theory.

As for the transmutationist hypotheses, among the botanists, the nominalistic concept of species remained prevalent until the nineteenth century: Schleiden and Nägeli were among his major bishops.

Further, cell theory was the botanical field that offered a theoretical landing to the theory of common descent, first theorised by the Schleiden (1863), a botanist: the origin of life starting from a first cell, conceived as a common ancestor developed within a primitive land characterised by completely atmospheric conditions differing from the current conditions. Schleiden was the undisputed authority in nineteenth-century botany and not only contributed to the cellular theory of Theodor Schwann (1810–1882), but also trained important botanists such as Hofmeister and Nägeli.

2.2 The molecular basis for the development of life sciences

For Schleiden, biology assumes not only a powerful reaction to the German Naturphilosophie, but engages in the study of all topics related to natural history by applying a scheme of chemical-

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[73] Brown (1773–1858) was a Scottish botanist known above all for his studies on the Australian flora, on the proto-plasma currents in the plant cells, and the fertilization of the orchids.

[74] Quotation.

However, until the 1970s, the role of the nucleus remained misunderstood: cell and protoplasm were considered almost synonymous, and the nucleus an unimportant cellular component that could indifferently be there or be missing.

[75] Henri-Joaquim Dutrochet (1776–1847) was a French physician and botanist; his theories are contained in Dutrochet 1828 and 1837.

[76] Elements de physiologie végétale et de botanique, 1815.

physical reductionism. Moreover, he introduces in cytology a method of verification thanks to which he established that the components of the plants and their structural elements are composed of cells that, depending on composition, determine the different functions of the various tissues.

Schwann extended these conclusions zoology, and in 1839 with his *Mikroskopische Untersuchungen über die Übereinstimmung in the Struktur und dem Wachstum of the Tiere and Pflanzen*, he demonstrated that all tissues, including those such as bones, even when highly developed do not exhibit any element of cellular origin; rather, they derive from primitive cells.[77]

The removal of a cellular identity attributable to the fundaments of organic life constituted the heart of cell theory.[78]

At this point, studies also began to determine the content of the cell walls: von Mohl called the viscous fluid contained in them "protoplasm" (1845).[79]

Thanks to the studies of von Mohl and the Austrian botanist Franz Unger (1800–1879),[80] the cell rises to the role of basic unit of study in the structure of the living world and the origin of the entire kingdom of plants.

Corti (1729–1813) first observed cell division, but Nägeli developed these studies into the discovery of the division of the nucleus and plastids (1844–1846). With proof that each cell originates from the division of a pre-existing cell, Ridolf Virchow dispelled the scientific validity of the theory of spontaneous generation. On the path traced by Virchow, Strassburger showed that the basic phenomena concerning the division of the nucleus and the cell occurs analogously in the plant kingdom as in the animal one.[81]

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[77] In the same year, Oken reached the same conclusions.

[78] In those years, the term "cell theory" referred to the theory of the free formation of cells, not to a functional description of the nucleus and the cytoplasm. Over time, the theory underwent a gradual shift of meaning.

[79] In 1835, the French zoologist called it "sarcode", while Purkinje in 1839 used the same term as von Mohl.

[80] Grundzüge der anatomie und Physiologie der Pflanzen, 1846.

[81] The principle condensed in the aphorism, "*Omnis cellula e cellula*", of the physician R. Virchow (1857) was universally accepted in 1857. The merit of having extended it to animals and plants belongs to Strasburger, as well as to Balbiani, van Beneden, Flemming, and Schleicher.

These new studies formed the basis for the new developments in life sciences in the nineteenth century: the search for general laws that will explain every singularity, the development of experimentation, the increase of chemical-physical analyses in the various scientific-descriptive fields, the increase in the number of researchers involved, further specialisations in research fields, applications in the medical, pharmacological, agricultural, food, breeding, and horticulture fields.[82]

2.3 The starting points for Darwinian botany

Much of these achievements, as we shall see, will influence Darwin's experimental work, but it was above all the question of plant reproduction and the significance of the characteristics of orchids that fascinated him.

Joseph Gottlieb Kölreuter confirmed with experiments on hybridisation (1761) the discovery of Rudolf Jacob Camerarius that plants reproduce through sexuality and that this sexuality is located in the stamens and pistils (1694).[83] His collaboration with Darwin revealed the problems related to the current biological understanding of the flower and the nature of the species.

The mystery of the fertilisation of flowers was revealed by the Reverend Christian Konrad Sprengel (1793) whose meticulous observations demonstrated the role played by insects, animals and, wind in the fertilisation of orchids. The subtle thread that bound Darwin to Sprengel was strained by Brown, and the consequences of this intellectual encounter are developed in this dissertation.

What is important to consider, and which will continually recur in Darwin's observations, is that the content of pollen grains and the depth reached by them in penetrating the female apparatus was first observed by Giovan Battista Amici in Tradescantia. Starting from this discovery, the microscope becomes the daily tool through which the botanist will observe the germination of pollen and pollen tubes and their contact with stigmatic surfaces.

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[82] Still, now the chemical applications in the botanical field allow the synthesis of a wide variety of pharmaceutical.

[83] It is on the basis of the discovery of Camerarius that Linnaeus, with his *Species plantarum* (1753), established the starting point of modern botanical nomenclature. In this work, Linnaeus classified about 6,000 species in 1,000 genera, which were assigned to 24 "classes" based on the number and disposition of the stamens. The classes were further divided into "orders" based on the number of pistils. These were artificial subdivisions on which Linnaeus organized natural groups at the species and genus level.

Amici failed to convince the international scientific community of his results, especially for the opposition of Schleiden, but in the end Hofmeister, Pringsheim, Strasburger, and Mohl confirmed the conclusions of the Modena scientist, reaching the same results.

Finally, Hofmeister conducted studies on the life cycle and the homologies of the reproductive organs, founding the phylogeny of the cryptogams and revealing the possibility of a relationship between cryptogames and phanerogames.

In Germany, research on cell division mechanisms led Eduard Strasburger to certify a functional cytological identity common to plants, fungi, and animals and to recognise meiosis as a common mechanism between the haploid and diploid phases of all those living beings that today we call eukaryotes. He also identified the chromosomes as a hereditary substance hypothetically located in the cell nucleus.

This series of discoveries, which occurred mainly in the second half of the nineteenth century, linked to the theoretical dimension of the theory of evolution, constituted the backbone of modern biology and the experimental background within which new important advances came to light, such as the hypothesis of an abiotic origin of life suggested by Nägeli (1883), based on his theory of micelles, and the proposal of a symbiotic nature of eukaryotic cells, from Il'ic Mecnikov.

3 THE WORK ON PLANT SCIENCES

Abstract

How and why did Darwin begin to study orchids? To answer this question, it is necessary to define the relationship that existed between the British naturalist and botany in general. After the long and grueling periods he dedicated to *Origin*, Darwin decided to dedicate his eyes and fingers to the study of plants, although he still had to finish reworking the drafts of the chapters of *Variation*.[84] He accompanied the writing with what he initially called a pleasant exercise in botany.[85] However, over time, his work took on the characteristics of an evolutionary study, and the results convinced him to perform an increasing number of original investigations. In 1860, he began to apply his theory to studies on sexual dimorphism in hermaphrodites, insectivorous plants and cross-fertilization in orchids. By the summer of 1861, he had meticulously recorded the structure and method of cross-breeding in most British orchids and was preparing a publication based thereon at the Linnean Society.[86]

From 1862 to 1880, Darwin published six botanical treatises in which he described the results of his experiments: on orchids, climbing plants, insectivorous plants, plant fertilisation, the different forms of flowers in plants of the same species, and plant movement.

why this radical study and search for botanical science?

Although Darwin did not consider himself a botanist,[87] in plants, he could see evolution in progress: his botanical works were recognized as an example of how natural selection made possible a different approach to botanical classification and allowed a new explanation of geographical distribution and plant morphology.

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[84] Darwin, 1868a.

[85] "As you say, there is an extraordinary pleasure in pure observation; not but what I suspect the pleasure in this case is rather derived from comparisons forming in one's mind with allied structures. After having been so many years employed in writing my old geological observations it is delightful to use one's eyes & fingers again", Darwin to Hooker, 6 November of 1846, Darwin Correspondence Project.

[86] Darwin Correspondece Project, Darwin to Hooker, 16 June of 1861.

[87] "…ought to have been treated by a professed botanist, to which distinction I can lay no claim", Darwin, 1877, Introduction, Pag. 1.

Therefore, it is possible to affirm that Darwin's botanical works were the instrument through which he tried to resolve the questions that had remained open in *Origin*. Furthermore, more generally, the botanical works represented proving grounds or *pièces justicatives* for his evolutionary theory: climbing plants became an irrefutable proof of the principles of the struggle for existence and the modification of organisms, showing the importance of organic beings' natural tendency to change and its close link to fertilization crossed. To produce fertile offspring (i.e., seeds), hermaphroditic organisms or those that employ self-fertilization must occasionally undergo cross-fertilization. Insectivorous plants made clear the salient aspects of the selection process, including variation, struggle and differential survival, where for the first time species belonging to the plant kingdom had developed adaptations similar to those found in the animal kingdom. The differing forms of flowers on plants of the same species could explain the relationship between hybridism and species origin. Finally, the power of movement in plants applied and demonstrated the concept of descent common to the most salient physiological aspects of plants and explores their meaning through a powerful number of experiments.

The general purpose that led Darwin to publish was to try to provide empirical evidence of natural selection and to use the theoretical results achieved in *The Origin of Species* to solve and reinterpret a series of apparently disparate and heterogeneous botanical phenomena.

3.1 The botanist Darwin

In the years that preceded and followed the publication of *The Origin of Species*, Darwin was engaged in the most varied areas of naturalistic research to explore issues that in the long run would have contributed decisively, even through channels often underground, to the philosophical and scientific maturation of the theory of common descent and the natural selection process.

He had been intensely involved for many years in the study of plant organisms, according to the scientific method of the Victorian age: Darwin's botanical work received wide praise both from his contemporaries and from later scientists.

After 1859, Darwin wrote another ten books, six of which emphasise evolution and adaptations in plants. First editions of Darwin's "plant books" appeared between 1862 and 1880.[88]

His research on plants developed on two tracks: Darwin intended to use plants as a test material for his hypotheses on transmutation and natural selection, but he ultimately addressed numerous

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[88] Quotation of Darwin's works…

questions of plant physiology that absorbed his activity down to the smallest details. Francis Darwin admitted that despite his intentions to study cross-fertilisation of plants from an evolutionary point of view,[89] the subsequent study of pollination captured him above all because of the irresistible thirst for understanding of floral biomechanics. The ability of botanical works to best express the validity of natural selection was, initially, a side effect of his true love for plants and yet proved to be the element on which he then concentrated more to convince scientists of the validity of his then-controversial theories.[90]

Huxley admitted that in the zoological field Darwin had become a master mainly thanks to his eight years' work on barnacles . In the botanical field, Darwin could not count on the same formative training, however: the mass of botanical examples accumulated and proposed in the first edition of *The Origin of Species* did not derive from his specifically direct knowledge of the subject.[91]

In general, Darwin never claimed to be a botanist; on the contrary, using a phrase attributed to Nägeli, he often presented himself as one of those botanists "who do not know one plant from, another".[92] Still, Darwin could count on the help of extraordinary friends and colleagues who were involved in botany and who exchanged letters, samples, analyses, observations, theories, and books for many years. The epistolary link he built with Hooker, Gray, Henslow, Lyell, Bentham, Müller, HC Watson, Knight, Kölreuter, Gartner, Huxley, and his other contemporary botanists was not only an inexhaustible source of information, theoretical proposals, and explanations, it was of ties that, once stipulated, provided a constant source of inspiration, support, company, and vigorous scientific and political empathy that alleviated and helped to contain the pain of the solitary daily scientific work.

In any case, *On the Various Contrivances* represented a turning point: the second edition allowed him to gain enough votes to become a correspondent member of the French Institute in the botanical section on August 1878,[93] news upon which he remarked,

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[89] Quotation.

[90] Darwin, F. 1889, The botanical work of Darwin, Annals of Botany, 13, IX-XIX.

[91] Darwin F, 1889, p. X.

[92] Darwin F, 1889, p. XI.

[93] Darwin F. 1887a.

"I see that we are both elected Com: Members of the Institut. It is rather a good joke that I shd be elected in the Botanical section, as the extent of my knowledge is little more than that a daisy is a compositous plant & a pea a leguminous one."[94]

Several eminent personalities expected this appointment, first of all Lyell, who had always considered it a scandal that Darwin had not yet been named within the French Institute. Evolutionary theories could be a brake, but their application occurred on arguments that Darwin had shown to control.[95] Not for *The Origin of Species*, but thanks to *On the Various Contrivances*, Darwin therefore received this appointment.

These books left various impacts on the development of scientific disciplines and the history and philosophy of science of the nineteenth century. Darwin carried out an enormous amount of research in this domain, from the 1860s until the time of his death. He often worked with his son Francis,[96] who was also the author of botanical studies, some of which were in German[97] (or, it would be more accurate to say, with his *sons*).[98] From these writings, initially published in the *Journal of the Linnean Society of London* and later republished with additional material in separate volumes,[99] the study of plants and the study of geological and zoological phenomena provided Darwin with the material on which he would build his evolutionary hypotheses.

One immediately notices when reading Darwin's botanical works his descriptions of plants as truly living beings, no less "alive" than animals.

He absolutely wanted to try to prove that the study of the vegetable kingdom could be as fascinating and surprising as the study of the animal kingdom. This goal was a matter that could hardly be

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[94] From Darwin to Asa Gray, 15 August 1878, Darwin Correspondence Project.

[95] Darwin F. 1889, p. XI.

[96] Like his uncle Erasmus, he graduared as a doctor but was disinclined for practice and became Charles' assistant in research in plants.

[97] Darwin, F. Über das Wachstum negativ heliotropischer Wurzeln, in *Arbeiten des Botanischen Instituts in Würzburg*, vol. II, 3, 1880.

[98] William E. Darwin was also the creator of many illustrations.

[99] *The Movements and Habits of Climbing Plants*, 2nd edition, John Murray, London, 1875 and *The Power of Movement in Plants*, John Murray, London, England, 1880.

taken for granted in his day, nor can it be today and this forced the introduction of a series of metaphors for the animal world, some of which were misunderstood.[100]

However, in his botanical contributions, Darwin should not be remembered only as a diligent experimenter. Darwin's botanical works can be approached in search of the necessary theoretical and philosophical preconditions of his laborious reorientation of knowledge—his rejection of the fixed vision of the natural world, explanation of life on the basis of secondary causes, departure from biblical creationism, and teleology in explaining natural events[101]—and the reasons for the specific connotations of his evolutionary conclusions: those that differentiate them, for example, from the conclusions of Delpino or Gray.

The transmutation was the frame constantly present for Darwin in authoring *The Origin of Species*, but the botanical works must be considered and interpreted along two main tracks: the naturalistic and the cellular approach.[102]

The dialectic of complex interorganic relations was studied by Darwin in relation to plants, which ceased to present themselves as theoretically impermeable systems but rather subject to variation; like animals, plants participate in the struggle for existence through a series of sophisticated adaptations and co-adaptations.

Darwin's botanical work further addresses the utility of these adaptations in the life of a plant, which aim to promote its success in the competition between living beings, and in the "natural selection" that this leads to. The botanical works do not represent the efforts of an amateur, nor do they shatter his research in a jumble of disciplinary interests of niches in which the evolutionary hypothesis loses clear application.

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[100] An example is the attribution of a brain to plants, which has been identified today with the radical apex as conceived by Stefano Mancuso. However, it was Darwin's son Francis who claimed that the plants had rational capabilities.

[101] In this respect, the author of *The Origin of Species* was aware of exposing himself to the attacks of eminent schools of thought: Quotation, Darwin, 1859, p. 310. However, as we will see, he could also count on the theoretical support of some friends: Quotation Hooker J.D. On the Flora of Australia, &c., F.R.S. (Introductory Essay.) 4to. 1859, p. xxv.

[102] Darwin, C. *The Movements and Habits of Climbing Plants*, 2nd edition, John Murray, London, 1875.

A very large number of experiments were added to the confirmations of the hypotheses that Darwin proposed along his observations. He succeeded in putting them into practice in an original and repeated way in the most difficult contexts: from sticks and stakes of various shapes and consistencies, through to raw fibres and mosses, extremely fine threads of linen, and cotton, to test the sensitivity of plants to touch; he also conducted precise surgical operations on the tips of roots and shoots, and surprisingly relied upon chemical substances.[103]

Even when ill, he did not cease to experiment on the plants he protected in the warmth of his room: it was not possible in fact to develop a heating system inside the greenhouses with which the wealthy houses of Victorian England were provided, so the plants could react better to experiments if placed inside the only room that had a fireplace.

The enormous work of the English naturalist received impulsion and stimulus from that of the scholars he cites as sources of inspiration and reference models for the verification or falsification of some of his observations: contemporary scientists coming mainly from central Europe.[104]

Thanks to these studies and collaborations, he succeeded to expand the range of his scientific interests, yielding increasingly sophisticated research.

3.2 The movements of climbing plants

If the botanical monographic debut of the British naturalist focused on the contrivances of the flowers of orchids, after that publication others followed, no less demanding, concerning topics and phenomena from which his scientific investigation had begun.

A large number of climbing species are fully investigated and become the subject of a sweeping publication which ran into a number of editions: *The Movements and Habits of Climbing Plants*.[105]

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[103] For example silver nitrate, used as a “caustic” or anaesthetics and organic mixture of oil and other substances.

[104] These included Sachs and De Vries, Ciesielski, Haberlandt, Kraus, Pfeffer, Strasburger, Von Mohl, and Wiesner. Among his sources we cannot forget French scholars such as Dutrochet and Batalin, together with some Americans as Asa Gray, and Delpino and Malpighi, and of course Linneaus.

[105] *The Movements and Habits of Climbing Plants*, 2nd edition, John Murray, London, 1875. Darwin divided climbing plants into four classes: plants that twine spirally or twining plants, those that irritable organs and that clasp any object and rise up on it (leaves, branches, or modified

After having read, on Gray's advice, the works of Palm[106] and von Mohl[107] on the subject, Darwin, not entirely satisfied,[108] decided to make a contribution that would explain the twining plants in a simple way.[109] The work, which initially took on the dimensions of a paper, interrupted the drafting of Variation and was published by the Linnean Society in 1865[110] and ten years later by Murray.[111] Darwin's operation consists of dividing his analysis into four plant species: twining plants,[112] plants with irritating organs clasping any object and rising up on it,[113] plants latching on using hooks, and

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petioles, often in tendrils), those that latch on using hooks, and those that rise up using radicles. While the third and fourth classes do not generally involve special movements and thus do not require in-depth examination, the first two are studied in great detail. This examination is undertaken not just because they are interesting, but because they "far exceed in number" the others in terms of variety "and in the perfection of their mechanisms", enabling them to rise up until they are in full light. The subsequent editions were *The Movements and Habits of Climbing Plants*, 2nd edition, John Murray, London, 1875; *The Movements and Habits of Climbing Plants*, 2nd edition revised, D. Appleton and Company, New York, USA, 1876; and *The Movements and Habits of Climbing Plants*, Final Text, John Murray, London, England, 1882.

[106] Palm, Ludwig H. Uber das Winden der Pflanzen: Eine botanisch-physiologische Abhandlung, Mit 3 Steindrucktafeln, 1827, Germany; second edition in 2018 by Pranava Books.

[107] Mohl von, Hugo Bau und das Winden der Ranken und Schlingpflanzen, Forgotten Books, 2018.

[108] In the autobiography, he expresses the need to overcome the mistakes contained in the explanations of his master Henslow (p. 129), while in the preface to the book on climbing plants Darwin admits to having been inspired by a paper by Asa Gray (Proc. Amer. Acad. of Arts and Sciences, vol.iv.Aug.12; 1858, p. 98) and to have read the two memoirs of Dutrochet on the subject (Des Mouvements révolutifs spontanés," &c., 'Comptes Rendus,' tom. xvii., 1843, p. 989; "Recherches sur la Volubilité des Tiges," &c., tom. xix., 1844, p. 295).

[109] Darwin, F., 1887a, From Darwin to Hooker, 10 June 1864.

[110] It was published June 12, 1865, in a double issue of the *Journal of the Linnean Society (Botany)*.

[111] Darwin, 1875.

[112] What characerizes these plants, as in the case of Asclepiadaceae Hoya and Ceropegia or in hops, is a revolving nutation which Darwin defines as a high speed circumnutation which allow plants to rise up through a very mobile stem. Circumnutation is an aspect that we see in this kind of plants

plants rising up using radicles. He focuses on the study of these climbing plants, since they grow in full light.

In relation to the members belonging to each of these categories of plants, Darwin devotes himself to the study of curvature movements to classify the main types, and later Darwin determines that the predominant movements in the plant kingdom are those of circumnutation, common to all growing organs, and from this universally present movement, the evolution of plants has the basis for the acquisition of the most diverse forms of movement, depending on the needs of the plant.

This universal basic movement is hereditary. It can be connected to light, like nictinastic movements, and it involves leaves, flowers, the seedling, the radicle. Moreover, it is the basis of gravitropic responses, which concern the stem, leaves, fruits and flowers, and phototropic movements.

The worldwide spread of creepers is due to the low investment of energy and matter they require to reach the light.

The quality of movement and sensitivity to contact develops from a minimum degree of specialisation, which we can find in twining plants (lianas) that need heavy supporting apparatus to cling, as well as in the leaf and tendrils climbers, which climb thanks to the competition of modified organs such as petioles and midbrids that contract, helping the ascent without the need for the help of powerful stems. The most sophisticated kind of movement Darwin notes is that of tendril bearers whose tendrils can originate from leaves, stems or modified flowers. The movements and habits of climbing plants was another proving-ground for the Darwinian principle of the struggle for existence and transmutation, influencing in several instances the fourth edition of *The Origin of Species*.[114] Indeed, the dense vegetation of thickets, hedges, and forests is the context for

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when they are winding in a certain direction, but another aspect is their adhrence to the support and the subsequent stabilitation that requires the contact for the substrate for the twining movement.

[113] Darwin subdivide them in leaf climbers, with functional leaves like the genera *Clematis* and *Tropaeolum*, and tendril bearers. The use of petioles and midbrids by leaf-climbers to climb, leads Darwin to put them in a evolutionary intermediate stage between twining plants and tendril bearers. Tendril bearing plants, like *Pisum sativum*, *Lathyrus* sweet peas, *Smilax aspera* and *Corydalis*, may derive their filamentory organs from leaves, but also from flower peduncles, branches, and perhaps stipules.

[114] Darwin, 1866.

competition for light and air, while the hooks and tendrils, as aids for ascent, are modifications of organs that once were a leaf.

3.3 The insectivorous plants

Two articles with preliminary information about Charles Darwin's studies of the insectivorous[115] plants *Drosera* and *Pinguicula* were published in 1874. In the first article, published in the *Gardeners' Chronicle*,[116] mention is made of some publications by the famous American botanist Gray, with whom Darwin had an intense correspondence, as well as of the studies of insectivorous plants that Darwin had not yet completed. It was hoped that the scientist's complete studies on this subject would be published shortly after. Another publication[117] included some of Darwin's observations on *Drosera filiformis*, during an excursion to new Jersey in 1874. These experiments were designed to assess the ability of this plant to bend its leaves partially or completely towards a possible prey, and Darwin took inspiration for his work from observations that the American scientist Mary Treat[118] had published in *The American Naturalist*.[119]

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[115] The term "carnivorous plants" was introduced only in 1942 by Francis Ernest Lloyd in *The Carnivorous Plants*, Chronica Botanica Company, Waltham (USA) 1942. This term was considered to be more correct because these plants feed not only on insects but also other arthropods or other animals. There are about 600 species of carnivorous plants throughout the world, comprising more than a dozen genera and families. Together with these, there are also about three hundred species of proto-carnivores that have some but not all of the characteristics required to be considered carnivores.

[116] Darwin, C. in *The Gardeners' Chronicle*, 4 July 1874, p. 15.

[117] Darwin, C. Memoranda on Drosera filiformis, in Canby W.M.M. Observations on Drosera filiformis, in The American Naturalist, 8, July, 1874, p. 396.

[118] Treat (1830–1923) was American entomologist and botanist, as well as a supporter of Charles Darwin's theory of evolution. She devoted her time to writing scientific articles and collecting plants and insects for other researchers, including Gray and Hooker. Treat published many articles in *The American Naturalist*, *The Journal of the New York Entomological Society*, and in more popular magazines. She worked with Darwin on the studies of carnivorous plants, and Darwin acknowledged her contribution in his book *The Insectivorous Plants* in 1875.

[119] Treat, M. Observations on the sundew, in The American Naturalist, 7, 1873, p. 705–708.

In 1875, Charles Darwin became the first to publish a complete treatise on insectivorous plants,[120] a work containing the results of about sixteen years of observations and experiments with this type of plant. The first edition of the book was published on July 2, 1875, and a second edition, edited by his son Francis,[121] was published in 1889 after Charles' death. This later edition contained a few corrections to the first edition that had been made by Charles, and some additions to the text and notes by Francis.[122] During his experimental studies into insectivorous plants, Darwin worked with a number of colleagues specialised in physiology and chemistry and, in particular, with Prof. Edward Frankland of the Royal College of Chemistry. His sons also helped him with the illustrations on the book: one, George,[123] worked on those in *Drosera* and *Dionaea*, while the other, Francis, made those of *Aldrovanda* and *Utricularia*. After the death of his father, Francis published a three-volume book in 1887 entitled *The Life and Letters of Charles Darwin*, in which he brought together his father's entire scientific correspondence with friends and contemporary scientists colleagues such as Gray, John Dalton Hooker and Lyell.

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[120] Darwin, C. *Insectivorous Plant*, John Murray, London, England, 1875.

[121] Francis Darwin (1848–1925) was a mathematician, a naturalist, and Charles Darwin's son. He worked with his father on experiments into the movement of plants and, in particular, into phototropism, and he was the co-author of the book *The Power of Movement in Plants* (1880). He became a member of the Royal Society in 1882, edited *The Autobiography of Charles Darwin* (1887), and published Charles Darwin's correspondence with other scientists in *The Life and Letters of Charles Darwin* (1905).

[122] The translation of the book into Italian was published in 1878, with the author's consent, by Prof. Canestrini and Prof. Saccardo of Padua University.

[123] George Darwin (1845–1912) was an astronomer and mathematician, as well as Charles Darwin's son. He was the first to develop the theory of lunar recession, in which he asserted that the moon was created out of the Pacific Ocean, and he also attempted to establish when this creation took place, by studying the velocity of the Earth. He went to Cambridge University, where he was given the professorship of Astronomy and Experimental Philosophy, one of the two highest posts in astronomy at the university. In 1892, he was awarded the Gold Medal by the Royal Astronomical Society.

Darwin's work was at the same time reconstruction and synthesis: referring to a tradition of studies that preceded him,[124] he investigated the matter by supporting his conclusions on hundreds of experiments and made a connection of all the facts that scientists before him were limited to describing in a disorderly fashion; thus, he created an overall picture.

He reviews all the sophisticated adaptations put in place to hunt insects: the tentacles on the upper surface of *Drosera rotundifolia* leaves;, its their particular characteristics (e.g., such as to induce the author to speak of nervous matter analogous to the nerves of animals and muscles);, the contraction capacity of *Dionaea* leaves and their digestion activities, also incredibly similar to animals' digestive processes; the deadly entrapment mechanisms present in the leaves of *Aldrovanda vesiculosa* arranged around the stem in a series of wheels; the even leaf-stalks resembling spokes; the fly-catcher leaves of *Drosophyllum lusitanicum*; the graminivorous and granivorous behaviour of *Pinguicula vulgaris*; the sensory antennae of *Utricularia neglecta*; the air-filled bladders of *Utricularia nelumbifolia*; the grids of *Genlisia ornata*, the anaesthetising liquid of *Nepentes pervillei*; the death-cell aquarium of the Bladdenwort *Utricularia vulgaris*; and the death chamber of *Genlisea ornata.* These various discoveries convinced Darwin and his readers even more that behind the perfection and the wonder so often praised by natural theology lay, in reality, a cruelty of the nature heralding indistinct massacres that represented an essential component of variation and the struggle for survival, as a part of evolution through natural selection.

3.4 Cross-self fertilisation

In 1876 *The Effect of Cross- and Self-Fertilisation* was published.

The idea that constitutes the thesis of this book was born in 1866, during the gestation of the chapters on the inheritance that the author was writing for Variation. In a series of experiments he realised that in *Linaria vulgaris*, the offspring of self-fertilizing plants were clearly less vigorous than those of others, specifically *Dianthus caryophyllus*. Now it needs to answer to the following question: what are the evolutionary consequences of cross-fertilisation? Following the observations of Kölreuter, Gärtner, and Naudin, he selected plant species belonging to families from different countries of the world and crossed them for ten successive generations.

He divided his experiments into specific series.

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[124] Linneo, John Ellis, his grandfather Erasmus su Dionaea, the Rev. Curtis of North Carolina, and others naturalist that came before him regarded plant's digestive fluid and several other characters.

The first series involved *Petunia violacea*, *Dianthus caryophyllus*, *Mimulus luteus* and some species of morning glory. The results convinced him that fertilising flowers with their own pollen for a dozen generations and growing the seeds under the same conditions allows them to fix certain characteristics, such as the colour of flowers, through the generations.

In the next series, he took six genera of the Scrophularia family: *Mimulus, Digitalis, Calceolaria, Linaria, Verbascum* and *Vandellia*. Cross breeding in *Mimulus* produced higher seed quality over three generations ; moreover, in nine generations it showed high polymorphism in the colour character.

In general and in the subsequent series of experiments, Darwin obtained observational results in favour of the recognition of a selective variation in cross-fertilisation: over the generations, the plants appeared to be more branched, with larger leaves and larger flowers and producing a higher number of capsules.

Whenever Darwin introduced genetic variability through crossbreeding, he discovered the superiority of generations compared to self-crossed plants.

He laid down as a general law of nature that the flowers were adapted to cross-fertilisation through the pollen of another plant: this adaptation involved a genetic variability that achieved greater resilience to ecological changes and a better structure conformation. Moreover the evolutionary advantage deriving from cross-fertilisation also explained the origin of the two sexes and their separation, or union, in the same individual. Furthermore, this book represented an important theoretical acquisition in the explanation of hybridism, another extraordinarily delicate issue within Darwin's theory of evolution that will be more fully addressed in his subsequent botanical publication.

3.5 The different forms of flowers on plants of the same species

In 1850, Charles Darwin embarked on a long series of botanical observations and experiments to explain the phenomenon of floral polymorphism. Darwin was encouraged to take an interest in this subject, and in pollination and the reproduction of plants, after observing something that might have appeared to contradict his theory of natural selection: most of the higher plants (Angiosperms) have hermaphrodite flowers. This suggests potential self-pollination of their flowers and, as a result, self-fertilisation, as well as a lower level of probability of crossbreeding and thus of variability between individuals.

Until this time, no one had yet demonstrated the meaning of heterostilia: no one had succeeded in concentrating on the fact that the pollen located on the stigma of a plant of this kind, although perfectly healthy, could have made no contribution in any illegitimate crossing.

Over the following five years, Darwin published five more works on other species, referred to as "dimorphic" and "trimorphic," because they present two or three floral morphs, respectively, characterised by pistils of different lengths. More precisely, it was possible to distinguish between long stylus and short stamen and short stylus and long stamen forms: both showed differences in the size of pollen grains, and Darwin called them "dimorphic" specimens. The third form, which the author called "trimorphic", presented three different varieties in the length of the stylus and stamen and in the size and colour of its pollen grains: each of them can present up to two sets of stamens, and between them, six series and three different types of stylus.[125]

The heterostyled species thus present two (dimorphic) or three (trimorphic) types of individuals (morphs) which can mainly be distinguished by the different lengths of their styles[126] as well as by other traits, such as the morphology of the stigma and of the anthers, the number and size of the pollen grains, the number and size of the seeds, and so on. These distinctions are crucial in determining fertilisation between the various forms: for example, fertilisation between stamens of the same height is always fertile. In fact, if a form is fertilised by the pollen contained in the stamen of another form placed at the same height, then the crosses between the dimorphic forms will be fertile, and in fact, Darwin calls them "legitimate marriages", while the "illegitimate" will prove to be variably fertile.

Darwin's observations of the reproduction of the higher plants and of the variability of floral structure started as he had begun drafting his *The Origin of Species*, and he continued to make them in later years, almost until the time of his death.

It was in 1859 that, in his garden at Down House, Darwin started up his first, meticulously scientific experiments on *Primula veris*. These were published in 1862 in the *Journal of the Linnean Society*,

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Linneo, John Ellis, his grandfather Erasmus su Dionaea, the Rev. Curtis of North Carolina, and others naturalist that came before him regarded plant's digestive fluid and several other characters.

forms, differing in the length of their pistils and stamens and in other respects.

126 Long styled, mid styled and short styled.

in a work entitled "On the two forms, or Dimorphic Condition of *Primula*". This case of variability had been known for some time, for it had already been described by John Henslow.[127]

Darwin realised that, although the specimens of *Primula* were hermaphrodites and could not be divided on the basis of sex, legitimate crosses gave rise to a superior offspring in force and size compared to illegitimate crosses. In addition, in 1838–1839, Darwin observed a similar floral dimorphism in a species of flax, *Linum flavum*, although he considered it to be simply a case of variability, without particular significance. It was only later on, when he carefully examined the cowslips growing in his garden, that he realised how the two forms were too regular to be considered in this way. He was helped by the contribution of 202 plants from the Isle of Wight thanks to his son William's collection and concentrated on the study of *Linum grandiflorum*, perennial and certainly flavum: he obtained more than eighteen unions, six of which were legitimate and, one more once, legitimate crossings proved superior. Yet he also realised that the percentage of the unions' sterility increased in proportion to the increase in the distance between the stigma and the stamens.

In 1877, his book *The Different Forms of Flowers on Plants of the Same Species* was published. It brought together all Darwin's observations, experiments, and speculations concerning sexual polymorphism of flowers on plants belonging to the same species. The subject covered included polygamy, dioecy, monoecy, and much space was devoted to the subgroup of heterostyled species among plants with hermaphrodite flowers, starting from publications in *Journal of the Linnean Society*.

According to Darwin, the heterostyly ensures cross-fertilisation: in other words heterostyly is one of the main mechanisms that makes possible the crossing of different individuals in species with hermaphrodite flowers.

Darwin analysed various characteristics in depth to evaluate their influence on the various possible crosses in terms of fertility: the length of the pistil, the shape and size of the stigma, the appearance

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[127] John Stevens Henslow (1796–1861) was professor of botany at Cambridge from 1827 to 1861. His friendship had a profound influence on Darwin's career, and not only because he was his tutor at Cambridge University. He pulled strings to make sure Darwin was given the role of naturalist on the Beagle, and Darwin wrote about Henslow, stating that "His knowledge was great in botany, entomology, chemistry, mineralogy and geology. His strongest taste was to draw conclusions from long-continued minute observations."

of the stigmatic papillae, the length of the stamens, the appearance of the anthers, the colour of the pollen, the size of the pollen grains, the size of the fruits, the size and weight of the seeds, data about the demographics of the natural populations, the frequency of different morph types in the populations, and more.[128] He used the term “legitimate unions” to define pollinations effected by pollen from stamens of the same length as the style of the receiving flower, while “illegitimate unions” captured those effected with pollens from stamens of a different length from that of the style of the receiving flower. He also made a number of observations of the pollinating insects and the ways that the species being examined were pollinated. In many cases, he also carried out pollination tests on the descendants, in order to compare the effects of self-fertilisation and cross-fertilisation on the fertility of the offspring.[129]

Darwin managed to capture the existence of plants belonging to the same species that had two or even three different forms:[130] they could interbreed with other plants, but only the crossing with plants having stamens at the same height could lead to perfect fertility for the seeds.

Establishing a distinction between legitimate and illegitimate unions, demonstrating that the former produce perfectly injured seeds while the latter are much more unstable, and setting theoretical general considerations on hybridism in nature allowed Darwin to construct a text that served as an aid only for the subsequent editions of *The Origin of Species*, but it was also a precious element for the horticulturists who knew now how to avoid sterility in the cultivation of fruit trees much more easily.

3.6 The power of movement in plants

With the drafting of the climbing plant, Darwin asked a new evolutionary question: if there were all those different classes of movement that had developed and on the basis of which it was possible to distinguish the plants, there had to be an original and primitive form of movement which was common to all plants and from which the movements of the climbing plants had descended.

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[128] The production of seed and fruit.

[129] In his studies, Darwin considered a large number of species, representing most of the genera and families known at the time to be heterostyled (thirty-eight genera and fourteen families, respectively).

[130] Long stylus shape, short stylus shape, half stylus shape.

His generalisations led him to postulate the existence of a class of circular movements influenced by light and gravitational force, which he summarised as circumnutation. He dedicated a treatise to demonstrate the existence and development of these movements.

He began his studies and drafts in the summer of 1877 despite his age and the illness that made him sick and allowed him few hours of work per day: Francis's help proved decisive.

No organ escapes the circumnutation process: many experiments thus investigated these activities in the plant kingdom and are mentioned in his famous essay on *The Power of Movement in Plant*, which contains about 150 illustrations of movement recordings,[131] as experimental evidence that each leaf-stalk and leaf perform the same behaviour, that the tip of each rootlet move digging along directions that draw small circles or ellipses, that this same movement is common to growing shoots, that plants use the night to sleep and can suffer from sleepless if deprived of daylight, and other fascinating behaviour patterns in botany. The most important observations developed in this work remain those of the nyctitropic (nyctinastic) movements, the movement of the seedling, the sensitivity and response of the radicle, the gravitropic responses, and the phototropic movements.

The circumnutatory movement is the common thread: in it, we find the origin of phototropism and gravitropism, epinasty, and hyponasty.

Observations on nictinastic movements[132] show that these closing movements contain the heat dispersion of the leaves during the sleep condition in cold environments and prevent the plant from freezing or from dangerous chilling. Darwin thus achieved the certainty of a hereditary basis for photoperiodism, but not only that: he was also the first to demonstrate experimentally that the apex of a radicle was sensitive to contact[133] and to describe a case in which the organ of the root moves away from objects touched and recognised as irritants.

Darwin's observations on the radical at the same time highlight his character as a plant physiologist and naturalist: he never tires of comparing his findings on the root apex with the analysis of the

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[131] To complete these experiments, he made use of a system of black sealing-wax strips on pieces of paper or manually marked a glass with the successive positions of the plant being studied.

[132] The experiments conducted concern the leaves of various dicotyledonous plants, in particular of the genus *Melilotus* and the aquatic fern *Marsilea quadrifolia*; all observations were made in winter conditions. He also observes the nocturnal closing of the leaves of *Arachis, Mimosa albida, Marsilea, Bauhinia* and *Oxalis* observing the double protection put in place by the leaves.

[133] Darwin, 1880, p. 131.

remote causes that are the reason for the sophisticated movements of the radicle. Not only is the radicle able to penetrate the ground thanks to its pressure capabilities, but it is also able to understand which parts of the soil offer the least resistance, how to dribble any obstacles to its descent, the most effective ways of getting to the ground, and the amount of humidity.

4 ORCHIDS IN VICTORIAN AGE

Abstract

Botanists' special interest in orchids was born in the eighteenth century. The first attempt to understand these species went hand in hand with classification. Carl Linnaeus conceived the plants in marital terms: they were husbands and wives united in a marriage of flowers.[134] This metaphor was nothing but the translation into literary terms of the Swedish classification system: plant sexuality was what allowed their distinction through names. The sexuality of plants was the same reason that led Darwin to study them and experiment on them. Years and years of study to answer the right questions started with his contact with the flowers of the orchids present in his garden. He was specifically curious about why orchids developed sophisticated and functional dimensions to build an intimate relationship with the insects belonging to the unique species that pollinate them.

The historical moment helped the naturalist, and he, at the same time, exploited it: in those years orchidmania was sweeping England, and orchids were flooding into the country by the millions from exotic, far-off places. A collection of orchids became a status symbol. Collectors were willing to pay very high prices for the rarest inflorescences. A real industry was created that also involved a collective imagination, fuelled by writers and illustrators; orchids became a member of the products protected by imperial trade routes that the British fleet supported and represented and that involved countless nurserymen and shippers. Being botanical collectors meant to have a specialised occupation, these botanists were men hired by botanic gardens, horticultural societies, governments interested in economic plants, and syndicates of private gardeners. However, men with another primary occupations (e.g., missionaries, consular officials, and supercargoes) made a remarkable contributions to the artificial redistributions of plants through their private means.

Among Darwin's many interests, however, botany probably ranked the highest. As a lover of plants, he enjoyed collecting them, and as with all orchids collectors, he learnt the method for preserving their colours before drying them.[135]

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[134] Endersby, p. 5.

[135] It involved smoking the blooms with a sulfur candle, Tyler Whittle, The Plant Hunters, Tales of the Botanist-Explorers Who Enriched Our Gardens, foreword by Chrles Elliott, Lyons & Burford Publishers, New York, 1997, V.

Darwin used all of this to extend his research to tropical orchids and to get his ideas to reach a huge number of readers, who were then all involved in this typically Victorian fashion: he tapped this fever for orchids and convinced his publisher Murray that a book on orchids would feed into this orchidmania. Eventually Darwin published two editions, with critical acclaim, which never sold more than 6,000 English-edition books by 1900. *On the Various Contrivances* was ground breaking and important, the mass of detail made for difficult and slow botanical reading.

The public pervaded by the orchid mania was also the one to which Darwin intended to dedicate the small treatise, however: not only historians of nature, therefore, but also classifiers, orchid lovers, and horticulturists were part of the audience of his readers, as well as of the large group of correspondents who stimulated and contributed to the writing of *On the Various Contrivances*.

4.1 Classification of new species of orchids

The first classification of orchids came about thanks to the work of Tournefort,[136] who strengthened the grouping of plants in general thanks to the choice of common features such as the corolla and the fruit. In this way, he more precisely distinguished the species within the systematic groups: he gathered generates together with larger groups he called “orders”.[137]

Among these orders he identified that of orchids, characterised by the asymmetrical arrangement of flowers. This classification remained constant until the eighteenth century, when botanists decided to recognise the orchid family.

The second recognition of this family took place in India: the Dutch Governor of the Malabar region of India,[138] Hendrik Adriaan Van Rheede, took care of publishing the Hortus Indicus Malabricus involving 200 botanical experts, including doctors and local monks, in a laborious work lasted more than thirty years. The result was twelve volumes dedicated to Indian botany,[139] and that made Van Rheede the first European to publish a detailed description of tropical orchids.[140]

These were orchids that grew on trees, and for this reason they were considered pests, but Van Rheede made it clear that they were not plants harmful to the trees on which they grew. Rather, the

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[136] Tournefort, Élémens de Botanique, 1964.

[137] They are not the current orders, but rather they are what botanists call families.

[138] The current state of Kerala.

[139] The images were produced by four soldiers of Dutch East India Company’s army.

[140] Van Rheedem preface to Vol. III of Hortus Malbricus.

trees were a support that the orchids used and, following Van Rheede's description, were called "air-plants".[141]

Starting with Van Rheede's publication, tropical orchids began to be imported into the Old Continent, and the classification work for these new flowers spread. The Royal Professor of Botany and Gardener to Queen Mary, Leonard Plukenet, published *Phytographia* (1696), a work in which he identified new species of orchids, and the German naturalist Engelbert Kaempfer published *Amoenitatum Exoticarum* (1712), in which he described numerous new orchids he had observed during his travels in Asia.

The turning point came with the work of Carl Linné, however.

4.2 Linnaeus

In the seventeenth century, botanical research was suggested and encouraged by collateral research in the medical field and by the desire to find exotic specimens able to retouch garden geometries with originality,[142] but the century of the Enlightenment, also known as Age of Elegance, was recognised as the "Golden Age of Botany". It was the century of classification, of the systematic search for plants, both on a professional and amateur basis, and of experiments.

The task of naming and describing new species played a fundamental role in the career of every eighteenth century naturalist and will also be inherited from the following centuries. However, the beginnings of these practices involved a series of problems, including how to definitively name new plants when the systems in use were divergent and required the adoption of different names.

On the basis of a biblical time scale and of the idea of fixation of animal and plant species, the recourse to the concept of *scala naturae* appeared not univocal: the hierarchical distinctions changed depending on the latitudes and when they began to translate and study religious traditions and cultural of foreign countries, and it was realised that different theories existed concerning the origin of the often irreconcilable living beings.

The 1700s was not, therefore, a century that saw naturalists unite under a single philosophical and scientific perspective.

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[141] We are dealing with those plants that botanists currently define as epiphytic or lithophytic.

[142] Tyler Whittle, 1997, p. 45.

Linné was influenced by reading an article by Sébastian Vaillant[143] where the French botanist stressed the need to refer to the stamens and pistils of the plants as their reproductive organs and, although the idea that plants possessed a sexual identity constituted a shock at the time, the Swedish botanist realised that the sexual organs were much more important than the petals in the classification. By reducing Vaillant's ideas and those of numerous other naturalists into a coherent, original, and comprehensive system,[144] Linné definitively named about 8,000 species of plants and about 4,400 species of animals.[145] He used his *Species Plantarum* (1753) to define the characteristics common to the Orchid genus.

The method used by Linné was then defined as the sexual system because on the basis of the count of the reproductive organs of each plant, it was possible to place that plant, with more precision than in past, in a hierarchy that saw the species at the initial level and the kingdoms at the highest, with a series of groupings in classes and intermediate orders.[146]

The simplicity of the Linnean method of identifying the method led explorers, doctors, naturalists, and plant lovers to use it to assign a position to newly discovered plants for the first time. The rapid diffusion of this method, thanks to the translation of the Swedish works also involved the diffusion

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[143] He was successor of Tournefort at Jardin du Roi in Paris.

[144] On the basis of Vaillant's intuition, Linnè refers to the numbers of masculine stamens to establish one-class plants and the number of female pistils for assignment to included orders. As for the flowers whose reproductive organs could not be seen, Linné gathered them together in a group he called the "cryptogams", whose marriages were hidden.

[145] Lisbet Koerner, "Carl Linnaeus in His Time and Place," in Cultures of Natural History, ed. Nicholas Jardine, James A. Secord, and Emma Spary, Cambridge University Press, 1996.

[146] This idea of hierarchizing the natural world pervades the *Systema Naturae linneano* that have absorbed the concept of *scala naturae*, but also the works of eighteenth-century zoologists, and is still perceived in Lamarckian thought: for Lamarck and the "transforming" zoologists, nature perfected the animal world through an "evolutionary scale"; an intrinsic desire to improve pushed the animals towards ever better anatomical structures and did not consider, instead, that the evolutionary processes are not univocal, but are shaped by different needs imposed by different environments.

of Linné's ideas,[147] allowing the identification and classification of the plants without continuous recourse to their usefulness in the medical field: in this way, the botany was progressively emancipated from medicine.

4.3 Orchids, society, and literature

The cultural and social framework that hosted the scientific interest of Darwin for orchids had peculiar characteristics: a typically Victorian passion for flowers in general, an increasingly widespread basis of botanical knowledge,[148] and the collection of exotic plants in private properties, a fashion rampant in the nineteenth century in the ranks of the middle classes.[149]

The orchids did not receive the attention of collectors and scholars only for their novelty and beauty: the company itself placed them in a grid of social belonging. In fact, starting from the industrial revolution, exotic and tropical orchids became the status symbol of people living in a wealthy and culturally elevated environment.[150]

On this assumption and to respond to ever-restless market demand, orchid hunters began to travel new routes, and they prepared to undertake distant journeys in dangerous and uninhabited areas,

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[147] There are many elements that permeate Linnaeus' work: for example the finalism of a nature perfectly and magnificently ordered and created in the mind of God; a concept of natural economy according to which the role of every living being is wisely administered and realizes a hierarchical system of perfection that presents no solution of continuity; a concept of living beings destined for the use and beatification of man and which in their specific and special creation reflect a rational order contained in the mind of God thanks to which it is possible to name and classify them; a method of classification that considers genus and species as real real entities, fixed and immutable, and that sets a binomial nomenclature; the use of the hybrid sterility criterion to determine whether or not two individuals belong to the same species; and the concept of a nature where survival is a struggle between individuals did not come conceived as events necessary to maintain the balance between species at the expense of these individuals and other theoretical generalizations formed the scientific background of the Linnaean classification and of the way in which the Swedish botanist looked at orchids.

[148] Scourse N. 1983. *The Victorians and Their Flowers*. Timber Press, Portland, OR, USA.

[149] Tyler-Whittle MS. 1970. *The Plant Hunters*. Chilton Book CO., Philadelphia, PA, USA.

[150] Tyler Whittle, 1997, p. 10.

fuelling the ambition that at the end of their journey they would have access to new and rare specimens or colonies of orchids.

Traces of this research began to show up at the end of the century: hundreds of forests were plundered in search of epiphytic orchids, and once the large areas containing orchid populations were stripped, most of them were completely eradicated and transformed into new habitat, so much so that several species survived only in captivity. One example is the *Laelia elegans*, which until 1847 grew abundantly under natural conditions on a small island in Brazil: starting from 1897, there was no living member of the species in that habitat.

The competition was such that the routes were kept secret or forgotten; in fact, the historical findings show maps with indications in kabbalistic symbols known only to a very restricted circle, or in some cases the comprehensible maps were nothing but forged documents that were diffused for a copying staff that would have fuelled many unsuccessful search attempts.[151]

The attractiveness of possessing a tropical orchid ended up drawing not only collectors, ready to pay dearly for the goods, but also orchid researchers: discovering an unknown species could represent the pinnacle of a scientist's career, but it could furthermore offer a source of livelihood for years. Above all, however, tropical orchids represented a prize: something that the market demanded continuously. This is an important trend for the national economy: not only were the individual noble families and the members of the industrial and mercantile bourgeoisie involved, but also botanical gardens and the scientific faculties demanded samples continuously: the exchange of seeds is famous among the Kew's Royal Botanic Garden and researchers working in various capacities in Brazil.[152] As we shall see, this will decisively involve the collaboration between Fritz Müller and Hooker.

In any case, in the Brazilian and Central American forests the variety of orchids was so rich that it pushed orchid pickers to risk their lives in search of new species. If the stories of these collectors

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[151] Tyler Whittle, 1997, p. 10–11.

[152] The Brazilian authorities prohibited the export of orchids from the country, so Kew sent a scientific expedition in search of seeds to import. The result was the departure of a steamer dubbed Amazonas, with the recommendations of Queen Victoria, from the port of Pará with a cargo of 70,000 seeds, of which only 3,000 sprouted into seedlings for Kew. Furthermore, 20,000 of them were reared and shipped out to Burma and the Malay archipelago.

were so full of dangers and failures,[153] they were also of secrets: the new species collected were exported, but few collectors intended to reveal their precise locations, and this secrecy represented a problem when foreign orchids became extinct in captivity.

Orchids were (and are) all over the world: there was a worldwide distribution of them and they were a very good example of a group that we could explain as having evolved from common ancestors over very different environmental regimes. In Britain, orchids were cultivated and sold as ornamental plants: collecting and growing orchids was a very popular sort of middle class activity in Victorian Britain, and many moderately wealthy or middle-class people had orchid windows in their houses.

With the abrogation of the tax on window-panes, the lowering of costs concerning the purchase of iron, and the significant improvement of greenhouse technology in nineteenth-century England,[154] the social situation presented a series of circumstances that reconciled a real mania for the tropical species epiphytic-lithophytic of orchids with the love for the collection of Victorian plants in whose catalogue we must mention tropical and temperate species of ferns, aquatic plants, *Rhododendron spp*., and palms, among others.

Overall, it is fair to remember that the craze for epiphytic orchids collected spontaneously turned out to be long lasting for two reasons.[155] Above all, there was no means to afford other types of plants: most of the middle class was certainly in great economic expansion in England, but did not own enough land to cure the culture of great groves of giant conifers and *Magnolia grandiflora* from North America or the arborescent *Rhododendron spp.* of the Himalayas. It was impossible to support construction costs and construction problems related to the building of huge tropical Amazonian houses for South American Victoria amazonica[156] and palm conservatories associated with Kew Gardens and the great private estates. The buildings of the time were based on small winter gardens and adjacent greenhouses connected to urban and suburban homes and to the heating

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[153] Tyler Whittle, 1997, p. 143.

[154] Woods M, AS Warren. 1988. Glasshouse: A History of Greenhouses, Orangeries and Conservatories. Aurum Press, London, England.

[155] Bernhardt P. 1989. Wily Violets and Underground Orchids: Revelations of a Botanist. William Morrow and CO., New York, USA.

[156] Coats P. 1970. *Flowers in History*. Viking Press, New York, USA.

systems of these houses, greenhouses that housed dozens of orchids from the tropics of the Old and New World.

A body of popular literature had also focused on didactic tales of how to collect and cultivate orchids, forcing readers to start a journey through tropical adventures when they sat in chairs to leaf through the books. The authors themselves recalled how the possession and display of such highly prized and hard-to-reach flowers conferred a special social status on their owners, because their cultivation and care required and at the same time showed good taste and horticultural expertise.[157]

The second reason concerned the reputation that collectors attributed to the flowers of these plants: at that time the orchids represented something unique, because the mass importation of these plants from their seeds or meristemic tissues remained impossible until the twentieth century.

4.4 Darwin and orchids

From youth to old age, plants and flowers were the passion of Darwin's life, his consuming interest and greatest love. His love for orchids was sudden and pervasive, however. As Janet Browne remarked in *Charles Darwin: The Power of Place*, "Even Darwin was surprised at his ardour for orchids that came over him in the middle of 1861, something like an unexpected love affair late in life." This love affair soon turned into an infatuation. Darwin writes, "I can not fancy anything more perfect than the many curious contrivances." He thus put aside a book on carnivorous plants and research on variations to experiment and unlock orchid secrets. He confessed, "I love a gambler and love a wild experiment." He called it a "hobby horse that has given me great pleasure to ride," and said, "I am intensely interested in the subject just as at a game of chess." Darwin furthermore decided to study orchids so deeply in part to show how complex structures could be explained by the mechanism of natural selection without reference to divine influence. Orchids were his proof of the reality of evolution. Did Darwin early love of flowers in general predetermine a long-term, and unusually personal, inquiry on orchids decades later?

Darwin's discoveries in botanical sciences were driven first by passion, as we can read in Francis' words: "I used to like hear him admire the beauty of a flower; it was a kind of gratitude to the flower itself, and a personal love for its delicate form and colour; I seem to remember him gently

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[157] Boyle F. 1893. *About Orchids-A Chat*. Chapman and Hall, London, England.

touching a flower he delighted in; it was the same simple admiration that a child might have."[158] This sort of passion led Darwin to observe the objects of his love with great accuracy.

The most plausible explanation for Darwin's orchidophilia remains with his seventh son, Francis (1848–1929): "He was probably attracted to the study of Orchids by the fact that several kinds are common near Down".[159]

More recently, Boulter[160] has reported on a notebook that Charles Darwin wrote in during his early days at Down house in the 1840s. Boulter insisted that Charles and his wife Emma transplanted orchids from the wild into their hothouse to better observe them.

By 1861, Darwin had amassed a sizable collection of orchids from collections at Kew and the commercial nurseries of James Veitch and son, as well as from gifts given by private collectors.[161] Addressing his father's research on orchid flowers, Francis wrote that in 1861 Charles Darwin gave part of summer and all of autumn to the subject. Some people have misread this statement and come to the conclusion that all Darwin's orchid research for the first edition of *On the Various Contrivances* began and ended in 1861. While it is reasonable to assume that it took Darwin ten months to write the book and that most of his dissections of exotic species were performed and recorded in this space of time, his correspondence indicates that his work in British species was older. In particular, there is Darwin's famous letter to the *Gardener's Chronicle* (4–5 June 1860) discussing his observations, before and during 1858, recording (insect-mediated) pollinia removal in flowers of *Ophrys muscifera.* Within the same letter, he contrasts these results with the absence of pollinia removal and self-pollination in *Ophrys apifera*. It was not until the second edition of *On the Various Contrivances* that Darwin (1877) finally released his data on poor pollinia removal rates in flowers of *Orchis morio* during the cold and wet season of 1860.

Based on collected correspondence, in 1860 Darwin first attempted to enlist other naturalists to make observations on orchid flowers native to Britain. He wrote Alexander Goodman More (1830–1895) on June 24, 1860, but More did not respond until the following year. In short, the belief that

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[158] Francis' words quoted in Haldane, J.B.S. *An Indian perspective of Darwin*, "Central Review of Arts and Science of Michigan State University", 3, p. 359.

[159] Darwin F., editor. 1896. The life and Letters of Charles Darwin, including an Autobiographical Chapter. Appleton and Company, New York, USA, p. 303.

[160] Boulter, 2008, p. 157.

[161] Siegel C. 2011. *Darwin and his love affair with orchids*. Orchid Digest 75:60–71.

Darwin began and completed his entire study on orchid floral biology pollination in 1861 does not withstand a reading of the first half of one sentence in Darwin: “I have been in the habit for twenty years of watching Orchids”.[162]

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[162] Darwin C. 1862c, p. 34–35.

5 THE ORIGIN OF *On the Various Contrivances by Which British and Foreign Orchids Are Fertilised by Insects and on the Good Effects of Intercrossing*

Abstract

For a book on variation, Darwin conceived a promise to readers to develop the theoretical generalisations contained in *The Origin of Species* in a synthesis characterised by compiling a larger body of observed phenomena, less amount of profundity to conjectural and plausible theorising, better profound acquisition of scientific knowledge and references. Darwin began to write notes for this book in January 1860.

Nevertheless, he was soon distracted from this new work to dedicate himself scrupulously to the plants.

Scientific observations of the plants, conceived as a preamble to a series of publications, began in 1841 when Auguste de Saint-Hilaire published physiological observations which suggested that the physical structure of plants in the genus *Goodenia* made cross-fertilisation impossible. Darwin was wary of these conclusions and tried to test them. The research on Goodenia turned out to be a dead end, but Hooker sent a pair of *Leschenaultia formosa*, a plant with similar floral morphology. At this point, Darwin began the study of the structure and reproduction of *L. formosa* and then moved on to sexual dimorphism in hermaphrodites, insectivorous plants, and cross-fertilisation in orchids: they were cases that offered all the ways to apply evolutionary thinking to projects that had fascinated him for decades.

Although Darwin felt guilty for diverting most of his efforts from variation to botanical publications,[163] at the same time he could not hide from his joy and his ever-increasing interest in addressing these new topics.

Darwin's *On the Various Contrivances*[164] was his first major publication after *The Origin of Species*.

Historians of science often refer to Darwin's first publication after 1859 as " the little book with the long title": *On the Various Contrivances by Which British and Foreign Orchids Are Fertilised by Insects, and on The Good Effects of Intercrossing*.[165] Originally published in 1862,[166] Darwin's

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[163] Darwin to Oliver, 20 October [1860], CCD(ref.5), VIII, 440.

[164] Darwin C., 1862c and Darwin C., 1877c.

[165] Darwin C. 1862c.

work on Orchids was both meticulous and stimulating: *On the Various Contrivances* compelled people from all over the world to send him correspondence and specimens, as acknowledged in his book. Accordingly, *On the Various Contrivances* enjoyed a second and much-expanded edition in 1877.

Actually, the version published in 1862 reported content not entirely unpublished; Darwin had anticipated the release of the book with two articles sent to Linnean Society.[167]

The first book Darwin published following *The Origin of Species* interpreted the morphology and biomechanics of flowers in the orchid family.[168]

5.1 The beginning of a paper

According to his autobiography, Darwin began to deal with cross-fertilisation by means of insects starting from 1839, but he had slowly accumulated observations and material on orchids in previous years. Hence, the observations made on the orchids took place when he had already realised the principle of natural selection in 1838. The letters that Darwin also exchanged with William Herbert[169] allow us to accept the hypothesis that he had already elaborated the Knight–Darwin principle, although he had not carried out sufficient experiments in this regard:

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[166] The first edition of the book came to light in 1862 and sold out quickly. A few months later, Darwin began receiving letters from numerous correspondents, including Fritz Müller from Brazil, from which he gained new knowledge about orchids and was made aware of certain mistakes in the original publication. After that time, new treatises on the fertilization of orchids came to light and carried out observations of many new facts: Darwin then chose the most interesting, gave a brief compendium to the publications, and he published his book again.

[167] Darwin, 1862a; 1862b.

[168] Darwin 1862, Darwin's treatise caused a great stir and was translated into many languages: the first Italian edition, which took from the second English one, came out in 1883. It was edited by the great Darwinist Giovanni Canestrini.

[169] William Herbert (1778–1847) was a British plant hybridizer and a poet and clergyman, belonging to the group of early evolutionists who believed in creationism but were sure of common descent and transmutation. Darwin defined him as the third greatest hybridizer who ever lived.

“[…]I have been led to believe, that amongst organic being producing seminal offspring there exist no such thing as a true permanent hermaphrodite—ie. that every individual occasionally, though perhaps very rarely, after long intervals is fecundated by a other indiv., in short that almost plant is occasionally fecundated as in as in diœcious genera— I am fully aware how presumptuous I must appear, to speculate on subjects on which I have made no experiments, & still more so in taking the liberty of addressing you but, if when at leisure in the country you will ever so briefly answer me these questions, I shall feel extremely grateful.”[170]

Moreover at that time, Darwin had not yet read Sprengel and was not sure of the role played by pollinators on plant pollination mechanisms: it was Herbert himself who made him aware that the possibility existed that insects fecundated flowers by pollen from other individuals.[171]

The observations on the cross-breeding experiments on plants, and also on some orchids, were collected in *Notebooks*,[172] but began in 1839.[173]

Beginning in 1841 and on the advice of Brown, Darwin began to focus on the relations between pollinators and flowers through voraciously reading Sprengel:[174] his copy of Sprengel’s book presents almost eleven pages of personal notes.[175]

Still in the very early 60s, Darwin became convinced that he wanted to publish a treatise, given the amount of material he had accumulated:[176] this desire began with a paper in 1861, preceded by a series of pressing requests to the *Gardeners’ Chronicle* about the pollination of *Ophrys apifera*,[177] a letter to Westwood to have pollen masses adhering to the body of hive bees and bumble bees for

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[170] From Darwin to William Herbert, 26 June 1839, Darwin Correspondence Project.

[171] From William Herbert to Darwin, 27 June 1839, Darwin Correspondence Project.

[172] Darwin, C. R. Notebook 1839–1844: Questions & experiments, in Barrett, Paul H., Gautrey, Peter J., Herbert, Sandra, Kohn, David, Smith, Sydney eds. 1987. Charles Darwin’s notebooks, 1836–1844 : Geology, transmutation of species, metaphysical enquiries. British Museum (Natural History); Cambridge: Cambridge University Press.

[173] Porter, Graham…p. 126.

[174] According to Ghiselin (Ghiselin, 1977), Darwin read Sprengel in the original German version.

[175] Di gregorio, Gill, 1990.

[176] Autobiography.

[177] From Darwin to Gardeners’ Chronicle, 4–5 June 1860, Darwin Correspondence Project.

possible transport to another flower,[178] one to Hooker on the descriptions received about the pollen masses of *Ophrys apifera* removed by insects,[179] one Goodman on the masses of *Ophrys* and the analyses performed on other orchids,[180] another on Stainton always concerning the *Ophrys* masses mentioned in the *Gardeners' Chronicle*,[181] and so on. The result was an unbroken series of correspondences in the coming years of almost 700 letters on the subject orchids[182] to testify as well as that which Darwin confided to Hooker to be the greatest interest of his life in a letter of October 13, 1861:

"I am desperately interested in subject; the destiny of whole human race is as nothing to the course of vessels of Orchids."[183]

The original intention was to write a long paper for the Linnean Society that Darwin had started during his stay in Torquay in July and August of 1861. At some point, however, as he confided to Murray,[184] he realised that the material he had accumulated could have been used for a separate publication: it was a collection of original facts that had engaged him for more than 20 years of observations and collection of notes.[185]

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[178] From Darwin to John Obadiah Westwood, 25 June 1860, Darwin Correspondence Project.

[179] Darwin to Hooker, 12 June 1860, Darwin Correspondence Project.

[180] From Darwin to Alexander Goodman, 24 June 1860, Darwin Correspondence Project.

[181] From Darwin to Henry Tibbats Stainton, 11 June 1860, Darwin Correspondence Project.

[182] Porter, Graham, 2015, p. 126.

[183] From Darwin to Hooker, 27 October 1861, Darwin Correspondence Project.

[184] From Darwin to Murray, 21 September 1861, Darwin Correspondence Project.

[185] As we have seen, Darwin began to speculate on orchids based on his theories starting in 1839. The passage from his autobiography testifies more precisely: "During the summer of 1839, and, I believe, during the previous summer, I was led to attend to the cross-fertilisation of flowers by the aid of insects, from having come to the conclusion in my speculations on the origin of species, that crossing played an important part in keeping specific forms constant. I attended to the subject more or less during every subsequent summer; and my interest in it was greatly enhanced by having procured and read in November 1841, through the advice of Brown, a copy of C. K. Sprengel's wonderful book, Das entdeckte Geheimniss der Natur.", Darwin 1967, p. 127.

Darwin demanded the judgment of Murray: he was doubtful that the publication of a small book on orchids could yield economic return for a publisher, and he feared that the public would end up getting bored by the highly detailed descriptions: in the end, it was about a bold experiment.[186]

Murray's reply reached Darwin two days after his proposal to publish a small treatise on the fertilisation of orchids: he consented without hesitation to the press and publication, allowing the author half of the profits of each edition.[187]

Darwin sent the manuscript in February 1862, and May 15 of the same year saw the publication of 1,500 copies. By August, almost half of the copies were sold,[188] and after this first peak, the editions slowly sold out.

The second edition of the book had the name *On The Various Contrivances by which Orchids are Fertilized by Insects*,[189], but the contents differed from those of the first edition, as did the reasons that led Darwin to publish again on the same topic after fifteen years.[190]

During these fifteen years, Darwin made numerous new and important observations on orchids that led him to introduce new conclusions, different classifications, and necessary corrections. Above all, during these fifteen years no less than forty treatises on the subject were published, treatises that all had their origins in that first publication. Furthermore, the first publication had generated a series of correspondences within which Darwin was continually updated by the observations and experiments of the other botanists on the subject, and the time had come to order them and add them to the previous ones for a new summary to be published.

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[186] From Darwin to Murray, 24 September 1861, Darwin Corespondence Project.

[187] From Murray to Darwin, 23 September 1861, Darwin Correspondence Project.

[188] Somewhat less than 2,000 copies: Freeman, 1977, p. 112.

[189] The term "fertilization" includes sexual reproduction, in other words the fusion of sperm and eggs. However in *On the Various Contrivances* we are witnessing the precise description of the sophisticated mechanisms by which the pollen masses are left on the stigmatic wall and the pollen tubes, in a second moment, lead the sperm towards the egg that is in the ovary, realizing what in modern terms we call "fertilization". However this last term was used only starting from 1872 with this semantic value and does not appear in the works of Darwin as in his letters (Porter, Graham, 2015).

[190] While the proofs of the first edition were corrected thanks the help of Henrietta, Francis was to correct proofs foor the second edition.

Both editions were translated into French and German while Darwin was still alive.[191]

5.2 Aims of the book

The book had several aims:

(a) Evidence for Knight–Darwin [192] law

The main assumption that the author intends to develop, starting from what is written in this regard is *The Origin of Species*,[193] is that no plant is fruitful by itself for an uninterrupted series of generations. To demonstrate this claim ,Darwin shows that the flowers of orchids are equipped with perfectly adapted contrivances to attract insects and involve them in cross-fertilisation, requiring the movement of pollen from one flower to another. Shape, colours, visual patterns, olfactory signals and smells, aromas, and nectar are all tools through which flowers attract insects. Then all the adaptations that allow the flower to adhere the pollen masses to the insect's body engage, as well as those to detach these masses or make them fall on the stigmatic surfaces of other flowers, thus achieving cross-pollination.

On the Various Contrivances is considered the main place where every conclusion is reached at the price of accurate and detailed investigation and demonstrative facts: the lack of these requisites

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[191] Quotation of book editions.

[192] Knight (1759–1838) was a British horticulturalist and botanist and the 2nd President of the Royal Horticultural Society from 1811 till 1838.

[193] Darwin attended the botanical lessons of John Stevens Henslow in Cambridge, who became his mentor: it was the latter who guaranteed the offer to the young naturalist for a place on the Beagle, and although Darwin did not write any specifically botanical work, he continued to observe and record as many plant details as possible during the trip. In 1838–1839, his speculations on the origin of the species we saw in the previous chapter convinced him to start a series of studies on the topic of cross-fertilization in orchid flowers by insects.

With the publication of *The Origin of Species*, Darwin had collected so many observations on fertilization that he felt confident enough to enunciate a principle that influenced his the entirety of his works after *The Origin of Species*: no organic being self-fertilizes itself for an eternity of generations.

could provoke a reaction of rejection by the scientific community.[194] The refusal by the scientists of some principles sustained in *The Origin of Species* constitutes one of the fundamental reasons for the publication of *On the Various Contrivances*, and Knight's law represents an example.[195]
Following an approach of thought already developed in Germany by Sprengel, in 1799 and after long-running experiments on garden peas, Knight declared that no plant ever fertilises itself for a perpetuity of generations. However, he did not causally ascribe his principle to any other fundamental natural law, and the scientific community forgot his legacy until the publication of *The Origin of Species*. In this book, Darwin presented Knight's law as one of the fundamental principles of the natural sciences: it was a fact that pervaded every aspect of nature that had been observed until the publication of Darwin's works.[196] Furthermore, Darwin often presented Knight's principle as intimately linked to the theory of natural selection, because it was the foundation of the ability to clarify and unify phenomena heterogens and because, like selection, he seemed to have universal value in the light of his research and the experience of many farmers:

"Those individual flowers which had the largest glands or nectaries, and which excreted most nectar, would be oftenest visited by insects, and would be oftenest crossed; and so in the long-run would gain the upper hand. Those flowers, also, which had their stamens and pistils placed, in relation to the size and habits of the particular insects which visited them, so as to favour in any degree the transportal of their pollen from flower to flower, would likewise be favoured or selected."[197]

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[194] Darwin 1877, p. 1: "Having been Blamed…"—in these terms Darwin describes reactions of Vicotiran scientists.

[195] We are referring to the principle according to which no hermafrodite fertilizes itself for a long series of generations.

[196] It will be also in *Variation* the further demosntration that breeding in-and-in diminishes the strength and productiveness of the offspring. Subsequently, with the publication of *Effects of Cross and Self Fertilisation*, Darwin evidenced that a costant crossing with other plants is essential to the production of the healthiest offspring.

[197] Darwin, 1959, p.43.

"…that is a general law of nature…that no organic beings self-fertilises itself for an eternity of generations"[198]

This meant that even for hermaphroditic organisms, for which self-fertilisation[199] is possible, it is possible to carry out cross-fertilisation thanks to the transport of pollen from one individual to another through the help of insects or the wind.

On the Various Contrivances is born, as Darwin presents it in the introduction, to confirm these two conclusions that he had reached in *The Origin of Species*, which should be linked.

In *The Origin of Species*, Darwin exhibited only general ideas in support of the opinion that higher organisms need, by virtue of a general law, crossover with another individual or, what's the same, that no hermaphrodite breeds itself for a long series of generations. He was attacked for establishing such a principle without demonstrative facts, the evidence of which he did not have the necessary space to produce. He wished to demonstrate in *On the Various Contrivances* that he did not express that principle without careful and detailed investigation. In other words, with reference to the two observations mentioned above, Darwin's book on orchids first of all aims to explain how fertilisation occurs in the individual species of these flowers and immediately to demonstrate how these physical and behavioural characteristics have evolved into mutual influence that flowers and insects pollinators have exercised to ensure cross-fertilisation at the expense of self-fertilisation. In fact, there is a primacy of cross-reproduction: according to Darwin, the descendants of crosses between different varieties or races show more vigour and fertility than do those descending from the same lineage.

(b) Evidence of the action of natural selection

On June 13, 1862, Alphonse de Candolle wrote a letter addressed to Darwin that complimented the research contained in the Darwinian paper "On dimorphic condition in *Primula*",[200] but at the same

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[198] Darwin, 1959, p.97

[199] Homogamic reproduction.

[200] Darwin, 1862a. Alphonse then asked his son Casimir de Candolle to write an abstract on the Darwinian text to be published for the Bibliothèque Universelle (archives des sciences).

time, addressing the theoretical content of *The Origin of Species*, he expressed scepticism about the possibility of admitting natural selection as main cause of evolutionary change.[201]

Darwin's answer reached de Candolle a few days later: Darwin was working on a book whose writing had seduced him. The job had cost him ten months, and the reasons that led him to pursue the publication of this work as follows:

The first was to demonstrate how wonderfully perfect the structure of plants is: First of all, according to Darwin the contrivances through which orchids are fertilised are as varied and almost equally perfect as any of the most beautiful adaptations of the animal kingdom. Hence the frequent use of analogies and similarities with zoological examples that could help the reader; but *On the Various Contrivances* also offered the opportunity to show that the study of organic beings can also be interesting for an observer who is perfectly convinced that the structure of each organism is subject to natural laws, evolution, and natural selection, as for the one who sees in every small particularity of structure the result of an immediate action of a Creator.

The second was to analyse the process and the effects of cross-fertilisations in nature: Darwin intended to demonstrate that the main function of these contrivances is the fertilisation of flowers with pollen carried by insects from another plant.

In the end, Darwin commented on selection, a statement that implicitly refers to the book on the fertilisation of Orchid, of which de Candolle would have found a copy attached to the letter:

"I am not at all surprised that you are not willing to admit natural selection: the subject hardly admits of direct proof or evidence. It will be believed in only by those who think that it connects & partly explains several large classes of facts: in the same way opticians admit the undulatory theory of light, though no one can prove the existence of ether or its undulations."[202]

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[201] From Alphonse de Candolle to Darwin, 13 June 1862, Darwin Correspondence Project.

[202] Darwin Correspondence Project, from Darwin to de Candolle, 17 June 1862. Darwin recorded a positive reaction from de Candolle towards the hypothesis of a transmutation of the species and on this subject the paper on Primula had played an essential role: "I have just had letter from Alp. De Candolle about Primula & he gives me facts & his queries show he appreciates the case, & about nat. selection.He says he goes as far as you about change of species, & he laughs at Linnæus' old definition 'Species tot numerasmus quot [...] sunt creatæ'.—But I think from his letter you go further; he says he wants direct proof of nat. selection & he will have to wait a long time for that.

It is no coincidence that Darwin added this comment immediately after having quoted his latest work in the letter: Darwin intended *On the Various Contrivances* as an example of how natural selection could be applied to the plant kingdom, and he was full of trepidation at the thought of laying down this fundamental law in a field not his own.

Darwin thought that the very particular structures and organs of orchids are not the result of the will of nature or of God's design, but rather the result of the action of natural selection, and the evolution from a general form of monocotyledonous flower of fifteen organs to a highly complex and specialised form is best explained by natural selection:

"The more I study nature, the more I become impressed with ever-increasing force, that the contrivences and beautiful adaptations slowly acquired through each part occasionally varying in a slight degree but in many ways, with the preservation of those variations which were beneficial to the organism under complex and ever-varying conditions of life, trascend in an incomparable manner the contrivances and adaptations which the most fertile imagination of man could invent."[203]

Before this book, there was no natural explanation for the sometimes bizarre colours and shapes of orchids. The only references were those obtainable from the treatises of natural theology, which did not present an explanation in terms of secondary causes. Darwin for the first time offers a utilitarian explanation of shape and colours, in relation to their attractiveness to insects.

In orchids, the need to promote insect visitation explained their structural modifications. Its original organs were gradually modified over countless generations to fit the complex and ever-varying conditions of life, particularly the requirement for cross-fertilisation.

(c) A new use of the concept of homology

Opticians do not wait for direct proof of undulation of ether. But Good Heavens what a higglety-pigglety letter I am scribbling to you, who have hardly a minute to spare.— It is a horrid shame, so I will stop.—", from Darwin to Asa Gray, 10-20 June 1862, Darwin Correspondence Project.

[203] Darwin, C.1889, pp. 285-286.

Another fundamental concept that Darwin wanted to disseminate was that of the common descent: through special creation it is not possible to account for the reasons that may have led the Creator to create the same organ that performs different functions in orchids and has reduced others to unnecessary rudiments. However, this series of phenomena can be explained in a simpler and more intelligible way if we start from the assumption that all orchids share a common monocotyledonous ancestor from which they evolved.

To demonstrate this assumption, Darwin starts looking for a basic floral form from which the forms of individual species are derived through divergent specialisations: it is not a question of referring to an ideal model but rather to a real and concrete ancestral structure from which to derive the phylogenesis of all orchids. In this regard, Darwin proposes a new use of the concept of homology: if we use this term to indicate those structures that are found in different species, because deriving from the same structure in a common ancestor,[204] then the study of homologies makes it possible to describe the history of the structures that we find in different species. Homology is thus linked to the history of a single ancestral structure from which the others derive after variations and modifications that succeed one another over time.

The study of homologies allows us to

- to understand in a more complete way the groups of organisms that we are preparing to study;
- to establish the number of possible differences accumulated within each group and their gradual development according to different evolutionary trajectories;
- to classify organisms more precisely and according to a historical-genealogical approach;
- to explain the monstrosities, vestiges and to show the meaning of rudiments;
- to reconstruct the form of the common ancestor or, in other words, the phylogenesis of groups; and
- to dissolve the metaphysics that surrounds expressions as a scheme of nature, an ideal type, basic plans, or ideas: Darwin saw much confusion in the use of these expressions by his contemporaries and he wanted to solve the semantic problems with a philosophical chapter on homology and scientific examples in *On the Various Contrivances*. In this sense, this philosophical work was a

[204] For example the forelimbs of mammals and the wings of birds are homologous, because they derive from forelimbs of a reptile that was the progenitor of both.

necessary step to clarify conceptually what he had prescribed in chapter 14 of *The Origin of Species*, as regards classification and the analysis of organs in living beings.[205]

Each of the points mentioned proved to be a novelty in the publishing field, but Darwin went further: his attention to floral morphology and anatomy led him to publish the first engravings of the cross sections of flower organs, with captions explaining each part in relationship to the others: another new tool for observing nature that naturalists need.

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[205] Darwin, 1872.

6 CLASSIFICATION IN *On the Various Contrivances by Which British and Foreign Orchids Are Fertilised by Insects and on the Good Effects of Intercrossing*

Abstract

In the chapter 14 of *The Origin of Species*, Darwin stated that one of the criteria for developing an effective classification is resemblance.[206]

However, some authors have offered interpretations according to which Darwinian evolutionism would not be innovative for the methodological foundation of the classificatory system Darwin adopted following *The Origin of Species*,[207] Darwin, although he made possible a plurality of approaches to the concept of species unifying the explanation of the different phenomena of speciation in his theory, did not propose new criteria for distinguishing species.[208] The naturalists would therefore be epistemologically justified in choosing the segments of the tree of life that they consider significant for a correct classification, but would not find any practical tools for how to conceive and classify the species.

However, with the publication of *On the Various Contrivances*,[209] Darwin disagreed with eminent botanists, changing the method of classifying several orchids. He made this classification according to a different theoretical approach to the concept of species compared to than what he had writtenote about for his previous classification ofn the barnacles, the biological concept of species he developed in *Notebooks,* and what he wrote about the meaning of species in *On tThe Origin of Species*.

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[206] “From the most remote period in the history of the world organic beings have been found to resemble each other in descending degrees, so that they can be classed in groups under groups. This classification is not arbitrary like the grouping of the stars in constellations”, Darwin, 1859, p. 363.

[207] Cristofolini, G. e Managlia, A. (a cura di) *Il giardino di Darwin, l’evoluzione delle piante*, Umberto Allemandi & C., Torino, Coordinamento redazionale Lina Ocarino, videoimpaginazione Elisabetta Paduano, fotolito chiaroscuro, Torino, finito di stampare nel mese di marzo 2009 presso Tipo Stampa, Moncalieri (Torino).

[208] Boniolo G. e Giaimo, S. Filosofia e scienze della vita, un’analisi dei fondamenti della biologia e della biomedicina, Bruno Mondadori, Udine, 2008.

[209] Darwin C. 1862; 1877.

The classic problem for those involved in botanical classification remained that of establishing the natural or merely conventional character of the groups of different generality used to put order to the large number of living forms: variety, species, and genus.

According to the Darwin of *On the Various Contrivances*, since these groupings are the result of the kinship relationships between the life forms on earth, they exist "naturally", and their study creates a genealogical tree able to illustrate the descendance relationships and the degrees of kinship between the orchids.

In this part, I attempt to demonstrate that in *On the Various Contrivances*, Darwin, even if he did not define the concept of species, elaborated sophisticated criteria for the demarcation of species on the basis of the degree of difference, according to a morphological characteristics of species, stripped of all essentialist claims, and following the doctrine of homologies, which offers the tools to grasp genealogical affinities and to construct a natural system of classification based on the history of organisms. The result was the building of a small treatise by which he showed to scientists that, applying his theory, it is possible to create a more detailed phylogenetic classification through a method that could help all naturalists and botanists to work, avoiding the problem of defining species according to typological thinking.

6.1 Different way of classifying

On the Various Contrivances embraces the classification of British orchids and several foreign species, their structural organisation, the correlation of their various organs, the adaptation of those organs to the functions which they are required to perform in a context of coevolution and pollination, and, in short, the study of particular phenomena in such a manner as to indicate any laws of homology by which species may be connected according to their common descent.

The generalisations are based not merely on descriptions of external characteristics, but on analysis of anatomical structure, through which Darwin has contributes both interesting observation and valuable discovery.

This book is furthermore an effective application of theory expressed in *The Origin of Species*[210] to the task of classification: Darwin tries to show how subjective the standards by which botanists estimate the value of characteristics often are; how loaded by preconceived ideas the balance in

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[210] Darwin 1859, 6th edition.

which they weigh them is; and how prone, in short, they were to assume that a change is in itself fundamental, because it shakes their systems to the foundation.

According to Darwin, to classify or re-classify the species of orchids, we must turn our attention to the "contrivances", a term borrowed from natural theology to indicate the infinite wisdom by which each created detail is adapted to the place and the purpose of which it was intended and designed by God.

However, some of these species will be reclassified by the author, and the source of these changes consists in developing a philosophical approach to the concept of species that differs from the nominalism extrapolated in some passages of *The Origin of Species* and the biological concept presented in *Notebooks*.[211]

Already two years before the publication of *The Origin of Species*, Darwin had softened his belief that the criterion of reproductive separation and geographical barriers was the only method for distinguishing species.[212] The convictions matured in *Notebooks* seemed to have faded for various reasons.

First of all, the study of plants continuously presented examples of organisms that did not reproduce sexually and for which a biological concept of species could not be applied. Furthermore, the use of terminology had changed: Darwin realised that talking about variety as an incipient species in zoological terms could not be done in botany. Thanks to help from Hooker, he realised that talking about plant varieties meant not only mentioning geographical breeds, or subspecies, but also individual variants within a local population, which could hardly be conceived as incipient species, given that the modality of speciation was clear and that using that terminology the boundaries between species and variety came to collapse.[213] But there are other reasons.

On the Various Contrivances author realised that the concept of species was strictly connected to the multiplication of the species and to the practice of classification. However, if it is true that the process of speciation is gradual, it is not the same to consider geographic isolation as the only mode of speciation. In fact, to consider incipient species, also the individual variations led Darwin to

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[211] This chapter is linked to what was written in the introductory part concerning the species problem in Darwin.

[212] From Darwin to Asa Gray, 29 November 1857, Darwin Correspondence Project.

[213] Mayr, E. One Long Argument. Charles Darwin and the Genesis of Modern Evolutionary Thought, Harvard University Press, Cambridge, Massachusetts, 1991, p. 42–3.

realise the presence of a different modality of speciation, a speciation within the territory of the parental species in response to an ecological specialisation. We can define it as a sympatric speciation, a theory which, according to David Kohn, Darwin elaborated between 1854 and 1858,[214] yet it is not still clear to scholars on the basis of what new observations and reasoning Darwin reached this new explanation for the multiplication of the species.[215]

Certainly when Darwin wrote *On the Various Contrivances*, he had by now personally understood the existence of a different form of speciation no longer due to geographical barriers. There were species that could vary within a shared space, and natural selection led to the development of a variation such as to influence the most important characteristics for the classification of flowers, those related to cross-fertilisation or autogamous.[216]

Darwin then began to abandon the attempt to define species univocally : the different concepts of species began to appear as criteria, rather than definitions, as methodologies to try to diagnose the species, since there were different definitions used by naturalists that made impossible the use of a univocal concept. According to Ernst Mayr, these conclusions Darwin in *The Origin of Species* to abandon the criteria for defining the species exposed in *Notebooks* and to give species a definition that gathered typological and nominalistic elements.[217]

However, what emerges from *On the Various Contrivances* seems to go in another direction.

From the first chapter of *On the Various Contrivances* , Darwin points out to readers his intention to stay within the classificatory tradition outlined by Lindley.[218] [219]

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[214] Kohn D. The Darwinian Heritage, Princeton University Press, Princeton, NJ, 1985.

[215] Sulloway, F.J. Geographic isolation in Darwin's Thinking: the Vicissitudes of a Crucial Idea, in Studies in the History of Biology", 3, pp. 23–65, 1979.

[216] See Mr. Moggridge's discovey in North Italy concerning *Ophrys apifera, aranifera, arachnites,* and *scolopax* Darwin 1877, p. 58–59.

[217] Mayr, 1991, p. 43.

[218] Lindley became one of the most important English botanists of the nineteenth century. He was a professor of botany at the University of London and in the Royal Institution of Great Britain. The classification of British orchids is based on the system that he developed in his *The Vegetable Kingdom; or the Structure, Classification and Uses of Plants Illustrated upon the Natural System*, Bradbury an Evans, London, England, 1846.

[219] Darwin, 1877, p. 6.

The features he addresses and consults in the works of other illustrious botanists concern above all the classification of the genera of the orchids,[220] but as far as the species are concerned, the author follows Lindley, to a point.
The most important reasons for which Darwin will impose a personal interpretation of the species of orchids, often diverging from that transmitted by tradition, are two: the substantially conventional nature of the current classification that was not satisfactory for him and the criteria through which he classifies species that he will apply in his analysis.
In fact, within *On the Various Contrivances*, we find the description of many forms on which there is no agreement among botanists: according to some a certain form may be a species, while to others it is variety, and Darwin does not forget to point out all those cases disputed from both and several other positions. For example, of a flower bed of *E. purpurata*, he writes,

"Mr. Oxenden also informs me that a large bed of E. purpurata (which is considered by some botanists to be a distinct species, and by others a variety) was frequented by 'swarms of wasps'."[221]

The conventional characteristic that distinguishes this classificatory conception concerns not only species, but also the agreements that botanists and naturalists have tried to achieve in distinguishing the main genera of orchids.[222]
This controversial situation was reported by Darwin to Hooker years before: the classification practice knew neither a common methodology nor, above all, a concept of species commonly shared as a basis for research:

"I have just been comparing definitions of species, & stating briefly how systematic naturalists work out their subject: […] It is really laughable to see what different ideas are prominent in various naturalists minds, when they speak of "species" in some resemblance is everything & descent of little weight—in some resemblance seems to go for nothing & Creation the reigning

[220] See Lindley's classification in Darwin 1877, 128.

[221] Darwin 1877, p. 102.

[222] See Cypripedium in Darwin 1877, p. 226.

idea—in some descent the key—in some sterility an unfailing test, with others not worth a farthing. It all comes, I believe, from trying to define the undefinable."[223]

In the pages of *On the Various Contrivances*, while specifying the disagreement between the scientists, Darwin cannot avoid sharing the same starting point for classification.

However, this is not a definitive programmatic indication: along the path of reading, the author will present cases in which, facing the weaknesses of the British systematic tradition, he will reset the classification of some species of orchids by applying a species concept that makes use of the morphological and physiological analysis of structure and function of the contrivances and of its doctrine of homologies: all this represents the definitive detachment from the fixist conception of the species to achieve an evolutionary synthesis on the origin of the orchids flowers based on the concept of common descent.

The organs on which Darwin concentrates his morphological descriptions most are sepals,[224] petals,[225] labellum,[226] nectary, stigma, rostellum, pedicel of the rostellum, anther,[227] pollen masses,[228] caudicle of the pollen masses and viscid disc,[229] stamens and pistils, and column.[230] The detailed description of each particularity of these structures is of the utmost importance in determining the belonging of the various forms to a given species.

When Darwin distinguishes the species from each other, he systematically refers to the description of the differences of these organs, which from now on we will call "contrivances".

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[223] Darwin Correspondence Project, from Darwin to Hooker, 24 December 1856.

[224] Lenght, width and shape of sepals.

[225] Presence, width, shape and lenght of petals.

[226] Shape, attachment and mobility of labellum, labellum margin, presence of labellum auricle and labellum nectar secretory glands, labellum lamina.

[227] Anther position (often relative to rostellum), anther orientation, anther apex.

[228] Pollinium number, shape and structure, pollen grain aggregations, pollen apertures, pollen color.

[229] Viscidium structure, viscidium number, pollinaruim stipe, pollinarium caudicles.

[230] Structure of the column, extension, vestigial components, appendages, viscidium number, viscidium structure, pollinia attached to viscidium by a hamulus or by a stipe, shape of pollinarium caudicles.

The description and distinction of species on the basis of exhibited morphological features was a common approach to naturalists and botanists. Herman Müller is himself[231] quoted by Darwin for his analysis according to the same method.[232]

When the activity of these organs is common, structural differences such as length, direction, form, and position become the first aspects to which he refers in distinguishing between species, for instance distinguishing their physiology.[233]

The positioning of the contrivances is also fundamental according to the author.

Each structure occupies a space and dimensions that are in relative proportion and structured with the other organs of the flower.[234]

The more Darwin describes the parts of the orchid, the more the reader is made aware that the mutual position and the shape of the parts of the contrivances are fundamental adaptations for pollination, mainly evolved by natural selection in a coevolutionary context, with the competition of other evolutionary factors that will be clarified by the doctrine of homologies.

However, not only the structures of the flower, but also components such as friction, viscosity, elasticity, and hygrometric movements are all connected to each other and come into play just to encourage the production of seeds. The coevolutive relationship establishes insects as the main subject according to which each structure and component of the flower is adapted.[235]

The presence or absence and modification of even one of these important characteristics common to all the English species and most of the orchids in the world, may involve the nomination of monstrous flowers,[236] but, and this is the most important thing, the differences in the contrivances can be such as to induce Darwin in *On the Various Contrivances* to express suspicion or implicit disappointment with well-established classifying results.[237] [238]

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[231] Hermann Müller was professor in the Realschule at Lippstadt in Westphalia, born at Mühlberg in Thuringia on September 23, 1829; he died at Prad in the Tyrol on August 25, 1883.

[232] Darwin 1877, p. 102.

[233] See Orchis mascula, morio, fusca, maculata, and latifolia in Darwin 1877, p. 15.

[234] See *Orchis pyramidalis* in Darwin, 1877, 16–17.

[235] See Vandeæ in Darwin 1877, p. 176.

[236] See *Orchis pyramidalis* in Darwin 1877, p. 38.

[237] See *Gimnanedia conopsea* and *Habenaria bifolia* in Darwin 1877, p. 40. This last case is significant because it involved more than one botanist. For example, John Lubbock also worried

On the other hand, with regard to *Peristylus viridis*, a variation on the discs is enough to push Darwin to express his doubts:

"Peristylus viridis.—This plant, which bears the odd name of the Frog Orchis, has been placed by many botanists in the genus Habenaria or Platanthera; but as the discs are not naked, it is doubtful whether this classification can be correct."[239]

Physiological differences are also important to Darwin, so much so that he does not hesitate to mention one of the most important American botanists and an old friend of his [240] regarding the physiological characteristics that may influence classification in species or varieties:

"P. hyperborea and dilatata have been regarded by some botanists as varieties of the same species; and Professor Asa Gray says that he was formerly tempted to come to the same conclusion; but on closer examination he finds, besides other characters, a remarkable physiological difference, namely, that P. dilatata, like its congeners, requires insect aid and cannot fertilise itself; whilst in P. hyperborea the pollen-masses commonly fall out of the anther-cells whilst the flower is very young

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about pointing out the disagreement between Darwin and the other botanists in terms of a morphological description: "*Habenaria bifolia* is by Bentham and other high authorities, considered as a mere variety. Yet, as Darwin points out, it differs in many important particulars. The viscid disc are oval; the viscid matter itself is of somewhat different character; the drum-like pedicel is rudimentary; the stalk of pollen masses is much shorter; the packets of pollen shorter and whiter; and the stigmatic surface more distinctly tripartite" (Lubbock, 1882, p. 177). As we will see, this kind of description will be only the methodological starting point with which Darwin will be convinced of the need for a new classification for *Habenaria*: the salient proof will be the analysis of the elements that allow its phylogeny.

[238] Darwin 1877, p. 65: Several times the author does not consider it appropriate to define *Gymnadenia conopsea* directly as an orchid, but prefers to mention the definition of the other botanists.

[239] Darwin 1877, p. 62-63.

[240] Asa Gray (1810–1888).

or in bud, and thus the stigma is self-fertilised. Nevertheless, the various structures adapted for crossing are still present."[241]

These last two species share a large number of structural characteristics, so much so that they are confused as two varieties of the same species, yet the process of fertilisation is totally different.

The Darwinian analysis allows us to understand how ineffective is the research of the essence of the species when we must distinguish two species from each other: the main observational fact that allows us to distinguish *P. hyperborea* from *P. dilatata* is not an essential character, indeed, but their different pollination strategy, capable of modifying and adapting the structure and physiology of the flower.

The analysis of differences in contrivances is not only an instrument to distinguish the classification of different species, but also to relocate genres.[242]

In general the number of morphological variations of the contrivances, and consequently the number of adaptations, is immeasurable and concerns the descriptions of genera, species, and varieties.[243]

In general we can conclude that when Darwin is talking about different species in the book, the first reference addresses differences in structure, after which come genealogy and history.[244] [245]

On the contrary to what is established in *Notebooks*, and despite that Darwin did not propose a definition of species in *On the Various Contrivances*, the species status is primarily inferred by the degree of morphological difference: the search for morphological differences therefore seems to be the source for the description of the species, but more than the reference to a morphological concept of species, it is a morphological criterion of demarcation of the species. This demarcation alone, however, is not sufficient to make sense of the author's abandonment of typological thought. In fact, the morphological analysis of *On the Various Contrivances* has sufficient depth to uncover the

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[241] Darwin 1877, p. 76.

[242] Cfr. P. hyperborea and dilatata in Darwin, 1877, p. 90.

[243] See the differences between *Ophreæ* and *Vandeae* in Darwin 1877, p. 153: if there are no limits to the different forms, dimensions and functions that the contrivances can take, then the typological assumption that the variation within each species is strictly limited is no longer sustainable.

[244] See *Calanthe masuca* in Darwin 1877, p. 161.

[245] See *Catasetum planiceps* in Darwin 1877, p. 193.

weaknesses of the typological concept of species: three of its most important assumptions, namely limited variation within each species, a clear solution of continuity that separates species, and an essence shared by similar individuals destined to distinguish species.

A fourth assumption of typological thought also exists, namely that each species remains constant in time and space. The reference to *Cephalantera* demonstrates how this point is also unsustainable, but here the author connects homological study to morphological analysis, and the role of homology in Darwinian classification is clarified in the following pages.

For the moment, we can conclude that in demonstrating that a variety has changed over time so much that it can be classified as a species, in *On the Various Contrivances* Darwin initially resorts to a morphological criterion of distinction.

6.2 The limits of morphological analysis

Once the principles of fixism have been overcome, the author continues with his analysis and continues to take a position even in publicly controversial cases, where the naturalists are aligned in defining a form as a real species or as a variety of a related species.

This willingness to engage controversy also marks a limitation: the morphological demarcation criterion does not always allow us to say whether or not a form is a variety of a related species with which it is compared. Often the morphological differences, even if compared with structure and function of characteristics belonging to other forms, are not sufficient or strong enough to convince Darwin to make a decision. Even regarding important differences between the organs of impollination, it seems that a final piece to express a definitive judgment regarding the classification of species is lacking. This is the case for *Ophrys arachnites*:

“Ophrys arachnites.—This form, of which Mr. Oxenden sent me several living specimens, is considered by some botanists as only a variety of the Bee Ophrys, by others as a distinct species. The anther-cells do not stand so high above the stigma, and do not overhang it so much, as in the Bee Ophrys, and the pollen masses are more elongated. The caudicle is only two-thirds, or even only half as long as that of the Bee Ophrys, and is much more rigid; the upper part is naturally curved forward; the lower part undergoes the usual movement of depression, when the pollinia are removed from their cells. The pollen-masses never fall spontaneously out of their cells. This plant, therefore, differs in every important respect from O. apifera, and seems to be much more closely allied to O. aranifera."[246]

If the important characteristics to be able to say that a form is not a variety of the *apifera* species are anther, stigma, pollen masses, and peduncle, which as we have seen above, belong to the class of adaptations for the pollination studied by Darwin, then according to the author on the basis of the differences in these characteristics, we cannot speak of *arachnites* as a variety of *apifera*. The distinction is clear, even if the author does not directly conclude it. In other words Darwin places himself neither with those who consider *arachnites* a species nor with those who consider it a variety of *apifera*: he has sufficient evidence to say that it is not a variety of *apifera,* and yet the morphological analysis does not allow him to fully demonstrate that *arachnites* is a variety of *aranifera* or is a species in its own right. Something is still missing.

In the case of *Habenaria*, the dissent is direct, and the analysis is meticulous, but the author adds considerations that are not limited to morphological analysis and allow us to grasp the missing ingredient to reformulate the classification of species.

Darwin finds himself in discussion with eminent personalities in the botanical world, yet he believes that his morphological analysis, which he had perfected in an eight-year study on barnacles, could make him right.

This is an example of the potential that the Darwinian method of analysis can develop in the classification field. As in the case of *Cephalanthera grandiflora*,[247] Darwin here makes use of precise and sophisticated morphological analysis and certain considerations taken from the study of homologies to distinguish two species.

Even if at the embryonic level, we can recognise the method that Darwin will apply to *Catasetum* and which we will see in the following pages: the author constructs an original classification, in contrast to the previous one, on the basis of

(a) a meticulous analysis of the contrivances based on a morphological criterion of demarcation of the species; and

(b) the study of homologies, which are concerned with linking the current state of some contrivances to the evolutionary history of the species and their descent from a common ancestor.

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[246] Darwin 1877, p. 51-52.

[247] As seen above.

"Habenaria bifolia, or Lesser Butterfly Orchis.—I am aware that this form and the last are considered by Mr. Bentham and by some other botanists as mere varieties of one another; for it is said that intermediate gradations in the position of the viscid discs occur. But we shall immediately see that the two forms differ in a large number of other characters, not to mention general aspect and the stations inhabited, with which we are not here concerned. Should these two forms be hereafter proved to graduate into each other, independently of hybridisation, it would be a remarkable case of variation; and I, for one, should be as much pleased as surprised at the fact, for these two forms certainly differ from one another more than do most species belonging to the same genus.

The viscid discs of the Lesser Butterfly Orchis are oval, and face each other. They stand far closer together than in the last species; so much so, that in the bud, when their surfaces are cellular, they almost touch. They are not placed so low down relatively to the mouth of the nectary. The viscid matter is of a somewhat different chemical nature, as shown by its much greater viscidity, if after having been long dried it is moistened, or after being kept in weak spirits of wine. The drum-like pedicel can hardly be said to be present, but is represented by a longitudinal ridge, truncated at the end where the caudicle is attached, and there is hardly a vestige of the rudimentary tail. In fig. 12 the discs of both species, of the proper proportional sizes, are represented as seen vertically from above. The pollinia, after removal from their cells, undergo nearly the same movements as in the last species. In both forms the movement is well shown by removing a pollinium by the thick end with a pair of princers, and holding it under the microscope, when the plane of the viscid disc will be seen to move through an angle of at least forty-five degrees. The caudicles of the Lesser Butterfly Orchis are relatively very much shorter than in the other species; the little packets of pollen are shorter, whiter, and, in a mature flower, separate much more readily from one another. Lastly, the stigmatic surface is differently shaped, being more plainly tripartite, with two lateral prominences, situated beneath the viscid discs. These prominences contract the mouth of the nectary, making it sub-quadrangular. Hence I cannot doubt that the Larger and Lesser Butterfly Orchids are distinct species, masked by close external similarity."[248]

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[248] Darwin 1877, p. 73-74.

It is not necessary address general appearance or geographical distribution: to the author, the meticulous description of the means of fertilisation is sufficient to justify his decision to consider *Habenaria bifolia* and *Habenaria chlorantha* two distinct species.

On the one hand, Bentham and the botanists who together with him represent a consolidated and prestigious systematic tradition on the basis of fixism and who consider *H. bifolia* and *H. chlorantha* as two varieties on the basis of the existence of forms of passage relative to the position of adhesive discs.

On the other hand, Darwin's morphological analysis shows specific differences in the position and the mutual arrangement of the discs, in the viscid substance that covers the disc, in the drum-like pedicel that in *chlorantha* is a continuation of the disc. In *bifolia*, by contrast, it is almost non-existent because it is replaced by a longitudinal ridge truncated at the end. Differences appear also between the rudimentary tail, which in *chlorantha* consists of the extremity of the caudicle and connects it to the disc, while in *bifolia* there is no, in the length of the caudicles, in the dimensions and colours, in the physiology of the pollen packs, and in the shape of the face stigmatic.

Let us dwell for a moment on the small and rudimentary appendix of the caudicle of *H. chlorantha* which in the author's words resembles a rudimentary tail.

According to Darwin, the doctrine of homologies has, among the various tasks, that of demonstrating the meaning of the rudiments. These are organs that in one of the forms of the same systematic unit are not yet in a condition of full structural differentiation and full functional efficiency. As we will see later, the rudiments, which seem apparently useless because they do not offer any current advantage, assume a fundamental role in Darwinian theory to establish the common descent in the populations. In fact, the main concepts of Darwinian evolutionary theory are two: natural selection and common ancestry, and the latter deals with elements that are not necessarily related to selection, but rather refer to the tree of life and the origin of organisms.[249]

This tail is small, curved, and extends above the drum; it represents a rudiment of extraordinary importance in terms of homologies.

Darwin writes,

"The little rudimentary tail of the caudicle projecting beyond the drum-like pedicel is an interesting point to those who believe in the modification of species; for it shows us that the disc has been

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[249] Sober, 2010.

carried a little inwards, and that primordially the two discs stood even still further in advance of the stigma than they do at present. We thus learn that the parent-form approached in this respect the structure of that extraordinary Orchid, the Bonatea speciosa of the Cape of Good Hope."[250]

The application of the study of homologies introduces an element completely alien to the classificatory tradition based on fixism and creationism: the transmutation of the species and their descent from an ancestor of which they still carry some inherited traits. Bentham and the other botanists had not conceived the classification of a concept of species that embraced the possibility that the varieties could eventually turn into new species. Darwinian classification, on the other hand, embraces the morphological analysis common to Bentham and the fissists but makes the concept of species free from any metaphysical reference to essentialism or creationism by introducing an evaluation tool that explains the existence of some characteristics on the basis of a common descent and of a transmutation of the species.

In the Darwinian view, it is not sufficient to distinguish between *H. chlorantha* and *bifolia* only and exclusively on the basis of morphological differences: *H. chlorantha* cannot be a variety similar to *bifolia* because it has a rudimentary character inherited from one of its progenitors, particularly resembling *Bonatea speciosa*. However, *H. bifolia* cannot boast the same lineage, because it is totally missing that rudiment: having two different ancestors, *H. chlorantha* and *H. bifolia* have a common ancestor too far in time to consider the two forms as a variety of the same species.

They are not two varieties of the same species, therefore, but two different species. To come to this conclusion, it is necessary to combine a morphological criterion to demarcate species, through which to address the analysis of contrivances, with a study that, thanks to the homologies, reconstructs a history made of inheritance and evolution.

The use of the doctrine of homologies expels every metaphysical claim of definition of the species and introduces the historical-genealogical study of characteristics, starting from the facts that demonstrate the transmutation of the species and their kinship by descent.

6.3 Doctrine of homologies[251]

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[250] Darwin 1877, p. 71.

[251] Originally, the term "homology" was used to distinguish a type of similarity that could be recognized between the characteristics of different organisms living under each variety of form and

In the chapter on the doctrine of homologies in *On the Various Contrivances*, Darwin defines homologous parts as modifications of the same primitive organ. In other words, if two or more species have an organ, a trait, or a characteristic handed down by the same, or a corresponding, characteristic belonging to a closer common ancestor, that is a characteristic that we can call "homologous". This definition in Darwin's theory implies the genetic heredity of traits, common descendancy and kinship, and the transmutation of species from a common ancestor; it is a study that proposes the calculation of the possible variations in the plan of the same group, starting from the typical and original shape of the flowers under examination. Moreover, it can provide exhaustive explanations of the origin of the monstrosities, the meaning of the rudiments, the process of modification that occurred in the braces over many generations, the perfect cohesion of anatomical parts that have different origins, the co-optation or the assignment of functions different from those for which the organs had originally developed and adapted, and the important role of useless organs.

The homologies are, according to Darwin, a fundamental cognitive tool: no organism can be well understood unless homologies are first clarified.

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function. This modern definition can be found for the first time in 1843 in *Lectures on the Comparative Anatomy and Physiology of the Invertebrate Animals* written by Richard Owen, considered one of the most important anatomists contemporary to Darwin. With Darwin, however, the term undergoes a semantic shift in genealogical terms: this resemblance of the characteristics that two different organisms possess is caused by kinship to a common ancestor from which organisms descend. Consequently, also the philosophical conception underlying the study of the homology changes after the publication of *The Origin of Species*, starting from Owen and up to the second half of the 800 the relations between the same organs in different animals, were described in terms of an identical divine design for the foundation of the creation of all living beings—a metaphysical theological interpretation that brought organisms back to an ideal model of departure. All this did not constitute a sufficient explanation for the author of *The Origin of Species* according to whom there is a link between all individuals, a common descent able to bring all living beings together in a tree of life: this was the cause of the inheritance of the homologous characteristics, and therefore the idea of the common ancestor was to replace the metaphysical conception of the ideal archetype.

From a philosophical point of view, to classify in exact categories the very dissimilar organs through the study of homologies means to eliminate the metaphysics that enveloped the concepts previously used by naturalists: to follow the homological study of the anatomist engaged in analysing the embryonic development of the living beings, the botanist totally absorbed in the comparative study of related monophyletic taxa, the zoologist fascinated by the discovery of the connection of two different forms through an intermediate one present in a parental form, or the palaeontologist looking for the existence of intermediate conditions in the fossils of ancestors. Such classification always means searching for the same object in different ways, that is, getting closer and closer to the knowledge of the real progenitor of the group and how it lived and developed in the past.[252] Still, in *The Origin of Species* the definitions that recur when Darwin mentions homology allow us to deduce that this study did not refer only to morphological characteristics and anatomical organs, but also to behavioural and physiological characters. This inclusion is a novelty compared to the tradition of naturalistic and medical studies that had conceived the concept of homology within a mainly anatomic scientific context. However Darwin presents an example taken from the chapter on instincts dedicated to species that live in different habitats but show a recent kinship on the basis of a homological affirmation of some components of their instinct[253] and the chemical, physiological, and cellular homologies that are explained on the basis of descent from a common ancestor, as Darwin summarises in the final pages of *The Origin of Species*.[254]

From this explanation, it follows that the concept of homology should be interpreted as a relation of similarity of characteristics and behaviours in different organisms due to the inheritance of the characteristic or equivalent instinct belonging to their common ancestor.

The doctrine of homologies forces Darwin to move from the simple comparison of morphological and physiological differences to the evolutionary history of the formation of a particular character. Nevertheless, the evolutionary history passes through the anatomical comparison: we could therefore say that it is not possible to establish homologies without starting from a morphological criterion of demarcation of the species, but at the same time it is not possible to establish the evolutionary origin of a characteristic with reference only to the pure morphological distinction of the characteristics of different species, which at the time of Darwin was dangerously imbued with

[252] Darwin 1859, p. 382.

[253] Darwin 1859, p. 234.

[254] Darwin 1859, p. 424–425.

influences of essentialist philosophy. In this contemporary search for proximate and remote causes in the description of the contrivances, the possibility of a classification that necessarily starts from morphological analysis is played out, but is then enhanced by a genealogical-historical analysis of components common to several flowers belonging to different species.

The doctrine of homology allows us to analyse and classify flowers starting from certain aspects of the phylogeny of specific characteristics and processes. *On the Various Contrivances* describes the following in great detail:

(a) a gradual transition of characteristics in *Orchis ustulata*:[255] Here we find an example of how one character can gradually transform into another: *Orchis ustulata* is placed halfway between *Orchis pyramidalis*, which has two distinct stigmas, and *Orchis mascula*, which instead represents a single slightly lobed stigma.

The analysis of the transverse rim that links the two lateral stigmas shows how a homological study that follows the series of existing passages, is the key to describe, as far as possible, the probable process of modification that occurred in beings for a long series of generations.

Other important aspects are reachable through the doctrine of homologies, though.

Goodyera's pollen masses do not agree with those of an authentic *Orchis*. However, it is the only *Neottiea* that has pollen grains gathered in large packets, just like in the *Ophrydee*, and, set at the top of the masses, a formation similar to that of the caudicle of an *Orchis*. It also has several affinities with the genus *Spiranthes*, such as the presence of a clinandrum between the stigma and the anther and a support of the rostellum. There is furthermore an affinity with the genus *Cephalanthera* in the filament of the anther and with the genus *Epipactis* in the structure of the rostellum and in the form of the rostellum.

All these organs so different in the same genus and so similar to the other apparently distant genera represent the morphological and physiological state of a group of orchids which, although for the most part extinct, included the common ancestors of all the before mentioned genera.

(b) The study of homology allows, therefore, the naturalist to recognise a link, like *Goodyera*,[256] to study how much a flower can be modified in many individual parts and observe how enormous the sum of variations have been from their typical shapes and original state.

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[255] Darwin 1877, p. 25.

[256] Darwin 1877, p. 105–106.

(c) The doctrine of homologies allows the discover also of the important cases that satisfy the principle according to which an organ not used for a long time tends to atrophy.

There is the possibility of fertilisation that does not require an exploding rostellum, as in the case of *Cephalantera*:[257] The description of its rudimentary rostellum allows the author to hypothesise the steps for which every single stage of a plant may prove useful and interesting and may develop by natural selection. According to Darwin, there is a continuous evolutionary development from the pollen masses of *Epipactis*, which bind to a functioning and developed rostellum at the anatomic stage of Cephalantera.

To describe the development, he resorts to *Neottia nidus-avidus*, an orchid fertilised through an exploding rostellum until the pollen is gathered and adhered in masses. However, as the flower grows old, the pollen loses consistency, becomes incoherent, and falls out easily or, in order to be brought back on the stigma, needs the help of small crawling insects. In this case, the self-fertilisation takes place and remains assured even in the event that the most important insects do not visit the plant. Furthermore, pollen in this state adheres much more easily to any surface. In this case, a small variation in the structure of the flower, added to a state of physical incoherence in the pollen at an earlier age, would lead to easier fertilisation, and would therefore be advantageous in terms of survival and reproduction, without the need for a rostellum exploding. A further development of these variations by natural selection could make the rostellum useless and no longer used.

Going back to the above principle, we will have a rostellum that atrophies and finally disappears. In this way, a new species with the name of *Cephalantera* forms in relation to the new contrivances used for fertilisation.

In this case, then, Darwin describes the formation of a new species on the basis of natural selection and atrophy of organs no longer used, and homological analysis allows us to understand how some organs can be suppressed or leave only useless traces of their primitive existence. This species will be similar to *Neottia* and *Listera*, but quite different in the contrivances suitable for fertilisation to be defined as a different species from the name *Cephalantera*.

(d) The doctrine of homologies allows the classification of very different organs in exact categories and the study of the original function of substances that are secreted by completely distinct structures. Take for example the viscid substance produced by the stigmas of most flowers and that

[257] Darwin 1877, 126–127.

one produced by the rostellum: from the comparison with *Malaxis paludosa* and the genus *Microstylis*, the primitive nature and purpose of the viscid substance is identical. It does not contribute to the transport of the pollen from one flower to the other; rather, it tries to hold the pollen sheets near the stigmatic cavity once introduced by the insects. Therefore the viscid substance that covers the rostellum originally had the function of retaining the pollen on the stigmatic surface: consequently it is a characteristic that originally and in ancient time belonged only to the stigma, but which has now also evolved into the rostellum;[258]

(e) Another aspect highlighted by the study of homologies is the reversion to the original form: it is a return to the characteristics of the ancestors, and in *On the Various Contrivances*, it is mentioned in relation to an anomaly within the *Epidendrum* genus witnessed by Fritz Müller. Darwin hesitates to quote Müller accurately: "Fritz Müller informs me that he has discovered in South Brazil an *Epidendrum* which bears three pollen-producing anthers, and this is a great anomaly in the order. This species is very imperfectly fertilised by insects; but by means of the two lateral anthers the flowers are regularly self-fertilised. Fritz Müller assigns good reasons for his belief that the appearance of the two additional anthers in this *Epidendrum*, is a case of reversion to the primitive condition of the whole group.*"[259]

(f) Another feature of the doctrine of homologies consists in recognising the evolution of structures that have been found in a rudimentary state and have been reused for a new function.

In the case of Malaxis paludosa, there is a cup-like clinandrum that protects the pollen masses: it consists of two membranes that represent the two upper anthers of the inner cycle in the rudimentary state, therefore not functioning as anthers do in the other orchids; instead, they are used for this purpose of protection.[260]

Darwin repeatedly insists upon the classificatory value of rudimentary and atrophied characters, which for a many years had been underestimated by naturalists because of their low physiological value or lack of meaning and role in the complex organic system of living beings. In *The Origin of Species*, he remembers,

[258] Darwin 1877, p. 134.

[259] Darwin 1877, p. 148.

[260] Darwin 1877, p. 131–132.

"Again, no one will say that rudimentary or atrophied organs are of high physiological or vital importance; yet, undoubtedly, organs in this condition are often of much value in classification. No one will dispute that the rudimentary teeth in the upper jaws of young ruminants, and certain rudimentary bones of the leg, are highly serviceable in exhibiting the close affinity between ruminants and pachyderms. Robert Brown has strongly insisted on the fact that the position of the rudimentary florets is of the highest importance in the classification of the grasses."[261]

All this is part of the more general consideration that an useless organ possesses an inestimable importance at the classification level, while the high physiological value of an organ does not determine its value in classification. According to Darwin, who never forgets to conceive an organism as an integrated system, the characteristics are all interrelated, and those conceived as useless hide correlations not only with the more or less important characteristics of the present time, but above all with characteristics and functions of the evolutionary past of a species: they therefore constitute a fundamental key to access the phylogenetic history of the species, and following the Darwinian classification based on a genealogical criterion achievable through the study of homologies, the useless organs can realise the definition of entire groups.[262]

(g) Different, but still included in the study of homology, is the case of the organs to which functions can be assigned that differ widely from their typical destination along the course of their gradual transition.[263]

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[261] Darwin 1877, p. 366.

[262] Darwin 1859, p. 367.

[263] In reference to this principle in *The Origin of Species*, Darwin writes, "In considering transitions of organs, it is so important to bear in mind the probability of conversion from one function to another, that I will give another instance. Pedunculated cirripedes have two minute folds of skin, called by me the ovigerous frena, which serve, through the means of a sticky secretion, to retain the eggs until they are hatched within the sack. These cirripedes have no branchiæ, the whole surface of the body and of the sack, together with the small frena, serving for respiration. The Balanidæ or sessile cirripedes, on the other hand, have no ovigerous frena, the eggs lying loose at the bottom of the sack, within the well-enclosed shell; but they have, in the same relative position with the frena, large, much-folded membranes, which freely communicate with the circulatory lacunæ of the sack and body, and which have been considered by all naturalists to act as branchiæ. Now I think no one

The first reference to structures useful for a certain function that are then co-opted to new functions is presented by Darwin precisely when he begins to talk about the genus *Catasetum*. Regarding the force with which the disc of pollinium is released in the direction of the insect's body, Darwin remembers that the pollen peduncles in the *Vandeae* are horizontal, elastic, and in tension so as to snap up, extracting the pollen masses from the anther lodges.

Instead, the peduncles of *Catasetum* are fixed in a curved position and, once freed for the bursting of the edges of the disc to which they are inserted, stretch with a force to push the pollen masses the anther lodges, and the whole pollinia to a distance of two or three feet beyond the antennas. This is a case where, according to Darwin, a series of modifications are affirmed to have been met with in different species, changing structures and capacities in new onesspecies.[264]

The description of these last two processes leads us to two further conclusions: the first concerns the philosophical consequences of the uselessness of some organs, while the second relates to the meaning of the modern concept of exaptation.

Design advocates had always placed the infinite wisdom of the Creator at the base of their arguments, which had finely crafted the highly sophisticated textures of internal structures and external relations between one species and another. In this explanatory framework, however, a justification for the existence of useless organs or rudimentary elements to be found in the anatomy of the orchids was not obvious. Moreover, a creationistic philosophy could not explain the meaning of the same organs of orchids performing different functions in time and the reduction of other organs to useless rudiments. Again, the purpose for which an omnipotent Creator would allow these kinds of processes was not obvious?

At the same time, saying that they belong to the body plan[265] of the class to which they belong is not sufficient to determine their role, their function, and their history. Above all, though, it is possible to find orchids in which organs are atrophied and apparently already completely useless, and others in which these organs are not present at all; this variation shows that they are not indispensable for the common *bauplan*. How can we demonstrate the derivation from an infinite

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will dispute that the ovigerous frena in the one family are strictly homologous with the branchiæ of the other family; indeed, they graduate into each other." Darwin 1859, p. 148–149.

[264] Darwin 1877, p. 179–180.

[265] Bauplan.

wisdom or from a unità di tipo about the organs that are themselves without function for the whole life of an animal?

On the Various Contrivances was able to answer these questions by setting forth a new way of understanding nature. The structural modifications of orchids became adaptations in order to promote insect pollination, and the study of homology postulates a common descent from a monocotyledonous ancestor: along countless generations, the original organs of orchids were modified to adapt to cross-fertilisation and the others to complex life conditions. No special creation and no more metaphysicalisic models of derivation, just explanation on the basis of whether secondary causes were sufficient to answer to the above questions.

As we will see, the orchid *Catasetum tridentatum* will provide an example of evolutionary explanation of useless and insignificant structure, a powerful methodological argument for evolutionary sciences, and a new method to classify the forms of orchid species.

The second consideration concerns the role played by functional reuse and co-optation within Darwinian evolution. This Darwinian formulation, which however already found zoological anticipation in *The Origin of Species*, was redefined by Ernst Mayr as pre-adaptations in cases where a trait develops for a certain function in a given selective context and is then employed to perform different tasks in changing conditions. They were then further relaunched and extended from Gould and Vrba into two essays from 1982 and 1986, with the term “exaptation” (Gould, Vrba, 2008) to include those cases called spandrels or plumes in which a trait is not born for selective reasons—but rather as effect of structure, a side effect of another, or in any case neutral with respect to the selection—and is then enrolled for the function it currently performs (Pievani 2003, 2008).

The case of the rudiments of orchids which are then reused falls into the category of spandrels, while *Catasetum* fully describes a classic example of exaptation.

The most important philosophical consequences that derives from this Darwinian treatment in the doctrine of homologies are as follows:

- Evolution does not occur *ex-novo* but reuses the material already available.
- Natural selection does not mould the organisms to they like, but starting from the material that is available, complying with the internal constraints that history has led to emerge in a contingent manner at all levels of evolution.
- We cannot say with absolute certainty that the usefulness of a trait and of a behaviour coincides with its historical origin.

- It is possible to respond to the objections of the anti-evolutionists, according to which an organ can serve no purpose until it is completely formed, so it would be impossible to hypothesise its presence as a result of gradual steps guided only by evolutionary advantage.[266]

6.4 Three genera in one species

In April 1862, Darwin offered a paper to the Linnean Society:

"On the Three Remarkable Sexual Forms of *Catasetum tridentatum*."[267] This paper aimed to solve a real enigma in the botanical field. According to orthodox naturalists and botanists, this was part of shocking and abnormal "ugly facts"[268]: *Catasetum tridentatum* was an orchid seen by Robert Hermann Schomburg[269] in 1836 and sent from Brazil and on different branches of the same individual specimen it contained flowers previously referred to three distinct orchideous genera and such genera had several species referred to them. In was an incredible exception because all botanist used to believe that these three genera grew separately and that most orchids were "perfect" or hermaphroditic, that is they contain both male and female parts in the same flower.

Catasetum is uniquely a masculine form, so to reach seed production it is necessary for the pollen masses to be transported on the stigmas of female plants:

"We shall, moreover, presently see that Catasetum is exclusively a male form; so that the pollen-masses must be transported to the female plant, in order that seed should be produced."[270]

The morphological approach can be seen from the moment when Darwin presents the *Catasetum callosum*: the analysis intends to deal with the similarities and differences between the various aspects of common contrivances of different species:

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[266] In the nineteenth century Darwin's adversaries contested with the same example promoted by the supporters of intelligent design: we will see in the chapter dedicated to teleology how Darwin explained the inconsistency in this argument.

[267] Darwin 1862b.

[268] Lyell to Charles Bunbury, 13 Nov. 1854, in Life, Letters, and Journals of Sir Charles Lyell, Bart., ed. Katherine M. Lyell, 2 vols. (London: John Murray, 1881), Vol. 2, p. 199.

[269] Sir Robert Hermann Schomburg (1804–1865) was a German explorer and naturalist.

[270] Darwin 1877, p. 129.

"The edge of the labellum is covered with papillæ; the cavity in the middle is small, and behind it there is an elongated anvil-like projection,—facts which I mention from the resemblance in some of these points between the labellum of this species and that of Myanthus barbatus, the hermaphrodite form of Catasetum tridentatum, presently to be described."[271]

But it is with *Catasetum tridentatum* that Darwin demonstrates how the application of his observations, and theoretical conclusions elaborated in *The Origin of Species*, to original subjects have a fundamental relevance in disclosing the mysteries of natural history.

The amazement of the botanists was incredible when it was discovered on the same plant flowers of *Catasetum tridentatum*, *Monachanthus viridis* and *Myanthus barbatus* considered to that moment as three completely distinct genera.

The discovery was published by Sir R. Schomburgk in the Transactions of Linnean Society, but others, as noted by Darwin, contributed to the discovery of intermediate or transitional forms between *C. tridentatum* and *Myanthus*.

Lindley himself commented with dismay the discovery that these cases shook the foundations of the ideas that scientists of the eighteenth and nineteenth centuries had formed on constancy in genera and species.

The consideration of the distinction of the sexes in orchids starts from observations of foreign authors and Darwin's correspondents: according to Schomburgk and Crüger,[272] *C. tridentatum* does not produce seeds and does not have the power to produce fruit, not even for self-fertilisation or even after artificial insemination.

However, Darwin noted, if *Monachanthus* is fertilised with the flowers of *C. tridentatum* it will always produce fruit.

This prompted him to study the female organs of *Catasetum tridentatum*, simultaneously with those of *C. callosum* and *C. saccatum*.

Unlike all other orchids, with the exception of Cypripedium, the stigma face was not viscous. This is a fundamental characteristic for securing the pollen masses when the break of caudicles happens.

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[271] Darwin 1877, p. 192.

[272] Hermann Crüger (1818–1864) was director of the botanical garden in Port of Spain, as well as a German botanist and pharmacist.

Cells of the surface of the cavity and the stigmatic canal were removed by Darwin, stored in alcoholic solution and analysed: he noted that they were elongated and containing an ordinary nucleus, but their number was much lower than the average of the cells present in the same structures in other orchids. Furthermore, these cells were more transparent and more connected to each other than the same cells in the most common orchids.

The *Catasetum* ovary also showed anomalies: it is shorter and has less deep grooves, moreover it is thinner at the base and more solid inside compared to *Monachanthus*.

Once again the Darwinian morphological analysis and the comparison with the other species allows to see in depth: in the three species of *Catasetum* the funicles are narrow and the eggs have a completely different appearance, they are thinner, more fleshy and more transparent than those of an incredible number of orchids that Darwin had already analysed.

They also assume the general position and appearance of eggs, but we cannot even call them such because it is not possible to find a micropile and nucleus and never once did the author find them inverse.

The Darwinian observations are then extended to the brevity, glabreness, and thinness of the ovary, the brevity of the podosperms, the particular state of the ovules, the lack of viscosity in the stigmatic face, and the transparency of the cells of the stigmatic face.

In the author’s words, these morphological and physiological observations are facts on which he bases his own deductions.

In a superficial analysis, the flowers of *Monachanthus* are quite similar in external appearance to those of *Catasetum*. However this similarity is insufficient for Darwin, who focuses on grasping the differences: the labellum occupies the same position, but is lower and has a crenate margin. Petals and sepals are folded and not as strongly stained as those of *Catasetum*. The bract at the base of the ovary is much larger. Column, filament, and anther are much shorter: the rostellum protrudes less. The antennas are completely missing, and the pollen masses are rudimentary. The homology allows us to explain this lack: the antennas are not there because there are no pollens to be expelled. Without them the presence of an organ destined to transmit the irritation produced by the contact with an insect to the rostellum is useless.

Darwin finds no trace of pollen discs or peduncles, which he believes have been lost during the transportation of the samples, but only rudimentary pollen masses remain.

There is no large stigmatic cavity, but a transverse fissure immediately below the small anther, within which Darwin will introduce a pollen mass. The cells are different from those of *Catasetum*.

In addition, the ovary is longer, thicker at the base and with furrows more distinct than that of *Catasetum*. There is also a difference compared to all other orchids: the podosperms are longer, and the eggs are more opaque and pasty than in ordinary orchids. From these facts, it appears, according to Darwin, that *Monachanthus* is a female plant.

According to Crüger and Schomburgk, moreover, *Monachanthus* produces a very high number of seeds.

Despite the apparent resemblance in external appearance, masculine and feminine flowers conceal a profound diversity in structures and tissues.

It is on the pollen masses, though, that we can observe the Darwinian method of classification at the height of its maturity and effectiveness.

He defines perfect pollen masses of the masculine form, and this observation is so important to Darwin that this detail is represented in the figure.

As regarding *Catasetum*, there is a plate of pollen organelles cemented together or waxy, the plate is folded on itself to form a sack with an open fissure along the lower face. Inside the fissure and in continuity and at its lower and elongated end, there is a layer of elastic tissue that constitutes the caudicle, the other end of which is fixed to the peduncle of the rostellum. There are internal and external pollen grains: the external ones are more angular, having larger walls and a more yellow colour than do the internal grains.

The gem is immature, and inside are two pollen masses, surrounded by two membranous pockets joined together, which are crossed by the two ends of the pollen masses and their pedicels. Furthermore, the two ends of the caudicles stick to the peduncle. Before the flowers blooms, the two bags containing the two pollen masses open and remain naked on the back of the rostellum.

As concerning *Monachanthus*, on the other hand, the two membranous pockets containing the pollens never open up, but gradually separate one from the other and from the anther. The tissue they are made of is dense and pasty. The solution of the puzzle is based on the analysis of useless rudimentary pollen masses of *Monachanthus*.

The pollen masses are rudimentary and, as with most rudimentary organs, their dimensions vary in shape and size: they have a circumference of about one-tenth of the masculine form.

They are arceolate, as shown by Darwin in the figure, and the lower extremity is extremely elongated, almost to the extent of piercing the external or membranous bag.

The fissure along their lower face which allows the passage to the caudicles is missing.

There are external and internal pollen grains: the external are quadrangular, but like the male ones, they have thicker walls than do the internal grains. Every cell has its nucleus, a fact that Darwin considers marvellous, because maintaining an embryonic characteristic is typical of rudimentary traits.

As Brown[273] had noted, in fact, in the first periods of development of the pollen grains of the common orchids a very small nucleus is visible: consequently, the rudimentary pollen grains of *Monachanthus* have been preserved, as it seems. Such preservation is common for embryonic characters in some organs rudimentary in the Animal Kingdom.

Not only rudimentary pollen masses and granule cells with rudimentary nucleus, but also rudimentary caudicles in these pollen masses of *Monachanthus*.

In fact, at the basis and within each urceolate pollinic mass is a small mass of brown and elastic fabric, which is nothing but the trace of a caudicle running along the thinned end of the pollen mass, but (at least in some specimens) it does not reach the surface, and above all, it never joins with any point of the caudicle. Caudicles that are so rudimentary and incomplete remain useless.

Despite the smallness and the abortive state, the pollen masses of the female forms placed inside the stigmatic cavity of female forms led to the occasional emission of a rudimentary pollen tube. This emission was witnessed by Mr. Crüger, who saw the ovary grow thicker when the petals withered, and after a week he saw it turn yellow and fall without maturing any seeds.

We see here an example of evolution by natural selection that, according to Darwin, is beautiful, as it shows how the organs can be transformed on the basis of small continuous variations. The female pollen masses are not evolved enough to be naturally transported and carried on the stigma, so they have not evolved the characteristics of pollination contrivances we have seen so far. Yet they represent an evolutionary stage common to all orchids, and therefore an evolutionary stage of a preceding ancestor. The organs change slowly and gradually, therefore at an ancestral stage, all the pollen masses were in the stage of the *Monachanthus*, although the current pollen masses of *Catasetum* belong to a successive state of evolution. Yet both the masses of *Monachanthus* and those of *Catasetum* possess and partly preserve their primitive properties and functions: a sign of a common evolutionary kinship.

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[273] Brown (1773–1858) was a Scottish botanist and friend of Darwin: he discovered the cytoplasmic streaming and described the cell nucleus.

Therefore every particularity of structure of the masculine masses is conserved in a rudimentary state in the female masses: this conservation means very close phylogenetic kinship, such as to force us to question the common interpretation according to which *Catasetum* and *Monachanthus* are different genera.

According to Darwin, these facts were known to naturalists. No others first reached Darwin's conclusions, however, because learned men, botanists, and naturalists had always considered useless organs not as rudiments preserved from heritability, as we have discovered in the study of evolutionary homologies, but as features created by an omnipotent hand and placed in their convenient place, to complete the "scheme of nature".

In this sense, the earlier botanists who believed in special creation thought that such pollen masses were meaningless ornaments, and in this way those botanists missed its evolutionary significance.

Since every characteristic feature of male pollen masses is represented in the female plant in a rudimentary state, we can no longer interpret these facts from a creationist perspective on species; rather, by applying a study of evolutionary remote causes we will obtain a reclassification of the flowers thanks to homological interpretation of the rudiments.

Myanthus barbatus is also occasionally found on the same plant as the previous ones.

Flowers differ greatly in their external appearance, but not essentially from the structure of the other two forms. They are in reverse positions, with respect to the latter; that is, they have the labellum at the bottom and edged with papillae in a singular way. The median cavity is small in size, and from the upper margin there is a singular curved and flat appendage that constitutes the prominence at anvil of the labellum of the masculine form *C. callosum*. Petals and sepals are stained and elongated, and the two lower sepals are folded. The antennas are shorter than the male tridentatum form, symmetrically arranged on the two sides of the corniform appendix at the base of the labellum and their ends, devoid of papillae that make them sour, almost entering the median cavity. The stigmatic cavity has a size halfway between that of the masculine form and that of the feminine form, covered with cells stuffed with a brown substance.

The ovary has a size double that of *Monachanthus*, and it is straight and crossed by evident furrows, but not so thickened in its point of union with the flower.

The eggs preserved in alcohol are opaque and pasty and resemble in every respect to those of the female form *Monachanthus*, but they are not so numerous.

The pollens reach about a quarter of the size of those of the male form *Catasetum*, but their disk and the peduncle are perfectly developed.

Darwin reports having lost the pollen, but Mr. Reiss gave the pollen a design in the Linnean Transactions that show they have a convenient size and have the cracks in which the caudicles are inserted.

In this form, male and female organs are perfectly developed, so *Myanthus barbatus* is the hermaphroditic form of the same species for which *Catasetum* is a masculine form and *Monachanthus* is feminine form and which we can now definitively call *Catasetum tridentatum*.

Moreover, in this case, the Darwinian method does not stop at the morphological analysis: the author notes that *Myanthus barbatus* resembles the masculine forms of the *C. saccatum* and *C. callosum* species, especially in the characteristics of the labellum, more than it resembles a masculine and female form of its own species.

These are similarities in general appearance and in structure. However, starting from the consideration that most orchids are hermaphrodites, Darwin deduces that the common ancestor of the orchids was probably a hermaphrodite, if this is the hermaphroditism and the general habit of *Myanthus* belong to the reversion to a common ancestor.

As we saw before, the reversion to the ancient characteristics of the species is another element belonging to the doctrine of homologies, which according to the author is characteristic of individuals who have undergone modifications that could harm their constitution or sexual identity. Darwin cites the example of *A. bezoartica*,[274] who chased to castration, develops horns with a completely different form from that in possession of the male of the same species.[275]

Of course, *Myanthus* has the reproductive organs of both sexes, but presents itself as a completely sterile form.[276] This means that his sexual constitution was modified, and this modification, according to the author, is the cause of his reversion.

Myanthus is hermaphrodite and has a reversion of characteristics to ancient species and, therefore, to a common ancestor; given its close affinity and analogy with the male members of *C. callosum* and *saccatum*, Darwin deduces that the progenitors of all *Catasetum* species had to be similar to the males of *callosum* and *saccatum*.

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[274] The male form of Indian antelope.

[275] This type of reversion can also be seen in the common ox, and Darwin makes direct reference to it in his *Origin of Man*.

[276] Darwin also reports the conclusion of Crüger, who has never seen intermediate forms producing seeds.

Once again, the Darwinian method has reconstructed the classification of three forms mistakenly considered three different genera, according to the modalities previously seen with *Habenaria bifolia*: morphological analysis and doctrine of homologies, or, in other words, analysis of differences starting from the morphological criterion of demarcation of the species and the study of the organs that testify a common descent starting from the transmutationist hypothesis.
The result is the demonstration that three sexed forms, commonly worn by three different plants and ascribed to three different genera, sometimes existing mixed together on the same plant, are wonderfully different from each other, "more than the male and female of the peacock", but belong to the same species.
The philosophical consequences of this operation are not limited to a happy classificatory ending of something that was previously considered an anomaly without any possibility of variation. Of course, the application of Darwin's theory does work effectively; even Crüger gives him credit and all the other botanists follow Crüger in this recognition: *Catasetum* is the male, while *Monachanthus* is the female of the same species, and what previously seemed like an unprecedented exception is, instead, a commonly observable condition, subjected to variation and perfectly classifiable following Darwin's operations.
Its effective application carries certain philosophical costs, however.
Before Darwin, most naturalists in describing and proposing a name for what they call "a new species" used that term to signify an originally distinct creation.
With *On the Various Contrivances*, Darwin intends to state no more than he actually knows: evolutionary thought through homology and high level descriptive practice of morphology. These are the keys for understanding the amount of structural differences within any taxonomic group and for defining and distinguishing a species. Thanks to this method, on which Darwin worked painstakingly, a systematist will not be haunted by doubt about whether a form could be in essence a species: the considerations of essence are replaced by the study of homology, so the daily work of naturalist is stabilised and enhanced.
The application of the study of homology was the proof that only evolution provided a coherent and productive scientific explanation of the contrivance that natural theology presented as evident examples of such sophisticated and beautiful adaptation that only a divine mind could have created.
In Darwinian work on orchids, we discovered that a species is, first of all, the result of a morphological approach. The constancy and distinction of a form from the other forms constitutes the first phase, research focussing on morphological differences to distinguish species from each

other and from varieties: the effective evaluation of real differences between individuals is the element that has the same importance as the study of homology: both are necessary for a correct classificatory practice.

In a summary of the analyses offered by *On the Various Contrivances*, we can define the morphological criterion of demarcation of species on the basis of contrivances: in establishing a species, the naturalist must determine the number of differences, the number and measures of points of differences, the physiological importance of the difference in a context of coevolution, the constancy of differences, and the presence and absence of gradual or intermediate gradations linking the forms.

6.5 Conclusion

The Darwinian classification system used in *On the Various Contrivances* is based on the morphological criterion of demarcation of the species and the doctrine of homologies, which in synthetic terms we could describe as analysis of differences or similarities and genealogy.

The study of homologies does not involve a substitution of the morphological criterion, but it rather allows us to go beyond the philosophical and scientific limits of the previous morphological analysis, thus enhancing the classification methodology. At the same time, genealogy, which includes similarity as the first evidence of a possible kinship, cannot disregard the evaluation of the degree of difference that develops during phylogenetic divergence.

According to Darwin, the placement and delimitation of taxa must correspond to these two criteria, and the choice of the characteristics on which to base the classification does not intend to refer to the largest number of traits that can be analysed, but rather focuses on the contrivances.

On a philosophical level, the considerations we can make are different.

We have seen how in *The Origin of Species* Darwin recalled the possibility of treating species just as naturalists treat genres: in a nominal sense.[277] This would have helped classificatory practices make them free from the research for the essence of the species, an elusive element in the consideration of natural history.[278] The research for the essence was a philosophical remnant inherited from concepts of fixed and creationist species and from typological thought, and it

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[277] In numerous passages, Darwin seems to support a nominal solution for the question of species: they have been collected and commented in Kottler 1978, p. 291–294.

[278] Darwin 1859, p. 425–426.

furnishes a reason Darwin seems to prefer a nominalistic approach which did not consider that the species were not real but artificial and arbitrary objects; rather, he wanted to fight conventionalism in classification and special creation that were incompatible with an evolutionary approach.[279]

With *On the Various* Contrivances, we can note that the element that shows how unbridgeable is the gap between typological conceptions and evolution is not natural selection, which may very well explain the phenotypic divergence, but the common descent revealed through the study of homologies. If the study of homologies contributes considerably to determine the classification status of species, the results achieved are based on the hypothesis that species can transmute: using the study of homologies in Darwin means, at the same time, applying a theory according to which species multiply and differ without the need to possess an essence, without the need to be created *ex-novo*. The philosophical principles of classification undergo a radical subversion without the need for the nominalistic interpretation previously presented from various studies on *The Origin of Species*: even if each naturalist has its own speciec concept, the real existence of genealogical resemblances and morphological differences cannot be denied. This claim certainly aroused opposition from naturalists and botanists tied to the Linnean classificatory tradition, but they themselves gradually became convinced of how effectively the Darwinian analysis could reveal new aspects in the recognition of the species and how deep it could go in recognising new traits and functions, so much to interpret the terms with which it refers to these structures differently from the books of botany of his age. In the case of pollinium, for example, the analysis is so sophisticated that it allows us to discover the history and functions of structural parts of the pollinium that were previously unknown and, consequently, to apply new names to distinguish them:

"In botanical works the whole structure between the disc or viscid surface (generally called the gland) and the balls of pollen is designated as the caudicle; but as these parts play an essential part in the fertilisation of the flower, and as they are fundamentally different in their origin and in their minute structure, I shall call the two elastic ropes, which are developed strictly within the anther-cells, the caudicles; and the portion of the rostellum to which the caudicles are attached (see diagram), and which is not viscid, the pedicel. The viscid portion of the rostellum I shall call, as

[279] Ghiselin 1969.

heretofore, the viscid surface or dise. The whole may be conveniently spoken of as the pollinium."[280]

Darwin, by providing a more complete explanation of the floral structure in general, allowed naturalists to create a new and powerful tool for classifying species within the natural system. Moreover, he invited the naturalist to grasp certain structural homologies among the living beings, which could well be interpreted as an indication of distant relations of parental and genetic filiation, and this interpretation became more persuasive as closely as it was accompanied by a realistic foundation of the natural sciences that measured itself on the explanatory effectiveness and on the superior capacity of generalisation that belong to this new method:

"The other and more general departments of natural history will rise greatly in interest. The terms used by naturalists of affinity, relationship, community of type, paternity, morphology, adaptive characters, rudimentary and aborted organs, &c., will cease to be metaphorical, and will have a plain signification. When we no longer look at an organic being as a savage looks at a ship, as at something wholly beyond his comprehension; when we regard every production of nature as one which has had a history; when we contemplate every complex structure and instinct as the summing up of many contrivances, each useful to the possessor, nearly in the same way as when we look at any great mechanical invention as the summing up of the labour, the experience, the reason, and even the blunders of numerous workmen; when we thus view each organic being, how far more interesting, I speak from experience, will the study of natural history become!"[281]

Moreover, this work demonstrates the meaning of philosophy in natural science. All the material collected by Darwin for this book did equip him to treat species philosophically, on the basis of accumulating facts and speculating on the subject of variation, species, and transmutation. These kinds of generalisations on species and transmutation could only arise from, and conform to, painstaking work with comprehensive natural-history collections, as Darwin had already done before with his eight-year taxonomic study on barnacles. This is the meaning of philosophical

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[280] Darwin 1877, p. 151.

[281] Darwin 1859, p. 427.

botany that, in Hooker's words, characterised the new Darwinian approach, as we can read in a letter from April 11, 1857:

"If you knew how grateful the turning from the drudgery of my 'professional Botany' to your 'philosophical Botany' was, you would not fear bothering me with questions— the truth in its positive nakedness is, that I really look for & count upon such questions, as the best means of keeping alive a due interest in these subjects. I indulge vague hopes of treating of them some day, but days & years fly over my head & all I do is done in correspondence to you, but for which I should soon loose sight of the whole matter."[282]

[282] Darwin Correspondence Project, from Hooker to Darwin, 11 April 1857.

7 CONTRIVANCES IN COEVOLUTIONARY CONTEXT

Abstract

Few authors prior to Darwin had methodically studied reproduction in orchids. One of the few was Sprengel,[283] in the late eighteenth century; another was Delpino, in the same period, as Darwin was carrying out his experiments. Both of them were studied and widely mentioned by Darwin.

The fundamental point is that without the help of insects, there cannot be fertilisation. Fertilisation starts from this premise, which Darwin reaffirms throughout the book and for which he distinguishes himself from some who preceded him; on the contrary, one could say that this is the first real difference, namely that fertilisation is achieved thanks to a flower and insect contest.

While Sprengel failed to give precise descriptions, despite the discovery of the need for insects, Robert Hooker described the structure of *Epipactis* in an extraordinarily precise manner, but underestimating the importance of insects, he adopted faulty interpretations.

Not recognising the function of insects does not allow a correct explanation of the structure of the flowers, while misunderstanding the mechanism of pollination leads to the same result.

Darwin overcomes both problems because he recognises that the structure of the flower is adapted to pollination, which needs insects.[284] Structure, pollination and insects are not made in their own

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[283] The belief that flowers could cross did not conceal from Christian Konrad Sprengel in *Das entdeckte Geheimniss der Natur*, from 1793, that insects are necessary for the transportation of the pollen masses, and he recognized the stigma position very well. However, in this regard escapes many admirable provisions probably as a consequence of the preconceived idea that the stigma normally receives pollen from the same flower.

[284] Every part of the orchid flower is peculiar. The perianth consists of six tepals arranged on two levels (technically, “verticils”) of three petals each. The three external tepals (one above, and two at the sides) are usually relatively undifferentiated, and are similar in terms of shape, colour and size, while the three inner ones consist of two upper elements, which are smaller and which come together to form a sort of hood that encloses the flower organs, and a lower, highly developed one. The latter extends forwards and downwards to create a sort of platform, known as the labellum, on which the pollinator insect can rest. This tepal may also extend towards the rear, creating a hollow appendage called a spur, in which nectariferous species secrete their nectar. The labellum and the

right, but are rather linked, thanks to the mechanism of natural selection in relation to fertilisation: fertilisation is necessity for the legacy of the most important structural varieties of plants. The flowering organ is the flower, so its parts will be adapted to the achievement of effective pollination, but pollination requires the participation of insects, so the parts of the flower will be adapted to favour the presence and entry of insects.

Darwin devoted much time to his study of orchids and considered their adaptation to pollinating insects as the finest example of his idea of evolution through natural selection. Following on from this idea, the mechanisms of fertilisation in orchids have often been used as an example of a coevolutionary process that, as a result of its mutual advantage, led flowers and insects to evolve together.

7.1 The development of the concept in the book

Indeed, following the classification of orchids established by Lindley,[285] Darwin was sure of the fact that in no other plant, nor hardly in any animal, are more perfect adaptations of one organ to the other and of the whole organism to the other organisms so far in the scale of nature than in the adaptations exhibited by orchids.[286] Darwin's fascination with orchids was due to the high degree of specialisation of their flowers, and the consequent specialisation of their plant–insect relationship.

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spur carry out the most important function in the complex relationship between the orchid and the pollinating animal.

The strucutre of the flower organs is highly sophisticated: the flowers are reduced, in the vast majority of species, to just one organ. Its filament is attached as a single unit to the style, forming the gynostemium, in such a way that the entire anther is located just above the stigma, and very close to it. The two sacs of the anther contain the pollen combined in two unified masses called "pollinia", each of which has an appendix called "caudicle" which ends in a sticky, adhesive disc called "viscidium". During the pollination, the two pollinia are removed entirely, as a result of the viscidium, which sticks to the body of the pollinator. Lastly, the ovary, which is large and elongated, may contain up to a hundred thousand ovules: hence, when pollination takes place, it brings about the contemporary fertilization of all the ovules of one plant with all the pollen of another.

[285] Darwin, 1877c p. 13.

[286] Darwin, 1877c p. 23.

This extremely close functional relationship between two organisms of different kingdoms presupposes the concept of coevolution.

In Darwin's *The Origin of Species*, coevolution was recognised as a dynamic process that drives the mutual adaptive evolution in interacting species.[287]

There is not a direct definition of coevolution in Darwin's orchid book. Rather he prefers talking about co-adaptations in relation to natural selection.

The discussion about coevolution in *On the Various Contrivances* focuses on individual orchid–insect interactions: Orchids are subjected to continuous and various interactions with a multitudes of insects, and such interactions are a fundamental driver of natural selection of marvellous and complex contrivances to pollinate and to reproduce and avoid extinction.

In *On the Various Contrivances*, coevolution implies tight ecological interactions between two or more species belonging to different natural kingdoms; consequently, coevolution is an evolutionary process that prompts the adaptation of a species in response to natural selection imposed by another interacting species, and the effects can be reciprocal.

The attraction exerted by the orchid on the pollinator is, in fact, effected in such way that there is a one-to-one relationship between individual species of orchids and pollinating insects, and this kind of relationship leads Darwin to assume that, as a general rule, the species endowed with short nectar or with a relatively wide entrance are fertilised by bees or flies, while those provided with a very long nectary or provided with a very narrow entrance are fertilised by diurnal *Lepidoptera* or nocturnal, like those with long, thin probosces. From this observation, it is noted that the structure of the flowers of the orchids and that of the insects that commonly visit them are in a wonderful relationship: the insects distinguish the flowers of the same species at a distance and pursue them as much as they can.[288]

Furthermore, the reciprocal dimensional and spatial relationships do not only concern the structures and reciprocal functions of the parts of the flower, but are also represented in the functions of the anatomies and the aetiologies of the species of pollinating insects. In this regard, all parts are so arranged that when insects visit flowers, pollen masses are almost certainly removed and carried to another flower:

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[287] Darwin, 1859.

[288] Darwin 1877c, p. 36.

"From the observations already given, and from what will hereafter be shown with respect to Gymnadenia, Habenaria, and some other species, it is a safe generalisation that species with a short and not very narrow nectary are fertilised by bees† and flies; whilst those with a much elongated nectary, or one having a very narrow entrance, are fertilised by butterflies or moths, these being provided with long and thin proboscides. We thus see that the structure of the flowers of Orchids and that of the insects which habitually visit them, are correlated in an interesting manner,—a fact which has been amply proved by Dr. H. Müller to hold good with many of the Orchideæ and other kinds of plants."[289]

Darwin further writes about *Spiranthes autumnalis* and on the purposes of the sophisticated arrangement of the parts:

"We thus see how beautifully everything is contrived that the pollinia should be withdrawn by insects visiting the flowers"[290]

Again, the term "contrived" is borrowed from the use that the literature of natural theology made of the meaning of "contrivance": terms that emphasised the intelligence of the Creator's design in regard to the finest details in the structure of living beings as a function of *economia naturae*. However, the meaning of "contrivance" in *On the Various Contrivances* differs wholly from the theological use of the term, because, for Darwin, contrivances are the result of the action of natural selection.

Since the selective pressures that each individual can exert on the other were expected to depend on the intimate nature and strength of the association, the ecological ingredients necessary for orchid-insects coevolution can be summarised in three main points:

(a) Orchids and pollinators must exhibit considerable inheritable variability.

(b) The variability of pollinator must have significant selective impacts on the morphology and physiology of orchid flower through a strong improvement of the orchid's fitness.[291]

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[289] Darwin 1877, p. 30.

[290] Darwin 1877, p. 111.

[291] This concept indicates the ability of an organism to survive, grow, and reproduce in competition with other organisms of the same species. The degree of fitness is given by the number of offspring

(c) Contrivances' diversity and variability must impact the evolution of the structural and behavioural traits of pollinators.

From these three elements we can say that the selective pressures imposed by continuous interactions between pollinator and flower determine specific and reciprocal phenotypical specialisations among specific species belonging to different kingdoms, which can lead to determinano delle reciproche specializzazioni fenotipiche tra determinate specie different forms of speciation.

7.2 Adaptation, natural selection e observational predictions

Although *On the Various Contrivances* offers no formal definition of adaptation, it is possible to observe that Darwin uses the term "adapted" to refer to the characteristics of an organism that show themselves to be well designed for the environment in which they live and able to foster them in the struggle for life.

Despite the use of a teleological language, both the adapted and the coadapted characteristics are due to the action of natural selection, although other evolutionary causes cannot be excluded. Both consist in a historical process of gradual accumulation of advantageous selected variations.

In these terms, the concept of adaptation is used to show that the perfection of organs, of which so much is spoken in the works of natural theology, are not of divine origin but rather are due to natural selection in a context of coevolution.

In *On the Various Contrivances*, natural selection is a process alternative to divine design, which reaches its maximum explanatory capacity in a coevolutionary context.

Hence, the structures and dimensions of contrivances are the result of the action of natural selection. If the small variations of structures do not bring any advantage or disadvantage to the owner, these remain in the species in which they appeared for the first time in a completely neutral way. However, if slightly reinforced or increased in the variation of other species that are otherwise similar or belong to the same genus, contrivances are of fundamental importance for purposes quite different from those relevant to species where these characteristics maintain a neutral function in the context of the struggle for the life:

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an organism generates during the course of its life. Nel caso delle orchidee, il rapporto con l'impollinatore dev'essere tale da aumentare la capacità riproduttiva della pianta.

“The anther-cells are remarkably open, so that with some plants which were sent me in a box, two pair of pollinia fell out, and stuck by their viscid discs to the petals. Here we have an instance of the first appearance of a trifling structure which is of not the least use to its possessor, but becomes when a little more developed, highly beneficial to a closely-allied species; for although the open state of the anther-cells is useless to the Spider Ophrys, it is of the highest importance, as we shall presently see, to the Bee Ophrys. The flexure of the upper end of the caudicle of the pollinium is of service to the Spider and Fly Ophrys, by aiding the pollen-masses, when carried by insects to another flower, to strike the stigma; but by an increase of this bend together with increased flexibility in the Bee Ophrys, the pollinia become adapted for the widely different purpose of self-fertilisation.”[292]

Natural selection works in detail by eliminating any element that may disturb fertilisation or turn out to be harmful, but preserving and perfecting the elements useful for the survival and reproduction of the plant. For this reason, for example, according to the author any variation of structure that does not help or reinforces the adherence of the adhesive discs to the body of the insect will be eliminated as completely counterproductive for its existence:

“Variations in the structure of the flower of an Orchid, unless they led to the viscid discs touching some part of the body of an insect where they would remain firmly attached, would be of no service, but an injury to the plant; and consequently such variations would not be preserved and perfected.”[293]

In addition, natural selection needs much time to act and, during Darwin’s century, it was impossible to study its effective action under experimental conditions. Some characters, however, appear to be gigantic with respect to the average and in conditions of coevolution appear as more effective examples of the Darwinian explanation.

If we take the nectary of *Angraecum sesquipedale*, we will notice its disproportionate length and its fecundation, which remains conditioned by the presence of nectar only in the lower and thinned part. In order for the nectar to be reached at those depths, an insect with a proboscis that is as long

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[292] Darwin 1877, p. 40.

[293] Darwin 1877, p. 73.

as the nectary, then 11–12 inches, must exist in a coevolutionary context. There are no such structured species in England, and in Madagascar, the birthplace of the *Angraecum*, such species were not found until the publication of Darwin's work. However, Fritz Müller[294] encouraged Darwin's observational prediction by noting the existence of Sphinx from South America with a spiral-shaped proboscis that, if distended, measured between 11 and 12 inches.

If the nectary is filled with nectar, even the butterflies with shorter proboscis will be able to feed themselves, but they will not be able to bring any advantage to the plant, because the pollen masses are at the end of the nectary, and it is necessary to insert the proboscis to the end of the nectary to remove the pollen. The proboscids cannot even be introduced until the pollen masses are released at the stigma or in the peristigmatic area.

If in Madagascar these butterflies of this size perished, the same fate befall *Angraecum*. However, if the latter were to become extinct, since the masses and nectar are at the end of the nectary and no other butterfly would have access except those with the exceptionally long proboscis, the latter would have a considerable loss. In this link we can understand how, thanks to the natural selection, the successive variations have been maintained to flow into the current dimensions. If the butterflies of Madagascar, due to selective environmental pressures, reached more developed dimensions or developed a longer proboscis to reach the nectary of *Angraecum* or other species with deep nectars, then we expect that those species of orchids that have received greater advantages in fertilisation, having deeper nectars thanks to their disposition to variation, would force the butterflies to push their proboscis up to the base. These plants will produce more seeds, and the progeny will inherit these characteristics.

The peculiarity of these changes is that they develop simultaneously in both the plant and the butterfly in the course of different sequences: Darwin calls these sequences a competition to reach a considerable length between the nectary and the proboscis. In this competition, where both subjects are the target of natural selection, the victory belongs to the flower: the selection target is stronger towards the orchid.

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[294] Johann Friedrich Theodor Müller (1821–1897) studied at universities of Berlin and Greifswald and obtained a doctoral degree in biology. He then began to study medicine, but after the failure of the Prussian revolution, to avoid dangerous complications for his life and career, he emigrated to Brazil in 1852 and dedicated himself to studying life in Atlantic forest and to teaching.

In fact, the *Angraecum* is prosperous, meaning that it has won in the struggle for survival with other species; it is common in many forests of Madagascar, so its spread has overcome geographical and ecological barriers, and it has a mechanism which restricts and forces the butterfly to introduce its proboscis as deep as possible to achieve the most nectar drops:

"If the Angræcum in its native forests secretes more nectar than did the vigorous plants sent me by Mr. Bateman,[295] so that the nectary ever becomes filled, small moths might obtain their share, but they would not benefit the plant. The pollinia would not be withdrawn until some huge moth, with a wonderfully long proboscis, tried to drain the last drop.* If such great moths were to become extinct in Madagascar, assuredly the Angræcum would become extinct. On the other hand, as the nectar, at least in the lower part of the nectary, is stored safe from the depredation of other insects, the extinction of the Angræcum would probably be a serious loss to these moths. We can thus understand how the astonishing length of the nectary had been acquired by successive modifications. As certain moths of Madagascar became larger through natural selection in relation to their general conditions of life, either in the larval or mature state, or as the proboscis alone was lengthened to obtain honey from the Angræcum and other deep tubular flowers, those individual plants of the Angræcum which had the longest nectaries (and the nectary varies much in length in some Orchids), and which, consequently, compelled the moths to insert their proboscides up to the very base, would be best fertilised. These plants would yield most seed, and the seedlings would generally inherit long nectaries; and so it would be in successive generations of the plant and of the moth. Thus it would appear that there has been a race in gaining length between the nectary of the Angræcum and the proboscis of certain moths; but the Angræcum has triumphed, for it flourishes and abounds in the forests of Madagascar, and still troubles each moth to insert its proboscis as deeply as possible in order to drain the last drop of nectar."[296]

The coadaptation maintains the historical[297] aspect of the adaptation process and allows the acquisition of a more precise predictive capacity: given a precise problem determined by the relationship of two species to each other and the environment and provided an excellent knowledge

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[295] James Bateman (1811-1897) British Horticulturist.

[296] Darwin 1877, p. 165-166.

[297] Phylogenetic.

of the biology of both species, we can generally predict how it is possible for those species to solve problems at the behavioural and anatomic level.

Based on his idea of coevolution, Darwin predicted the existence of a pollinator with a mouthpiece long enough to reach the nectar at the extremity of a very long spur (20–35 cm), and in 1903 this particular pollinator with whom the orchid establishes a species-specific relationship of mutual benefit was discovered, initially called *Xantophan morganii praedicta*, with the subspecific epithet to remember this correct observational prediction.

8 TELEOLOGY

Abstract

On the Various Contrivances occupies a very particular role in the academic production Darwin and in his battle for evolutionism.

Research on the relationship between flowers and insects carried out during the first twenty years after *The Origin of Species* had increased the abundance of theoretical reflections that served as a prelude to different interpretative strategies, as regards the clash between supporters and opponents of teleology.

A recent literature has collected numerous approaches to the subject concerning the relationship between teleology and Darwinism, which have reached divergent conclusions.[298] However, here we have dealt with and will deal in the third part only with what emerges from *On the Various Contrivances*, from the correspondence of the Darwinian botanists, and the works of the latter were influenced by Darwinian writings on orchids.

One of the implicit purposes that prompted Darwin to publish *On the Various Contrivances* was what Gray called the flank movement:

"I just received and glanced at Bentham's address, and amused to see how your beautiful movement with the Orchid-book has nearly overcome his opposition to the Origin."[299]

Gray wrote this letter just before the review he was to provide to the American Journal[300] about Darwin's book, which took place in November 1862.

In all this, an outflanking manoeuvre was seen and interpreted consisting of the publication of this small treatise to answer and contradict all those who had attacked *The Origin of Species* for the anti-religious implications of Darwin's greatest work.[301]

To reinforce this interpretation, the continuation of a letter sent to De Candolle is often cited:

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[298] Mayr, 1973, Moore, 1979 and Ghiselin 1981.

[299] From Asa Gray to Darwin, 2-3 July 1862, Darwin Correspondence Project.

[300] Gray, 1862.

[301] Pancaldi, 1984.

"Under my hearty congratulations of Darwin for his striking contributions to teleology, there is a veil of petite malice, from my well-known that is the idea of design, while he is bringing the neatest illustrations of it!"[302]

If, in fact, all those sophisticated and refined adaptations so minutely described were traced to an interpretation that made them the proof of a providential plan of nature, one might think that the author of *The Origin of Species* had no intention of breaking with the religious tradition. Rather, he had written *On the Various Contrivances* to reconcile it with evolutionism. This was Gray's position, and this position would consist of a circumvention manoeuvre: the adaptations so minutely described by the author would constitute a work capable of instilling in youth the ancient finalistic conception of nature.

However, I believe that the flank movement is many other things within the Darwinian strategy, none of which, however, has to do with a reconciliation with *The Origin of Species*' detractors, who hated the anti-religious consequences of his work: rather, the most important meaning consists in a conversion of those who criticised *The Origin of Species*' methodological framework.

I provide two proofs in favour of this criticism: in a first section, where I will try to indicate that Darwin had no intention of giving new life to teleology through the study of complex reciprocal adaptations between flowers and insects in fertilisation. A second section instead discusses the main content of the third party, with the final results of the flank movement.

8.1 The debate

Georges Cuvier had methodologically and philosophically set up the analysis of vital phenomena, arguing that mechanistic conceptions and chemical laws entailed limits in the field of understanding the differences that separated the phenomena of the world organised by the phenomena of pure

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[302] From Asa Gray to A. de Candolle, 16 February 1863, in Letters of Asa Gray, edited by Jane Loring Gray, London, Macmillan, 1893, p.486.

matter: these theses were then amplified thanks to the work of von Humboldt[303] and, as we saw earlier, of Dutrochet.[304]

During the first part of the 1800s these themes were taken up and linked to the philosophical speculation of Treviranus[305] and of idealistic and Kantian philosophy: a series of internal causes and effects underlying the bodily activity of each living organism were recognised, an internal purpose capable of distinguishing life from inanimate bodies. Not only that, this rational principle of finality also influenced interorganic relationships: unlike objects or artefacts, living organisms were able to regulate external conditions based on their state or to regulate their state according to external conditions. It was thanks to this principle that it was possible to explain the instincts of animals and the rational faculties of man: a rational principle that mutually linked all the organisms together and justified an external purpose that would then be taken up by Delpino and applied to ecological relations.

Whether it was through the works of natural theology or through the philosophical speculation of scientists like Delpino, in the first part of the nineteenth century the conception of the existence of a finality of which the entire living world was imbued informed and scientific works[306] and the interpretations of readers who tried to account for the phenomena of adaptation.

The finalism also influenced explanations concerning the useless elements of life: the rudimentary organs[307] could be explained only in terms of a function assumed in the past and then no longer required.

The topic on which the teleological explanations concentrated most, especially those that followed *The Origin of Species*, like that of Delpino and Gray, concerned the variations that emerged between one generation and another within populations.

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303 Alexander von Humboldt (1769–1859), German naturalist and geographer, brother of Karl Wilhelm, his vision of vital phenomena emerges especially in *Aphorismen aus der chemischen Physiologie der Pflanzen*, Leipzig, 1794.

304 Dutrochet, 1837.

305 Treviranus, 1818, 1831–33.

306 Timothy Lenoir, 1981.

307 This is what remains of the organs in the past that were well developed but no longer useful in the current life of the individuals who carry the traces.

If Darwin at the time of writing *The Origin of Species* conceived variation as the raw material on which the action of natural selection was exercised, without claiming to establish the ultimate causes of the variations but entrusting their eventual conservation to the uncertain outcome of the struggle for survival and thus describing an evolutionary process that did not present any intentionality or tendency to refinement, on the other hand, even in the attempt to bring order to the phenomena still little understood in inheritance, the teleologists maintained that the variations were the product in a predetermined design, and therefore the whole of evolution was to be interpreted as the intentional action of a divine intelligence. This was a common element in the finalistic philosophy of Delpino and Gray's religious teleology.[308]

According to H. Müller,[309] this was also a position shared by Axell, for which that of evolution was a process of increasing perfection that was reflected and could be found in the adaptations and internal organisation of living beings.[310]

Therefore, *On the Various Contrivances* represented the occasion and the need for Darwinian botanists who did not share the randomness inherent in the selective mechanism and the contingency on which the evolutionary process was based, to try to reach a theoretical conciliation between finalism and Darwinism.

8.2 Contrivances

To convince his publisher, Darwin presented the project according to a more or less explicitly apologetic purpose:

"Like a Bridge-water Treatise the chief object is to show the perfection of the many contrivances in Orchids"[311]

The Bridge-water Treatise comprised the eight works commissioned to the Royal Society of London by the testamentary will of Francis Henry Egerton, the eighth earl of Bridgewater, to

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[308] Gray, 1876a, p. 9–10.

[309] Muller, 1883, p. 19–20.

[310] Another element in common with Delpino e Axell (1843–1892) was the deep valuation of Sprengel's work.

[311] From Darwin to Murray, 21 September 1861, Darwin Correspondence Project.

describe the power, wisdom, and goodness of God as manifested in creation. Within the theological context of these works, the term "contrivance" had found its root meaning: the contrivances responded, in the collective imagination imbued with the explanations of William Paley, to the functionalist and utilitarian conception of structures perfectly adapted to their ecological niches of belonging. This understanding was also increased by Owen's version of a transcendental anatomy that had so much influenced naturalists between the 1940s and 1950s.[312]

If we find a clock in the woods, Paley argued, then there must be a watchmaker. In the same way, animals and plants have been created, and if we talk about contrivances then we must assume a contriver and a purpose for which the contriver has produced that specific contrivance.

Consequently, it was no coincidence that Darwin chose the term "contrivance" as a banner to show off in the title of the publication on orchids: he wanted to show that contrivances could exist without the need for a contriver that had devised them, since most of the adaptations are the result of natural selection, and in this evolutionary process there is no privileged purpose or direction.

However, others found Darwin's intentions harder to perceive, leading to a long-running debate about the roles of design and teleology in Darwin's works. The focus of this confusion is Darwin's use of the word "contrivance", often combined with metaphors that explicitly compare organisms to human-made artefacts.

The confusion over the apparent teleology of *On the Various Contrivances* arises from viewing evolution in a religious context, yet the book is better understood as part of Darwin's project to close the apparent gap between plants and animals. Orchids possessed several of the features that Darwin found so compelling in the animal world: according to him, an examination of their many beautiful contrivances would exalt the whole vegetable kingdom in most persons' estimations.[313] He concluded his detailed analyses of orchids by describing them as wonderful and often beautiful productions, so unlike common flowers, particularly because of their many adaptations, with parts capable of movement, and other parts endowed with something so like, though no doubt really different from, sensibility. Because orchids possessed something so like sensibility,[314] they effectively redesigned themselves, turning their flowers into traps for unwary insects. Natural selection was, of course, Darwin's only real process in action; the competition to survive and breed

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[312] Smith, J. 2006.

[313] Darwin, 1877c, p. 2.

[314] Darwin, 1877c, p. 285.

ensured that favourable variations became more common, while unfavourable ones declined. Comparing orchids to artefacts was not intended to hint at the possibility of a divine contriver, but to imbue the flowers with agency; in Darwin's writing, apparently for the first time in botanical history, plants have strategies with which to achieve their goals: Darwin's are crafty orchids.

The shift of meaning in the term "contrivance" makes it a product of natural selection rather than of an omniscient and omnipotent Creator who designs organs animated by a profound benevolence towards the human race begins with *The Origin of Species* and finds its fulfilment in *On the Various Contrivances*: the author intended to avoid the terminology developed in the texts of natural theology, but decided to use the term "contrivance" to subvert the meaning it had previously acquired. Precisely for this reason, *On the Various Contrivances* can be seen as an anti-Bridgewater treatise. In fact, the words that Darwin adds in the introduction read,

"This treatise affords me also an opportunity of attempting to show that the study of organic beings may be as interesting to an observer who is fully convinced that the structure of each is due to secondary laws, as to one who views every trifling detail of structure as the result of the direct interposition of the Creator."[315]

Indeed, the Darwinian study of the floral pollination mechanism translated what for natural theology represented the pinnacle of the perfection of the creative force in brilliant evidence, favouring instead the action of natural selection in the role of the main process of evolutionary change in nature. *On the Various Contrivances* was the first of the botanical volumes entirely dedicated to this purpose.[316]

8.3 New explanatory possibilities opened by the presence of randomness

Darwin conceived ecological relationships as a complex intertwining of circumstances in which chance played a very important role.[317] Although other Darwinian botanists did not find space for this type of consideration, but endeavoured to explain in teleological terms every process or

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[315] Darwin, 1877c, p. 2.

[316] Freeman, R. B. 1977. The works of Charles Darwin: an annotated bibliographical handlist. 2d ed. Dawson: Folkstone, p. 112.

[317] Cfr. fetilization of *Coryanthes*.

adaptation, in *On the Various Contrivances* Darwin tried to maintain a philosophical neutrality on the subject, without directly criticising the teleology. Instead, he exploited many of the observations and conclusions reached in the book to criticise the scientific contributions that came from the defenders of a finalistic ordering of the natural world.[318]

The fertilisation of the orchids did not appear to the author's eyes as the result of the action of a natural rationality and of a parsimonious use of the means in view of very precise ends; rather, it could depend on completely accidental events like the random bath of an insect inside a mellifluous hollow of *Coryanthes*,[319] which forced the insect then to come out of a narrow passage near stigma and pollen masses. Inevitably, the masses could, depending on the case, either stick to the body covered with the insect's sticky substance or leave it to lean on the stigmas, or both. Yet, the unscheduled bath of insects, which could fall into the basin during the attempts to eat, and the quantity of liquid that was simply going to wet the insects, were phenomena devoid of intention or rationality. This interpretation, as we will see in the third part, personally involved Crüger, director of the Trinidad botanical garden, whose description admitted the presence of elements devoid of intentionality in the fertilisation of *Coryanthes*, and Delpino, who instead decidedly rejected the interpretations of Crüger and Darwin's views in *On the Various Contrivances*.

What Darwin had to fight in any case, as with *The Origin of Species*, was the use of a teleological language: if the *Coryanthes* liquid did not owe its origin to an insect priming function, it still maintained its purpose of moistening body and wings of insects finding accidentality more precisely in the fall and consequent involuntary bath.

However, as Pancaldi has pointed out, the criticism of teleology is methodological: the same organic substance, like the same organ or apparatus, can perform different functions[320] because they are observable and conceivable as means to satisfy the opportunism of nature rather than a finalism inherent to all aspects of life. Specifically, a liquid usually secreted by orchids to lure insects is used in *Coryanthes* to wet their wings and facilitate their exit through a bucket spout,[321] allowing fertilisation of this plant.

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[318] As for example Linneo, Sprengel e Delpino.

[319] Darwin, 1877, p. 174.

[320] Nectar can serve as a food, a bath in which to become covered with viscid substance or excrement, Pancaldi 1984, p. 29.

[321] Darwin, 1877, p. 175–176.

In this way, the concept of randomness moves to a different speculative level: not only can random events that favour pollination happen, such as the fall of insects in a basin filled with liquid, but also the conversion of a function has a character that is completely random, a means certainly advantageous but obtained through a series of innumerable attempts without a planned direction starting from a genetic variation common to all the specimens of *Coryanthes* and, ultimately, to all organisms. Consequently, the evolutionary phenomenon is conceived as a contingent process, and precisely in this philosophical conclusion lies the unbridgeable gap that separates Darwin and the Müllers from the positions of theologians such as Sprengel, Delpino, Gray, and Cuvier, as well as from natural theologians and Axell.

8.4 Change of function over time

The influence of Cuvier and its finalism as a condition of existence of an individual within nature, the Aristotelianism contained in the functional approach of natural philosophy, and the Platonism that pushed anatomists to look for an ideal model in the functions of the organisms were overcome by Darwin, who proposed a concept of homology that was completely incompatible with research of the ideal type, because it was connected to the phylogenesis of individuals. It was no longer a question of applying a study of functions on the basis of the comparison with metaphysical archetypal models, but to trace the history of a common ancestor that really existed in the natural world that puts in crisis all the definitions of adaptation or anatomical form based on the actual utility of an organ.

Darwin felt that in this way it was also possible to account for the existence of some structures that the finalistic explanations tried in vain to explain: people who believe in a design can think that the Creator, with infinite wisdom, arranged the infinitely complicated relationships of internal structure and the external relations of species to species.

This explanation cannot comprehend the casual existence of useless organs and rudimentary elements in the anatomy of orchids, however. They are not compatible with the harmony that the infinite wisdom the Creator is able to build. At the same time, saying that they belong to the body plan[322] of their class is insufficient to determine their role, their function, and their history.

Above all, though, orchids can be found in which organs are atrophied and apparently already completely useless, while others lack these organs entirely. These variations show that they are not

[322] The *bauplan* of zoological considerations of natural philosophy.

indispensable for the common *bauplan*. How we can demonstrate the derivation from an infinite wisdom about the organs that are themselves without function for the whole life of an animal? These parts are, however, useless in in the classification, because they reveal the hidden plot of tree-shaped genealogical relationships that binds all organisms more or less distantly related to each other:[323] no longer an element to be fathomed for teleological explanations but elements of constant research in the morphological work of the naturalist who includes them as evidence and part of an explanation based on the concept of common descent. Still, that's not enough: *On the Various Contrivances* recognises these useless elements, such as vestiges and rudiments, as constraints on the action of natural selection, which keeps them as neutral in the struggle for survival but entails limits. Not everything in nature is adaptation, and adaptations are not a perfect result. The evolution does not consist in a progressive implementation by natural selection oriented to reach perfection; rather, it is a contingent historical path that must respect the limits as it works on the available material.

In this sense, we can understand how, according to Darwin, that what seems a completely superfluous appendage may realize a magnificent change of function in time, as it happened in *Catasetum*.[324] On this point, Darwin wrote to Hooker:

"It seems that i cannot exhaust your good nature. I have had the hardest day's work at Catasetum and buds of Mormodes, and believe I understand at last the mecanism of movements and the functions. Catasetum is a beautiful case of slight modification of structure leading to new functions. I never was more interested in any subject in all my life than in this of Orchids . I owe very much to You."[325]

These results involve the concept of function that developed in the nineteenth century. Within the philosophy of design, an organ fulfilled a specific function, understood as the role that that organ played in the life of organisms, and this term was dangerously used as a synonym for adaptation, or a concept related to it, to explain its usefulness: that is, it tended to explain adaptation based on the current function of a structure. In reality, with *On the Various Contrivances*, we witness an attempt

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[323] Sober, 2009 e Darwin, 1877.

[324] As we have seen in pages dedicated to the study of homologies.

[325] Darwin to Hooker, 13 October 1861, Darwin correspondence Project.

to distinguish function from adaptation, precisely because the use of an organ can change over time and because the evolution of organisms is never finished. Darwin thus intends to use the term "function" simply to indicate the role or the mechanism that an organ puts into action at a given time, releasing it from its history or, in other words, from the historical consideration of fitness obtained based on adaptation by natural selection.

To base this semantic distinction between historical adaptation and current function, *On the Various Contrivances* details cases of change of function over time, because thanks to these data it is no longer possible to sustain the notion that an organ, a structure, or an apparatus with a current function is evolved as an adaptation to this same function.

The change of function over time[326] has another philosophical consequence, though.

Darwin's adversaries, particularly the supporters of natural finalism, attacked the selective gradualism of *The Origin of Species*, claiming that an organ until it is not completely formed cannot offer any evolutionary advantage. If an eye is useful because it performs the function of sight, they argued, as they can be advantageous the apparatuses and tissues of which it is composed, each of which taken individually is insufficient to perform the visual function. The selection could not explain an advantage for the components or the incipient stages of the organ, while an explanation based on a project carried out in view of that particular function by a superior intelligence, better filled the gaps that the Darwinian evolutionary description did not seem to able to fill.

Yet, *On the Various Contrivances* proposes precisely an answer to this finalistic or creationist conception: there are organs that have evolved historically by performing a specific function and then converted to play a different role or used in completely new ways. The examples are various, as we have seen in the chapter on homology, ranging from *Catasetum* to the labellum of some species of the genus *Serapias*, which from visual and olfactory signals evolved into a food reward for insects.

If the same organ may have performed different functions during the evolution of living beings, then we can conceive evolution and nature as composed of parts of every living being that served in modified forms different roles and that were part of living structures of very ancient and different organisms. This is the material on which natural selection works.

On the Various Contrivances provides the reader with all the evidence that supports the distinction between remote and proximate causes and leads us to argue that the author did not conceive

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[326] What today is best known by the term "exaptation", coined by Gould and Vrba in 2008.

evolution as a new or special creation of organs, tissues, apparatus, structures, forms, and species by a designer. Precisely on the change of function over time, Darwin wrote to Fritz Müller:

"I have re-read many parts; especially that on cirripedes with the livliest interest. I had almost forgotten your discussion on the retrograde development of the Rhizocephala.[327] What an admirable illustration it affords of my whole doctrines! A man must indeed be a bigot in favour of separate acts of creation, if he is not completely staggered after reading yr essay; but I fear that it is too deep for English readers, except for a select few"[328]

8.5 Conclusion

In general, Darwin was against finalistic scientific explanations. This conclusion we can draw from the following:

(a) The correspondence with Gray shows us a position that does not compromise with any philosophical concession towards a direction imposed by the Creator.

(b) The quotations of Delpino, Linnaeus, Sprengel, and others who accepted the finalism in their scientific explanations are always linked to the discussion around case studies where Darwin criticises and refutes attempts made by other botanists to suggest the possibility of a teleological interpretation of floral reality.

(c) the choice to present *On the Various Contrivances* at Bridgewater constituted a strategy to have readers consider, as in contrast to the treatises of natural theology, that natural contrivances can no longer be explained in terms of a design.

(d) Darwinian explanations can explain what natural finalism fails to explain.

(e) None of the Darwinian explanations in *On the Various Contrivances* are compatible with teleology.

Finally, in the book, an antiteleological conception of ecology emerges: the utilitarianism that regulates the coevolutionary relationships implied by fertilisation, the possibility of explaining nature on the basis of secondary causes without recourse to religious dogmas, the opportunism of the species involved in the struggle the survival, and the awareness that the contrivances are not

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[327] It was about a change of functons from cemented ducts converted in nutritive filaments on the basis of which Müller advanced the hypothesis of a derivation of Rhizocephala from barnacles.

[328] From Darwin to Fritz Müller, 18 March 1869, Darwin Correspondence Project.

perfect. These elements, combined with what has been said so far, lead us to recognise a use of metaphors and teleological language that the author deployed of necessity, but not because he recognised an effective purpose in natural processes.

Returning to the flank movement that opened this chapter, certainly one of the aspects contained in the Darwinian strategy was to clarify the explanatory limits of natural theology in the description of the wonderful organic adaptations, to show how much more effective a scientific explanation could be based on the common descent and natural selection.

In the face of these indications, the teleological interpretation of the quotation from the letter of Gray shown in the abstract cannot be supported. In his support, we could add Darwin's answer to the letter of the American botanist:

"Of all the carpenters for knocking the right nail on the head you are the very best; no one else has perceived that my chief interest in the orchid has been that it was a "flank movement" on the enemy.– I live in such solitude that I hear nothing, & have no idea to what you allude about Bentham & the orchids & Species. But I must enquire. By the way one of my chief enemies (the sole one who has annoyed me) namely Owen, I hear has been lecturing on Birds, & admits that all have descended from one, & advances as his own idea that the oceanic wingless Birds have lost their wings by gradual disuse."[329] [330]

However, Gray's direct reference to Bentham explains how Gray had the political function of the book in mind. Although Darwin calls it an allusion he is unaware of, he immediately realises the connection implicit in Gray's words between Bentham, *Orchidee* and *The Origin of Species*: as if Darwin were admitting that if there were a function between the book of orchids and the change of opinion that Bentham has developed towards *The Origin of Species*, he knew nothing about it directly, covering the book's hidden intentions with the usual modesty and calmness of a Victorian gentleman. This exchange is a prelude to what we will see in the third part of this paper, but which

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[329] Owen, R. 1859. On the classification and geographical distribution of the mammalia, being the lecture on Sir Robert Reade's foundation, delivered before the University of Cambridge, in the Senate-House, May 10, 1859. To which is added an appendix "on the gorilla," and "on the extinction and transmutation of species." London: John Parker.

[330] Darwin to Asa Gray, 23-24 July 1862, Darwin Correspondence Project.

Darwin has difficulty in not recognising in this letter: he once again takes up the term "enemy", first mentioned in Gray's expression, and not to refer to an abstract concept or the philosophical consequences of natural theology, but to the person of one of the scientists who most violently had criticised *The Origin of Species*. In relation to these characteristics, we must include the "enemies" to which the flank movement is addressed: the scientists who had ostracised or underestimated the theories contained in *The Origin of Species* and those that the author of *On the Various Contrivances* wanted to convince to change their minds by showing them a correct methodological application of *The Origin of Species*' theories to a series of original topics, studied systemically.

9 SPRENGEL

Abstract

The first occasion in which Darwin cited his studies on Sprengel's work occurred in 1841, when he felt compelled to reply to an article in the *Gardeners Chronicle* that claimed the bees were under indictment, considered the main suspects for having ruined bean crops by making potholes in the flowers in search of nectar. According to the author, if one wanted to save bean crops, nests and female bees must be destroyed as soon as the bean flowers flourished. Darwin undertook to defend what he considered to be industrious and extraordinarily intelligent creatures. In fact, the presence of bees was to be interpreted according to dynamic costs and benefits, and the benefits were ordinarily higher than the costs in the specific case. In fact, given the need for flowers to transfer pollen thanks to the competition of bees,

"If all those flowers, even hermaphrodite ones, which are attractive to insects, almost necessarily require their intervention, as is supposed with much probability by Christian Sprengel, to remove the pollen from the anthers to the stigma, what unworthy members of society are these humble-bees, thus to cheat, by boring a hole into the flower instead of brushing over the stamens and pistils, the, so imagined, final cause of their existence!"[331]

This chapter intends to explain how the Darwinian reformulation of the Knight principle was not a completely original result: its maturation rises gradually, starting from a development process and new observations activated for the first time in the year in which the news of the taking of the Bastille was beginning to excite public opinion and revolutionary consciences throughout Europe. In the summer of 1789, a German Pomeranian botanist during his quiet and patient examinations noticed that there are flowers that cannot be fertilised except with the help of insects that can transfer, by contact or flying, the pollen from the stamens to the stigma. His name was Christian Sprengel, and in 1793, when the Terror began to spread throughout Europe, echoing the upheavals that characterised it, he published *Das entdeckte Geheimniss der Natur im Bau und der Befruchtung der Blumen*,[332] where he proposed for the first time in the history of botany the idea that the

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[331] Charles Darwin, "Humble-bees", Gardeners' chronicle, 21 August 1841, 550.

[332] Sprengel, 1793.

flowers' colours, structure, smells, and secretion of honey were adaptations to insure fertilisation by insects, but also reached the hypothesis that nature seems to mean that no flower will be fertilised by means of its own pollen. It will then be Darwin who will develop and link these two conclusions together in his writing on orchids.

9.1 Brown

Darwin first studied Sprengel because he was interested in the role of pollen transfer modalities in the context of plant fertilisation. At that time, the scholar who had most worked on the same subject was Brown, and his studies had focused on *Asclepiadeae* and *Orchideae*. In 1831 and 1832 he had decided to communicate the results of his work on the mechanisms of pollination directly to Linnaean Society.

Brown had come to the conclusion that to understand pollination, it was necessary to patiently and meticulously analyse the structure and action of the sexual organs of *Asclepiadeae* and *Orchideae*. After numerous observations, the British botanist came to the conclusion that in orchids, and in most plants, cross-fertilisation took place in which the transfer of pollen played a fundamental role, but in this he also recognised that he had not been the first to notice it:

"The authors whose opinions or conjectures on the mode of impregnation in Orchideae I have to notice, may be divided into as such have considered the direct application of the pollen to the stigma as necessary: and those who – from certain peculiarities in the structure and relative position of the sexual organs in this family, –have regarded the direct contact of these part as in many cases difficult or altogether improbable, and have consequently had recourse to other explanations of the function. […] In 1793 Christian Konrad Sprengel asserts that the pollen masses are applied directly to the secreting or viscid surface on the front of the column, in other words to the stigma, and that insects are generally the agents in this operations."[333]

In the same article, but this time dealing with the history and functions of structures suitable for fertilisation in *Asclepiades*, Brown wrote,

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[333] Robert Brown, "On the Organs and Mode of fecundation in Orchideæ and Asclepiadeæ", *Transaction of the Linnean Society of London*, XVI 833, 685-745, pp. 685, 687.

"In 1793, Christian Konrad Sprengel, who adopts the opinion of Jacquin both with respect to the pollen masses and pentagonal stigma, further states, that this stigma has a secreting upper surface or apex, and is formed of two united bodies, each of which conveys to its corresponding ovarium the fecundating matter, consisting of the oily fluid which exudes from the surface of the pollen mass. He also considers insects as here essentially necessary in impregnation, which they effect by extracting, in a manner particularly described, the pollen masses from the cells, and applying them to the apex of the stigma. And lastly, as extraordinary activity of the insect is necessary, or at least advantageous in the performance of this operation, that activity is, according to him, produced by the intoxicating secretion of the nectaria."[334]

From the historical-scientific point of view, it was an important novelty, because before Sprengel and thanks above all to Kölreuter,[335]

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[334] Robert Brown, "On the Organs and Mode of fecundation in Orchideæ and Asclepiadeæ", *Transaction of the Linnean Society of London*, XVI 833, 685-745, pp. 717.

[335] Before Sprengel, it was known that pollination was an essential condition for seed production, but it had not yet been sufficiently proved how the pollen masses were conveyed and brought into contact with the stigma. It was believed, after numerous observations, that in diclinic plants the pollen masses were transferred from the male flowers to the female ones thanks to the action of external agents such as the wind. The explanation for the pollination of hermaphrodite flowers instead postulated a dusting of the stigma with pollen coming from the same plant when the flower was still closed: no collaboration of external agents, therefore, rather a movement of the sexual organs. This type of mechanical fertilization was foreseen in the flowers both in the flowers in which the stamens overtop the style, which were therefore considered in upright position, and in those in which the stamens are surmounted by style, considered the pendulous position.
Any consideration of the direct and necessary action of insects in pollination was, however, completely excluded from the botanical explanations: it had been noticed that some flowers contained honey, and this attracted insects, but it was believed that the latter occasionally shook the flower, causing the fall of the pollinia. The influence of these events was considered completely irrelevant. The only exception remained the observation made by Chalcis Psenes regarding the fertilization of *Ficus carica* (Ficus in Amoen. Acad. I), which remained undervalued until 1761, however, when Kölreuter demonstrated the concurrence of insects in the pollination of

the phenomena in which insects approached the flowers of the plant and tested pollination were known, but sporadic and entirely random phenomena were retained; rather, the rule of self-fertilisation dominated unchallenged. Brown was one of the few to make public Sprengel's battle to dispel this faulty explanation.

From the Darwin's autobiography, it emerges that Brown was also the first to report Sprengel to Darwin.[336]

However, it is important to highlight that Ghiselin is not convinced that Brown led Darwin to read Sprengel, stimulating in this way his interest in orchid pollination.[337] According to Ghiselin, Darwin was experimenting on a range of flowers as early of 1839: the correspondence with Hooker show they began discussing irritability of orchid flowers as early as 8 December 1844 and, about the same matter of reactions of irritated flowers, there is moreover a letter addressed to W. D. Fox in 1857, from Darwin, asking his cousin to observe any *Mormodes spp.* in bloom in a private collection at Oulton House:

Curcubitaceae, Irideae, Sambucus and *Viscum*. From that moment on, botanists' observations began to focus on the behavior of insects and sexual organs: Kölreuter had also shown that in *Malvaceae, Epilobium* and *Polemonium,* the maturation of sexual organs at different times prevented self-fertilization: it was therefore necessary to have the action of insects carrying pollen from younger flowers up to the pistil of an old flower.

However Kölreuter, in accounting for the pollination of most of the flowers, remained anchored to the traditional scientific explanation, which although erroneous continued to boast the support of most botanists, and so it was until the appearance of Sprengel's book and the works of F. J. Schelver and August Henschel. These new studies recognized the importance of an external agent in the fertilization of the pistil, but Henschel and Schelver underestimated the role of insects and were led astray until they considered the sexuality of the plants non-existent, while Sprengel, after having shown that the ancient explanation of the pollination contrasted with factual data, brought the sexuality of plants back into a place of importance within the description of the adaptations of flowers to insect fertilization.

[336] Quotation.

[337] Darwin 1877d, p. xvii–xviii.

"I work all my friends: Are there any Mormodes at Oulton Hothouses or any of those Orchideæ which eject their pollen-masses when irritated: if so will you examine & see what would be effect of Humble-Bee visiting flower: wd. pollen-mass ever adhere to Bee, or wd. it always hit direct the stigmatic surface?"[338]

9.2 Sprengel's observations

During the second half of the eighteenth century, studies on interorganic relations had intensified, or, in other words, on the ecological relationships of organisms: naturalists, starting from Linnaeus and his students, were increasingly occupied with relations between species in their concrete life within the ecosystem of belonging.

To define the complex reciprocal relationships that are established between the organisms for the satisfaction of their primary needs they used the term "*oeconomia naturae*." Each of the phenomena that occurred within the *oeconomia naturae* were ordered according to a finalistic design: food chains, prey–predator relationships, and the relationships between the various natural kingdoms in general were regulated by a providential, sometimes inscrutable, plan in which the species did not act only selfishly but also to the advantage of the other species in order to maintain a balance that was theologically called the harmony of nature.

This particular philosophy of eighteenth-century biology, once applied to the relationship between insects and flowers in the context of pollination, had produced and informed *Das entdeckte Geheimins der Natur im Bau und in der Befruchtung der Blumen*.

The importance of Sprengel is capital because he was the first to introduce in the scientific explanation of the pollination of flowers the hypothesis that the structure and form, the colours and the smells of the orchids were adaptations made in order to recall the insects. It was an open door to a new natural universe to be observed and scientifically explained, a new light thrown on the most important phenomena of flower life: Sprengel had recreated, from apparently insignificant observational details, the perfect work in his treatise. He had finalistically given birth to a Creator who had foreseen everything, a Creator who had to be defined as "wise author of nature who has created one hair without a defined purpose."

In 1787, studying the honey drops placed under the petals of *Geranium selvaticum,* Sprengel realised that the nectary of the greater part of the flowers was structured in such a way as to remain

[338] Darwin Correspondence Project, Darwin to Fox, 8 February 1857.

protected from the rain and reachable only through a specific aerial trajectory available only to insects: if only the insects could easily reach the nectary, Sprengel reached the conclusion that the nectar was secreted just to feed the insects and was protected so that they could get it pure and uncontaminated.

The following summer, Sprengel analysed the *Myosotis palustris*:[339] he realised the magnificent chromatic contrasts between the blue of the petals and the yellow of the circular ring that delimits the mouth of the corolla and deduced that it had to be a signpost guide for the insects. These were the first theoretical speculations on the characteristics of flowers starting from an adaptive purpose: he continued his observations and realised that the other flowers also presented variously coloured points or lines at the entrance of the nectary and concluded by analogy that these were ways to indicate access to a food reward that defined path-finders or honey-guides.

Subsequently, Sprengel also realised the usefulness of a chromatic gradation in the floral variation: if the particular colour is useful to guide the insect close to the nectary or near the corolla once the insect has rested on the flower, the brilliant colours serve to capture the attention of insects from a long distance.

What led Sprengel to consider the characteristics of flowers as adaptations for insects was the study of irises: from the beginning the German author had considered the whole flower as a contrivance for use by insects, but some examples of irises could fertilise themselves without the help of other external agents. Thus, in 1789 he made a distinction: the flowers that secrete honey, protect it from the rain, and are equipped with colours to indicate the position of the corolla are those who need the competition of insects for pollination. The methods of pollination that occur when the flower is fertilised by insects, are the brushing of pollen from the anthers caused by contact with the hairy parts of the body of insects: insects approach to feed on honey, touch the anthers, and transmit pollen to the stigma.

Each observation contained in his book guarantees this conclusion through a long series of patient observations and acute reasoning. In hundreds of flower species, some autochthonous, others cultivated, he searches for the five theoretical premises for this type of pollination to take place:

(a) the presence of a nectary, and therefore of pebbles that work and secrete honey;

(b) the presence of a honey-receptacle (i.e., a structure or tissue that contains secreted honey);

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[339] More commonly known as “forget me not”.

(c) a floral device[340] that allows protection of the honey from the rain;

(d) visual or olfactory tricks[341] that allow the insect to find honey—in the case of flowers already seen, bright colours, extension of the corolla, and coloured spots that signal[342] the entry of honey-receptacles;

(e) the impossibility of self-fertilisation; and

(f) the presence of insects that approach the flowers to feed themselves by coming into contact with the anthers.

Sprengel's book is an analysis of all these points, and his research leads him to conceive the existence of contrivances that recall and help insects in fertilisation.

Unfortunately, and although Sprengel had noticed cases in which pollen is transported by another flower through insects, he did not consider this to be the central process in cross-fertilisation.

He used the term "dichogamy" to indicate those plants in which the two sets of sexual organs did not develop simultaneously, and he was very close to recognising what was later called the Knight–Darwin principle. Sprengel, in fact, carrying out experiments on *Hemerocallis fulva*, realised that this plant could not be fertilised by his own pollen and he deduced that, since in nature very many flowers are of only one sex but even more seem to be flowers of dicogamic nature, which acted in such a way that it did not allow the flowers to be fertilised by its own pollen.[343]

However he failed to tie together the considerations that the contrivances realise the collaboration of the insects, which in turn favour cross-fertilisation, as well as the fact that self-fertilisation leads to worse results than those observable with cross-fertilisation.

Patient and acute observations and comprehensive and accurate interpretations in observation and reflection with such admirable results are the characteristics that allowed the botanist to achieve results so important that had nevertheless been neglected by most of the new generation naturalists, who, instead of verifying the accuracy in his descriptions and continuing Sprengel's research (trying to achieve an ecological understanding of the relationship between flower and pollinator) turned to studies of anatomy and embryology.

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[340] Saftdecke.

[341] Saftmal.

[342] Path-finders.

[343] Sprengel demonstrated through experiments upon the yellow day lily that plants impregnated from their own stamens cannot be made to set seed at all.

9.3 Darwin on Sprengel

Darwin analysed Sprengel's work both in *The Origin of Species* and in *On the Various Contrivances*, revaluating it for all nineteenth century botanists, because he was fighting the finalistic conception. The evolutionary point of view was completely unknown to Sprengel: he could not admit, within the philosophy of eighteenth-century biology, that the process of evolution by natural selection replaced the providential harmony of nature in explaining the relations between flowers, insects, and birds and that adaptations developed for cross-fertilisation.

Darwin needed Sprengel's analysis to re-declare the principle of Knight, however,. In 1857 and 1858 he published data on the pollination of *Papilionaceae* to show how useful the presence of insects was to carry out fertilisation and that, above all, fertilisation encouraged with pollen originating from a different plant.

He took a step forward, recognising that the crossing with pollen belonging to different plants was mainly due to the concurrence of insects, but, a little like Sprengel, he could not yet connect these data with the greater value of cross-fertilisation with respect to self-fertilisation, merely theorising that the absence of insects could cause a decrease in productivity.

The decisive conclusions came with *The Origin of Species* and *On the Various Contrivances*.

In *The Origin of Species* Darwin recognised the priority of the hypothesis that all hermaphrodites make occasional or habitual recourse to two individuals for the reproduction of the species to Sprengel, namely Knight and Kölreuter.[344] Furthermore, Sprengel had the merit of having discovered the methods of flowers to prevent the stigma from receiving pollen from the same flower[345] and Darwin credited the hypothesis that the peripheral flowers developed colours to attract insects: in his eyes it was a very advantageous action for the fertilisation of plants, but immediately he remarked, for the avoidance of any finalistic misunderstanding, that if Sprengel's statement was true, then natural selection had come into play.[346]

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[344] Darwin, 1872, p. 162.

[345] Darwin, 1872, p. 163–164: Sprengel, and more recently Hildebrand, discovered that in *Lobelia fulgens* some samples showed anthers opening before stygma was ready to fertiliaztion.

[346] Darwin, 1872, 208.

In *The Origin of Species* and *On the Various Contrivances*, Darwin confirmed Sprengel's demonstration that the reciprocal position of the reproductive organs and their maturation at different times posed a serious limitation to self-fertilisation.

In *The Origin of Species*, he summed up Sprengel's observations with those of Gärtner and Köleuter in the chapter on hybridism: if the crosses between closely related individuals develop, the fecundity of the offspring suffers a sudden decrease or stops, on the contrary also an occasional cross with individually distinct varieties will increase the vigour and fecundity of the offspring.[347] These data, if viewed in the light of Sprengel's results on the mechanisms that orchids maintain to avoid self-fertilisation, to the notifications of Fritz Müller on orchids, of Hildebrand on *Hippeastrum* and *Corydalis*, of Herbert on *Hippeastrum aulicum,* and of Darwinian studies on orchids pushed author to admit another principle: in some species abnormal individuals, and in other species all individuals, can be more easily hybridised than fertilised by pollen from the same plant.[348] Darwin was always particularly attentive to these previous studies, because it was understood that, as far as plants are concerned, the sterility of the crossed species derives from some principle independent of natural selection.[349]

With the publication of *On the Various Contrivances*, he showed that the structure and contrivances of the flowers were sophisticatedly adapted to lead the insects to release the pollen of other plants on the stigmas of the flowers on which they had rested, and so on: these contrivances, with the exception of a few species, concerned not only British orchids but also those from around the world, upon which Darwin based his conclusions and his analyses of samples received or of indirect observations.

Finally, Darwin had succeeded in developing Sprengel's insights not only in terms of explanatory content[350] but also in methodological terms: he had inherited the methods by which to discover and interpret the minute adaptations of flowers.

Despite their theoretical disagreement, Sprengel conceived the adaptations as perfect creations of an omniscient and omnipotent divinity,[351] and Darwin instead excluded the final causes to introduce

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[347] Darwin, 1872, 341.

[348] Darwin, 1872, 343.

[349] Darwin, 1872, 354.

[350] Contributions from Sprengel to which Darwin will refer in On the Various Contrivances will be about O. latifolia, O. morio, Epipactis latifolia, Listera ovata, and O. militaris.

the theory of natural selection[352] and the common descent. Both were convinced that the study of floral morphology was the starting point in attaining knowledge of the underlying relations of the natural economy. From this premise each drew inspiration to build his personal scientific enterprise.

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[351] He ramined still a devoted son of a clergyman.

[352] A long and continuous process of gradual adaptive refinement.

10 THE USE OF IMAGES IN *On the Various Contrivances by Which British and Foreign Orchids Are Fertilised by Insects and on the Good Effects of Intercrossing*[353]

Abstract

The graphic aspect of a scientific treatise seems to be taken for granted today, but it represented an important novelty when Darwin published the *Orchid* book.

The author had only one drawing in *Origin*, but the small treatise on orchids abounded in sketches. The innovations related not only to the transversal sections of the anatomical descriptions of the orchids, but also to the aesthetic conception that underlay each graphic reproduction. If before drawings had been used to depict the beauty of nature, which in turn demonstrated the perfection of the creative mind, in *Orchid*, beauty could no longer be conceived as a theological proof. Rather, it was shown to be the result of a utilitarian evolutionary race, where the flower tries by all means to win insects' visits and achieve cross-fertilization. The beauty that explained natural theology was the proof of a creation made with the blessing of man. The beauty that explained natural selection had nothing to do with aesthetic taste and human faith, but was the result of a struggle for survival. Some saw in this conclusion a weak point in the theory of natural selection. [354] However, Darwinian botanists took it as a source of inspiration to continue to draw and exchange increasingly precise and complete sketches that explained pollination in order to publish these and bring to completion another aspect of the flank movement. This chapter explains the reasons.

10.1 The work inside the book

When Darwin wrote about orchids, he initially thought of a publication in the Transactions of the Linnean Society. However, after completing the paper, he realised that the length of the text and the number of necessary illustrations made the road to publication of an article impractical.[355]

During the drafting of the paper, Darwin had hired G. B. Sowerby[356] to make the images and lay them out,[357] as a full and accurate account of the parts structure must be accompanied by the

[353] Darwin, 1877.

[354] The Duke of Argyll argued that selection could not explain the beauty that God had infused into natural creatures.

[355] From Darwin to Hooker, 24 Settembre 1861, Darwin Correspondence Project.

drawings.[358] The Darwinian supervision of the work took place in Down, and in 10 days Sowersby prepared the drawings: however, the enterprise proved far more difficult than expected. The agreed cost for the drawings was 11 pounds, but it proved impossible to draw on a wood.[359] However, Darwin trusted Sowersby both for the transfer of the drawings to wood and for the supervision of the incision.

The importance of the illustration was crucial for the British naturalist: he had strongly wanted an artist he trusted, and he was ready to pay for his own images without resorting to works already used in botanical treatises. He intended to ensure the realisation of the entire work even while the possibility of cost absorption by the publisher was envisaged.

Orchis mascula effectively represents the innovations introduced with *On the Various Contrivances* in the field of scientific illustrations:[360] it was primarily a wood engraving rather than a lithograph. Lithographs were the most commonly used medium to depict a horticultural image, but Darwin wanted to mark clearly a difference between the use of botanical images and the use of horticultural images, reaching a level of precision required and obtainable only with images belonging to the botanical field. The artistic effect and contrasts of chiaroscuro took second place to the accuracy and precise delineation of the anatomical details required by natural history studies, and for this reason even lithographs were no longer considered useful by the author of *On the Various Contrivances*.[361]

Another element that characterises *O. mascula* like all other illustrations is that there are no colours present. This absence seems a paradox, given that the colour represents one of the proofs from the action of natural selection that has acted over time to ensure that flowers able to attract and guide

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[356] George Brettingham Sowerby II (1812–1884) was one of the most important contemporary illustrators of Darwin.

[357] It's interesting how Darwin speaks about Sowersby's work: "I am much indebted to Mr. G. W. Sowerby for the *pain* he has taken in making the diagrams as intelligible as possible" (Darwin, 1862, p. V). The inlay of wise anatomical and graphic representations is described by the author of *On the Various Contrivances* in terms of the painstaking labor that characterizes scientific progress.

[358] Introduction, XVI, p. 3.

[359] From Darwin to Murray, 21 October 1861, Darwin Correspondence Project.

[360] Darwin, 1877, p. 8–12.

[361] From Darwin to J. de C. Sowerby, 13 April 1850, Darwin Correspondence Project.

insects to contact with the nectary are favoured in the fight for survival. Above all, if we consider that the historical context was that of the orchid mania, the orchids were one of the favourite subjects in the horticultural publications, and several artists had specialised in colour lithographs with remarkable success.[362]

However, the answer to this paradox rests on material questions: the cost for colour lithographs far exceeded that of wood engravings, and Darwin, knowing that the publication would come to weigh on the funds made available by Murray, considered it unthinkable to risk such an expense important for a small treatise of which he was not sure. It would have received a sufficiently large success to repay all the printing costs.

Another element that could be expected from the author is the use of techniques typical of the illustrations used in horticultural publications, and in fact there are some diagrammatic portraits, but completely absent are the specimen portrait and composite portrait. Although most of the illustrations consisted of partial portraits of the flower, the images focused mainly on the structure and physiological capacity of the pollen and on the reproductive system. If there is any presence of the composite representation technique, it is used for a detailed anatomical comparison typical of botanical illustrations. The Darwinian intent, however, inherited from the Linnaean tradition, was to demonstrate how fertilisation occurred and through which contrivances. As such, describing *Orchis mascula*, Darwin requires that pollen be depicted in their different phases of curvature at a distance of 30 seconds placed on a pencil that imitates the action of an insect's proboscis.[363]

The images that Darwin used in *On the Various Contrivances* were as follows:[364]

- six drawings concerning *Orchis mascula* on page 8, two drawings depicting the physiology of pollen of *Orchis mascula* on pencil on page 12;
- seven drawings of the structure of the *Orchis pyramidalis* flower on page 18;

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[362] The most famous was Walter Hood Fitch, who worked at Kew and also became the official illustrator for Botanical Magazine. He had been the author of for the drawings depicting *Primula* in the papers published for the Linnean Society.

[363] Darwin, 1862, p. 15. The author will use the same technique of depiction of pollens seen in the various phases of pollination on a needle to imitate the proboscis of a moth and with the addition of an anatomical cut of *Orchis pyramidalis* devoid of sepals and petals. This consisted of the comparative technique used in *On the Various Contrivances*.

[364] See Darwin, 1877.

- a drawing depicting head and proboscis of *Acontia luctuosa* with adherent seven pairs of pollinia on page 31;
- two images on the structure of *Ophrys muscifera* on page 46;
- two images relating to the pollens of *Ophrys aranifera* on page 50;
- an image related to a pollinium of *Ophrys arachnites* on page 51;
- two images relating to the structure of *Ophrys apifera* on page 53;
- an image of the structure of *Peristylus viridis* on page 62;
- two images related to the depression movement of the pollen masses of *Gymnadenia conopsea* on page 65;
- three images related to the anatomy of *Habenaria chlorantha* on page 69;
- two images of the adhesive discs of *Habenaria bifolia* and *Habenaria chlorantha* viewed vertically from the top and to the same degree in the magnification scale on page 74;
- three images of the anatomy of *Cephalanthera grandiflora* on page 81;[365]
- two images of *Pterostylis longifolia* taken from Australian orchids by R. D. Fitzgerald on page 87;[366]
- four images of the anatomy of the flower of *Epipactis palustris* on page 94;
- an image of the structure of *Epipactis latifolia* on page 101;
- five images on the structure and anatomy of the contrivances of *Spiranthes autumnalis* on page 107;
- images on the structure of *Listera ovata* on page 116;[367]
- five images of *Malaxis paludosa* partially copied from Bauer on page 130;
- an image of *Masdevallia fenestrata* on page 136;
- three images on the contrivances of *Dendrobium chrysanthum* on page 139;
- four images of the genus *Cattleya* showing: anther, top of the column, pollen masses, rostellum, stigma, column, labellum, nectary, ovarium, or germen;

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[365] Given this detail a dispute arises, as Bauer reports the flowers in the fullness of anthesis being much more explained than they are in the image of *On the Various Contrivances*, yet Darwin underlines that he never saw the flowers in the state described by the drawings of Bauer.

[366] The decision to copy the figures from Fitzgerald's text reflects Darwin's will to favor the reciprocal position of the parties.

[367] Partially copied from Hooker in Philosophical Transactions, 1854, p. 259.

- one image to illustrate in detail the structure of the *Vandeae* column on page 150;
- four images reproducing pollen masses of *Oncidium grande, Brassia maculata, Stanhopea saccata* and *Sarcanthus teretifolius* in different physiological contexts on page 154;
- three images of a pollen of *Ornithocephalus* taken from a sketch by Fritz Müller on page 160, which describes the different forms that the pollinium reaches starting from the insertion in the rostellum up to the hygrometric movements;
- two figures of *Calanthe masuca* on page 161 showing pollen masses, two stigmas, mouth of nectary, labellum, viscid disc, and clinadrium after pollen masses are removed;
- one image of *Coryanthes speciosa* taken from Lindley's Vegetable Kingdom, showing labellum, backet of the labellum, fluid-secreting appendages, and bucket spout on page 174; and
- five images of *Catasetum saccatum* depicting anther, antennae of the rostellum, disc of pollinium, filament of anther, ovarium, labellum, pollen masses, pedicel of pollinium, stigmatic chamber, column, and pollinia on page 182–183.
- two images of Catasetum tridentatum showing anther, pollen peduncle, antennae and labellum on page 194
- two images: the first illustrating anther, anthennae, rudimentary pollen massess, stigmatic clef, two lower sepals of Myanthus barbatus; the second showing the profile of Monachanthus viridis on p. 199.
- an image of Mormodes ignea showing anther, pedicel of pollinium, stigma, labellum, latera sepal on page 209;
- an image of Cychnoches ventricosum showing small column after the expulsion of a pollinia, anther filament, stigmatic cavity, labellum, two lateral petals, sepals on page 156;
- a diagrammatic section of a flower-bud showing the column placed upright, anther, pollen masses, filament of anther, pedicel of pollinium, disc of pollinium, stigmatic chamber, stigmatic canal leading to ovarium
- two images containing anther, rudimentary anther scudiforme, stigma and Cypripedium labellum on page. 227;
- image with cross section of an orchid flower for the study of homologies on page 236;
- image with rostellum of Catasetum on page 242;
- image with disc of Gymnanedia conopsea on page 267.

10.2 Differences from the previous tradition

In the use of the illustrations, Darwin falls into a precedent tradition, for example with ornithological and agricultural studies, modifying it considerably. The traditional illustrations and the conventions on the basis of which these were made were not for him: there was no rational connection of illustrations, textual descriptions, and explanations that made the reader able to observe and distinguish very different orchids.

This combination, which the author tried to make on the page, was easier to apply thanks to the fact that *On the Various Contrivances* was not a purely classificatory treatise, but an attempt to explain the relationships between anatomical structures and the fertilisation process.

One of the most innovative and difficult-to-accept elements for the Victorian public was the aesthetic implications of *On the Various Contrivances*. If with the treatises of natural theology the readers were used to observing and interpreting the beauty of nature as evidence of a divine design and an element created for the use and enjoyment by the human species, Darwin now invited readers to observe the beauty of the flowers, their colours, their ornamental apparatuses, and the delicate and elaborate structures as an example of transmutation of the species reached through natural selection and according to other evolutionary processes in relation to the advantage offered by the cross-fertilisation implemented thanks to the competition of the insects.

With *On the Various Contrivances*, beauty began to appear in the eyes of the readers in a completely different way than it had before: beauty as an element to be found on the natural scale of progressive implementation in the perfection of organisms gave way to an evolutionary and physiological description of beauty in terms of secondary causes. No longer a gift to man as a superior creature, nor a result of a divine delight operating in every creative expression of the natural world, beauty became rather a strictly utilitarian means through which individuals could ensure cross-fertilisation and the species maintained their survival.

It was therefore a new aesthetic philosophy that was born within the scientific naturalism and obtained not a few oppositions.[368]

The combined use of schematic illustrations and pictorial images was a license that Darwin took from the botanical conventions of the time, above all because his was not authoring a classification treatise: Darwin decided to contain a mix of various representational techniques, and he considered himself free to choose and innovate. For this reason, *On the Various Contrivances* was filled with

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[368] An example of this new method of observing botanical nature is in Ruskin, J. Proserpina, Createspace Independent Pub, 15 giugno 2015.

pictorial illustrations of orchid flowers, most of them accompanied by small figures that expressed in detail the anatomical patterns drawn as small incisions that opened the flower to an invasive look. Although not all the illustrations reproduced the whole flower, in most of them the petals were removed to give space to the exact position of the sexual organs: this is perfectly observable, for example, from the image of Orchid mascula presented in a drawing from G.W. Sowersby.[369]

If the theological intent to show the beauty reserved by the Creator for human bliss falls, what remains is an illustrative narrative that implicitly clarifies the role played by natural selection, adds evidence to the ubiquity and importance of variation, and subjects readers to the importance of evolutionary explanations in accounting for the emergence of cross-fertilisation and species diversity.

If in *The Origin of Species* we were dealing with a diagram in which the concept of common descent was first depicted, in *On the Various Contrivances* the depictions that detail cross-fertilisation through a variety of elaborate "contrivances" we have the description for the first time of the action of natural selection. In fact, the detailed descriptions contained in the captions at the foot of each illustration were another element of detachment from the 800 floral taxonomic tradition: a relationship is built such that visual contents made no sense without the textual explanations of the fertilisation process in which the contrivances were involved and vice versa. What Darwin tried to establish was a relationship between image and word that definitively demonstrated the structure and function of these sophisticated contrivances and linked them to an explanation that could no longer be based on the dogmas of natural theology.[370]

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[369] Darwin, 1862, p. 18.

[370] Smith, J. 20016, p. 155.

11 THE MISTAKES OF *The Origin of Species*

Abstract

The profound changes that the author of *The Origin of Species* introduced in the way of understanding the balance of nature, the struggle and mutual destruction of organisms, and the relationship between the abundance and variety of life immediately became the target of a crossfire.

Darwin expected attacks against the content of his theory and overall, as we will see, on his criticisms about the fixity of species. He was not prepared for the attacks that his methodology was to receive from the leading philosophers[371] and scientists of his day.

The problem was that most of Darwin's work appeared not to respect the methodological categories proposed by Whewell and Herschel. In the nineteenth century, in fact, the worth of a scientific discovery was determined by the works of the most important philosophers of science, who were concerned with defining the validity of inductive investigation. For the philosopher, it was a matter of establishing the boundary between theory and research, both from a philosophical and scientific point of view. The culture of Victorian England required the observance of precise methodological canons on the basis of which scientists could open up new areas of knowledge.

If this did not happen, a series of ethical judgments served to undermine the aura of scientificity that served as a dividing line between works by naturalists in the field and works by authors of surreal novels.

Consequently, although *Origin* presented a long chain of empirical evidence,[372] it was difficult to recognize the method that linked these data to the originality of *Origin*'s conclusions, and many scientists dismissed them as weak and fanciful speculations. Hence, the philosophical-scientific problem became philosophical-moral: if a theory is not able to correctly explain the phenomena, then the behavior of the theorist is incorrect: he is arrogant in his speculation, and devoid of respect for and recognition of the truth of the facts.

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[371] John Herschel, William Whewell, and John Stuart Mill remained convinced that *The Origin of Species* was simply full of conjectures: from a philosophical point of view, Darwin's evolutionary theory was weak and wrong, and it proved nothing.

[372] Which became increasingly detailed in the following editions.

This depicted the author of these generalizations as a traitor to the moral virtues that formed the personality and method of a great man of science, such as patience, earnestness, discipline, humbleness, exactness, meticulousness, an indefatigable attitude towards work, and cautiousness.
Origin seemed to be a work without such virtues, and this was the greatest obstacle to the diffusion of the Darwinian revolution. The purpose of this chapter is to prove that, in contrast to what is commonly believed, what created a stir, before Darwin's conclusions, was his failure to observe the method prescribed by Victorian philosophy of science.

11.1 First judgements

From the beginning, only a few of Darwin's friends supported the content of *The Origin of Species*: Hooker, Lyell, Gray, Wallace, and Huxley in a more or less extensive way.
However, it did not escape Gray, who accepted the possibility that one species could vary in another, that the extension of this theory to the whole organic world represented a problem not only scientific but also philosophical and religious.
Heartened by the theoretical conclusions of his esteemed colleagues about the work he was counting on to defend himself against unscientific attacks,[373] Darwin did not hide his intention to convince even the new generations of naturalists:

"Your approval of my book, for many reasons, gives me intense satisfaction; but I must make some allowance for your kindness & sympathy. Anyone with ordinary faculties, if he had patience[374] enough & plenty of time could have written my book.— You do not know how I admire your & Lyell's generous & unselfish sympathy; […] We shall soon be a good body of working men & shall have, I am convinced, all young & rising naturalists on our side."[375]

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[373] From Darwin to Hooker, 25 December 1859, Darwin Correspondence Project.

[374] As we will see, the Darwinian insistence on patience is the reflection of a moral feeling of the time: the Victorian scientist had to distinguish himself first of all in this virtue.

[375] From Darwin to Hooker, 14 December 1859, Darwin Correspondence Project.

While Darwin anxiously awaited a reaction from Bentham,[376] the first criticisms began to emerge: J. E. Gray[377] accused him of reproducing nothing more than the Lamarckian conclusions so ridiculous and inconclusive that he had pushed Lyell and others to attack him for 20 years.[378]

Thanks to the interest of Lyell and Hooker, papers by Darwin and Alfred Russell Wallace were published in 1858 at the Linnaean Society, and Haughton was, in all probability, the first to comment on them publicly. He read the first prints of the paper of two naturalists and criticised the contents of a paper of the Geological Society of Dublin which he received on February 9, 1859. They were then reported in the newspaper of the association, and his reaction was gathered in a direct and ferocious critique:

"This speculation of Mess. Darwin and Wallace would not be worthy of note were it not for the weight of authority of the names under whose auspicer it has been brought forward. If it means what it says, it is a truism; if it means anything more, it is contrary to fact."[379] [380]

The title of the Haughton review was "Biogenesis" and appeared in the *Natural History Review* in 1860.

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[376] From Darwin to Hooker, 14 December 1859, Darwin Correspondence Project.

[377] John Edward Gray, the keeper of the zoological department at the British Museum, had assisted Darwin with his work on *Cirripedia*.

[378] Darwin Correspondence Project, Darwin to Hooker, 14 December 1859.

[379] From the notice enclosed in the letter from Darwin to J.D. Hooker, 3 May 1 859, in Frederick Burkhardt and Sydney Smith (eds), The correspondence of Charles Darwin, 7 (1858-9) (Cambridge, 1991), 29

[380] Darwin later commented in his autobiography that this was the only response to the papers, summarising Haughton 's verdict as "all that [was] new in there was false, and what was true was old" Nora Barlow (ed.), The autobiography of Charles Darwin, with the original omissions restored (New York, 1958), 122.

His newly published summary in the *Annals and Magazine of Natural History* in 1863 was equally critical,[381] because Darwin's dry speculations appeared to Haughton arrogant to the point such as to compare them with Lamarck's ideas and some of Buffon's conclusions. It was not just arrogance, but also the dissemination of irreverent ideas: *The Origin of Species'* theories could be applied to mankind, and this could not be tolerated. Linked to Malthusian speculations on population growth. The value of Darwinian conclusions had the same scientific dignity as did animal magnetism,[382] and for this reason it was not worthy of being the object of any interest.
On April 30, 1860, Darwin noted in a letter to Hooker that "Haughton has been down on us with full force."[383] Writing again on 5 June he made it clear that he did not think the review was a fair one:

"Have you seen Haughton's coarsely-abusive article of me in Dublin Mag. of Nat. History? [...] I never knew anything so unfair as in discussing cells of Bees, his ignoring the case of Melipona, which builds combs almost exactly intermediate between Hive and Humble-bee. What has Haughton done that he feels so immeasurably superior to all us wretched naturalists and to all political economists, including the great philosopher Malthus?"[384]

Darwin was referring to Haughton's critique of the evolution of beehive cell construction: starting from the consideration of a potentially unlimited variation, the Darwinian theory contemplated the possibility of an increase in efficiency in the use of wax, and Haughton, in the footsteps of Darwinian reasoning, attempted to show that in listing a series of real and hypothetical

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[381] Samuel Haughton, 'Biogenesis', Natural History Review 7 (1860), 23–32, reprinted in David L. Hull (ed.), Darwin and his critics: the reception of Darwins theory of evolution by the scientific community (Cambridge, MA, 1973), 216–28.

[382] Mesmerismo.

[383] In Frederick Burckhardt et al. (eds), The correspondence of Charles Darwin, 8 (1860) (Cambridge, 1993), 181.

[384] Darwin Correspondence Project, Darwin to Hooker, 5 June 1860. For the original discussion of bee-cells see Charles Darwin, On the origin of species by means of natural selection (London, 1859), 224-35.

developmental stages, one could see that the least-efficient stage belonged to that of a species that still exists.

Darwin rejected Haughton's critique: his description of the Melipona cells was a very brief synthesis dealing with an example of an intermediate stage of cellular construction development. Haughton had interpreted it as the final stage and had constructed a completely hypothetical mathematical model, devoid of adherence to real facts and purely functional to the quantitative calculation of the use of wax by bees. Wallace's response to the bee-cells[385] was also not long in coming.

In general, there was no specularity between mathematical models and naturalist methodologies, so it was really lacking in consistency to try to describe the evolutionary processes within formal and reductionist cages. In this way, we can read the words of Darwin when he writes to Gray that the subject of the author of the review Biogenesis, as well as chemist, geologist and mathematician, "shows immeasurable contempt of all who are not mathematicians."[386]

The truth is that the same speculative characteristic we find in Hughton's critique is also present in the thinking of many other scientists with a mathematical background, such as William Thomson.[387]

11.2 Inductives and analogical mistakes

Mathematics was not be the only obstacle, however. Even the culture dominated by the idea of a finalistic design in nature did not help to definitively explain a mechanism based on chance and errors, as was the case in the explanation of natural selection.

Darwin was aware of the effort required of scientists with this type of training to get out of their own interpretative schemes, and the lack of correspondence with Haughton seems to suggest that he had surrendered from trying to convince the mathematicians and naturalists who studied the structural mechanisms of the living in search of a perfection that was the basis of every intelligent design of a Creator.[388]

These frustrations added to the fact that he was convinced that the explanation of the mechanism of

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[385] Alfred Russel Wallace, 'Remarks on the Rev. S. Haughton's paper on the bee's cell, and on the origin of species', Annals and Magazine of Natural History 12 (1863), 303.

[386] From Darwin to Gray, 8 June 1860, Darwin Correspondence Project.

[387] Hull, Darwin and his critics, 228.

[388] Samuel Haughton, The principles of animal mechanics (London, 1873), 238.

natural selection offered by his writings and those of Wallace had not made it clear how exactly the process took place, leading him to write to Hooker about Haughton and Harvey:

"This Review, however, & Harveys letter have convinced me that I must be a very bad explainer. Neither really understand what I mean by natural selection.— I am inclined to give up attempt as hopeless.— Those who do not understand, it seems, cannot be made to understand."[389]

The biologists seemed not to want to deal with the critical articulation of a complex of metaphors that characterised the theoretical exposition of the process of natural selection. For this reason Darwin failed to teach them the effort to conceive the complexity of a nature irreducible to mere competition or cooperation or to the coexistence of both: as we can see from the words of the last letter, his suffered perception of the complexity of natural history was not shared by its critics, who, to defuse its ambiguity, reduced it to simplifying, hasty, and liberating formulas.

Darwin repeated the same points in letters to Lyell on June 6[390] and to Gray[391] two days later.

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[389] Darwin Correspondence Project, Darwin to Hooker, 5 June 1860.

[390] "Did you read Haughton in Dublin Mag. of Nat. Hist.? He is more coarsely contemptuous than even Mr Dunns in N. British & overdoes everyone else in misrepresentation. I never knew anything so unfair as his ignoring in his remarks on Bee's cells the almost exactly intermediate comb of Melipona; & so in many other cases. It consoles me that he sneers at Malthus, for that clearly shows, mathematician though he may be, he cannot understand common reasoning. By the way what a discouraging example Malthus is to show during what long years the plainest case may be misrepresented & misunderstood." Darwin Correspondence Project, Darwin to Lyell, 5 June 1860.

[391] "A review in last Dublin Nat. Hist. Review. is the most unfair thing which has appeared,— one mass of misrepresentation. It is evidently by Haughton, the geologist, chemist & mathematician. It shows immeasurable conceit & contempt of all, who are not mathematicians. He discusses Bees-cells, & puts a series, which I have never alluded to, & wholly ignores the intermediate comb of Melipona which alone led me to my notions. The article is a curiosity of unfairness & arrogance. But as he sneers at Malthus, I am content, for it is clear he cannot reason. He is a friend of Harvey, with whom I have had some correspondence. Your article has clearly as he admits influenced him: he admits to certain extent natural selection, yet I am sure does not understand me. It is strange that very few do, & I am become quite convinced that I must be an extremely bad explainer. To recur for moment to Owen. He grossly misrepresents & is very unfair to Huxley. You say that you think the article must be by a pupil of Owen; but no one fact tells so strongly against Owen, considering

In Haughton's view and that of many other naturalists, natural selection was not able to explain the ordinarily complex structures such as, for example, the anatomical parts that made up the muscles of the uterus. The perfection inherent in the pressure movements of all membranes during childbirth so that the foetus was not injured could not be strictly related to this function or, in other words, designed for this purpose. Instead, with the theory of natural selection, a theory that Darwin had borrowed from Lamarck according to Haughton, the whole system would have been the result of chance or fortune, which in the past had linked to the advantage of the mother and her children to an acquired advantage during the struggle for survival in an ancestral past. Nothing that concerned the birth of the nurses could be explained by the natural condition, as nothing that concerned the perfectly engineered construction of the cells of a beehive could be explained by the same theory.
Rather, the assumption that nature acts in the most functional way had to be applied to them to understand an analysis of the anatomical structures of geometry, mechanics, and mathematics justifying this approach on the basis of a Platonic philosophy.
In the philosophical context, to conceive species as populations of different individuals who must constantly achieve adaptive compromises to cope with multiple constraints imposed by a complex and ever-changing environment
Even one of Darwin's teachers, after reading the manuscript, was disappointed and offended. According to Sedgwick, *The Origin of Species* was even more mischievous than *Vestiges*: the same "dish of rank materialism" but served up without the "ignorant absurdities," and he was not the only one to think so. Many of Darwin's detractors indicted *The Origin of Species* to be unfettered speculation[392] on the basis of Sedgwick's Discourse.[393] These accusations also ricocheted through the notorious 1860 meeting of the British Association at Oxford. Starting from the same year, all those who engaged in discussion or review of Darwinian work began with the assumption, shared by Sedgwick, Owen, Wilberforce, and Haughton, that the theory must have a fatal mistake, as it was unseemly in the building built by Darwin, lacking careful induction. It was an event judged as a crime within the scientific community, because the inductive methodology was considered the only

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his former position at Coll. of Surgeons, as that he has never reared one pupil or follower.", Darwin Correspondence Project, Darwin to Gray, 8 June 1860.

[392] Owen 1860, Samuel Wilberforce 1860.

[393] Sedgwick, A. (1833). A discourse on the studies of the university (1st ed.). London: John Parker, pp. 250, 256, 263.

true path of legitimate science. Not searching for this path prompted a host of hostile reviews and comments for Darwin.

The Darwinian building itself seemed to offer the side to the attack of the enemy: it was possible to observe how Darwin had inductively achieved the concept of common descent, but the passage from artificial selection to natural selection consisted in the use of analogy, and for the interpreters, the use of the analogy within a hypothetical deductive system could represent a dangerous and misleading guide.

However, most of these assumptions seemed to be questioned by Darwin's work: scientists believed that he established by induction all living species descended from four or five common ancestors for animals and for the same number of progenitors or a lower number for plants. The next step was the use of analogy: for the interpreters of Darwin's thought, the step towards the deduction of a single common ancestor, a single primordial organism, represented dangerous analogical reasoning. Living beings could have a similar physical constitution and a similar chemical composition, an identical structure of cellure, analogous laws of cerscitation and reproduction. Yet the analogy could be shown as a misleading guide.[394]

The unjustified use of analogical reasoning was not the only weak point in Darwin's work, according to the critics. Darwin further offered reasoning in terms of evolutionary change in species without explaining when and for how long these changes could be possible. The most logical answer was, Thanks to the accumulation of all the centuries that characterise geological eras. But where were the confirmations? The fossil record was insufficient to justify all the intermediate varieties that should have preceded the currently existing species.

It was precisely in this that the use of the analogy manifested its deepest methodological weakness: if the missing links are not there, we cannot prove that there has been an evolution from the first progenitor to the species under examination. Proposing, by analogy, that these ancestors have existed in the past means setting up historical research that manages to find them, their fossils, or their historical traces. The presence of these tests could confirm the correctness of the work, and yet these trials were lacking, and the analogy was insufficient to lead one to believe that, although unattainable for the moment, they persisted.[395]

If Darwin's theory was scientific, critics wondered, why did the use of the analogy and the failure to

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[394] Anon. 1860. Darwin on the Origin of Species. New Englander 18 (70) (May): 516–519.

[395] Anon. 1860. Darwin on the Origin of Species. New Englander 18 (70) (May): 516–519.

observe an inductive method make it so weak?

Why had not we yet succeeded in discovering the missing rings, the progenitors of the various species of birds, fish, primates, flowers, and trees that could be interpreted as natural pasts?

Why would scientists have to exclude the intervention of a divine and rational mind or a providential and lateral plane of the Creator in the name of such a weak analogy?

11.3 The weakness of transmutational theories

The situation of the transmutation theory also worsened the situation.

The work *Vestiges of Creation* and Lamarck's treatises had aroused not a little disturbance in British public opinion: bold conclusions that seemed to make the creation of an intelligent Creator unnecessary.

Both the anonymous author of *Vestiges* and Lamarck were able to activate the hatred of the British cultural establishment, and this reaction put scientific education under the control of natural theology. When it seemed by then that nobody listened to even the echo of the transmutationist hypotheses, which could now be found in the dusty shelves of the bookcases next to the books of fairy tales, suddenly a new book appeared proposing with more force, exactness, and boldness the same theory culturally banned in recent past. In the light of the foregoing, Darwin's theory was interpreted simply as a heresy that sought to propose an alternative explanation to creationism.[396]

The subsequent and inevitable discussion would have had to do with the origin of humanity: in fact, if according to Darwin every living being should be explained in terms of secondary causes, the status of human beings was thrown into question. He had not dealt with the place of human being in *The Origin of Species*, but the intellectual community had made profound criticisms of this eventuality: Darwin's theories prompted them abruptly to avoid those who used them to demonstrate the foundation of man's moral and intellectual qualities on a natural or material basis. The conscience, the ontological leap that separated human beings from animals and plants, and the immortality of the soul represented taboos: naturalistic speculation could not be totally ignored, however, because it was an intellectual field owned by religion and metaphysics. Although most of the British intellectual community elected not to accept any element of Darwinian theory in relation to these topics, the British social context and times did offer a certain kind of harbour to such

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[396] Anon. 1859. [Review of] Origin of species. Saturday Review 8 (24 Dec 1859): 775–776.

hypotheses: neither imprisonment nor death were imposed upon those who supported these ideas, unlike in previous times.

Nonetheless, the publication of these theories was a crime against the notions of the cultural and social powers of the time.[397]

In the 1960s, therefore, a battle against the ideas of Darwin that sounded like heresies had just begun: his own book would have fallen victim to the theory, forgotten, because in a position to compete with more brilliant, more correct theories, it would have been revealed incapable of surviving in the competitive field of science due to the inability of its author.[398]

To argue that species, genera, orders, and classes of animal and vegetable life belong to a tree of life would not have led to any innovation in the systematic practice and development of a new concept of species. Establishing that the evolution had nothing to do with the act of a creative force would have been conceived as an attack against the cultural and religious establishment and consequently stopped before becoming a reality that could be shared within the scientific community. To slow down and to make gradual the modification of the theory is still conceived by many scientists as an unattainable axiom. To suggest that the main evolutionary process was a blind and without purposes natural selection would have sounded contemptuous and unsustainable.

If the only way to show how natural selection acts is an analogy with the ways in which humanity handles variation in the domestic state, then the whole theory is nothing but the birth of the imagination of its author. In other words, it is a fantasy that needs the theoretical support of practically eternal geological time, if compared with the biblical prescriptions: but there are no facts that can prove both assumptions. Even demonstrating that biblical times are much more extended, the suggestion that natural selection can cause the formation of new species remains a hypothesis whose logic is not at all stringent: Darwin's weakness was not in the contents but also in his reasoning, by which he could not bring new evidence to his thesis.

In spite of everything, copies of *The Origin of Species* were sold, and it was necessary to prepare new reprints. During the spread of his ideas among scientists, three general orientations towards his work coalesced: those who intended to explain the origin of species on the basis of the theory of special creations with immutable characteristics, those who supported a spontaneous generation of

[397] Anonymous, 1860. Natural selection. All the Year Round 3 no. 63 (7 July): 293–299.

[398] John William Dawson, "On the Origin of Species," *Canadian Naturalist*, 1860, *5*:100–120, 119–120.

species, and those who supported the transmutationist theories. Among the latter, the youngest naturalists sought sources of inspiration and, often with misleading simplification, referred to De maillet, Oken and the author of the *Vestiges* to look for arguments on the power of physical agents to modify varieties and to Lamarck to discover that organised beings can change as a result of their own acts. It was an immature reception, but the cultural ferment that it fed was more concrete than ever.[399]

However, the possible realisation of a paradigm shift within the natural sciences led even the most important scientists to read *The Origin of Species* and to take a position in the fierce debate that could no longer be ignored:

"[…] and unless Darwin and his followers succeed in showing that the struggle for life tends to something beyond favoring the existence of certain individuals over that of other individuals, they will soon find that they are following a shadow. The assertion of Darwin, which has crept into the title of his work, is, that favored races are preserved, while all his facts go only to substantiate the assertion, that favored individuals have a better chance in the struggle for life than others. But who has ever overlooked the fact that myriads of individuals of every species constantly die before coming to maturity? What ought to be shown, if the transmutation theory is to stand, is that these favored individuals diverge from their specific type, and neither Darwin nor any body else has furnished a single fact to show that they go on diverging. The criterion of a true theory consists in the facility with which is accounts for facts accumulated in the course of long-continued investigations and for which the existing theories afforded no explanation. It can certainly not be said that Darwin's theory will stand by that test. It would be easy to invent other theories that might account for the diversity of species quite as well, if not better than Darwin's preservation of favored races. The difficulty would only be to prove that they agree with the facts of Nature."[400]

As we will see, the words of Agassiz will change, especially in response to suggestions and facts from one of the most famous Darwinian botanists: Fritz Müller, the ardent defender of Darwinian theories.

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[399] Duns, J. 1860. [Review of] On the Origin of species. North British Review 32 (May): 455–486.

[400] Agassiz, J. L. R. 1860. [Review of] On the Origin of species. American Journal of Science and Arts (Ser. 2) 30 (July): 142-154.

It is important now to note that, as did Agassiz, many others strongly opposed Darwin: William Jardine intended to emphasise that the assumption of such a pervasive variation principle of natural reality, so powerful as to be the first cause for the transmutation of species, was something scientifically impossible. The Darwinian principle of divergence appeared more like a tool for science fiction literature capable of captivating the collective imagination, but it had no credit for entering the scientific literature, and those who tried to apply it in the natural framework did no more than expose themselves to public and bitter defeats.[401]

Powerful and excommunicating criticisms arrived, indeed, precisely from the scientific community to which Darwin belonged. The dominant paradigm of the philosophy of European science had been influenced above all by advances in physics during the previous two centuries. Philosophers and scientists sought to work together to ensure that the philosophical generalisations resulted in consistency with the latest realisations. In this context, transmutational theories could not obtain verifications or falsifications, as they did for phenomena and physical models, in which it was possible to deduce a single observational consequence and checking it. The hypotheses of the natural sciences were not purely mathematical and could not be translated into deductive form, so in the eyes of physicists and philosophers of science, and although Darwin had collected a great deal of data, it was not possible to deduce from these precise and unassailable inferences. One could only theorise a series of more or less possible conclusions.[402]

11.4 The Darwin's inductive malpractice

Most strongly opposed by the philosophers and scientists of Victorian culture was the detachment from the properly scientific method that Darwin had adopted by writing *The Origin of Species*. The attacks on this treachery were fierce. John Leifchild attacked Darwin's book on the origin of species in an anonymous form in the journal Athenaeum[403] in the form of a methodological criticism: Darwin emerged as a writer of remarkable imagination and immense pride, capable of pushing him to multiply his assumptions without restraint and every time finding himself faced with the presence

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[401] [Jardine, W.] 1860. [Review of] On the origin of species. Edinburgh New Philosophical Journal n.s. 11: 280–289.

[402] William Hopkins, "Physical Theories of the Phenomena of Life," *Fraser's Magazine*, 1860, *61*:739–752, *62*:74–90, esp. pp. 739–740, 84–85, 90–91.

[403] The most important weekly culture magazine in England.

of contrary facts and consequently using it was the work of a dreamer.

It was Sedgwick's criticism that Darwin should leave no doubts about methodology that Darwin took most seriously:

"[…]I have read your book with more pain than pleasure. Parts of it I admired greatly; parts I laughed at till my sides were almost sore; other parts I read with absolute sorrow; because I think them utterly false & grievously mischievous— You have deserted—after a start in that tram-road of all solid physical truth—the true method of induction […]Many of your wide conclusions are based upon assumptions which can neither be proved nor disproved. Why then express them in the language & arrangements of philosophical induction? […]Acting by law, & under what is called final cause, comprehends, I think, your whole principle. You write of "natural selection" as if it were done consciously by the selecting agent. […]There is a moral or metaphysical part of nature as well as a physical. A man who denies this is deep in the mire of folly […]Were it possible (which thank God it is not) to break it,[404] humanity in my mind, would suffer a damage that might brutalize it—& sink the human race into a lower grade of degradation than any into which it has fallen since its written records tell us of its history. […]Passages in your book, like that to which I have alluded (& there are others almost as bad) greatly shocked my moral taste […]Lastly then, I greatly dislike the concluding chapter—not as a summary—for in that light it appears good—but I dislike it from the tone of triumphant confidence in which you appeal to the rising generation (in a tone I condemned in the author of the Vestiges),[405] & prophesy of things not yet in the womb of time; nor,

[404] Here Sedgwick refers to the link between the material and natural world and the moral and metaphysical one.

[405] Sedgwick had attacked the transmutationist position that Chambers presented in *Vestiges of the natural history of creation*, but Darwin wrote to Lyell about this review: "I have been much interested with Sedgwick Review; though I find it is far from popular with non-scientific readers. I think some few passages savour of the dogmatism of the pulpit, rather than of the philosphy of the Professor chair; & some of the wit strikes me as only worthy of Broderip in the Quarterly. Nevertheless it a grand piece of argument against mutability of species; & I read it with fear & trembling, but was well pleased to find, that I had not overlooked any of the arguments, though I had put them to myself as feebly as milk & water", Darwin to Lyell, 8 October 1845, Darwin Correspondence Project.

(if we are to trust the accumulated experience of human sense & the inferences of its logic) ever likely to be found anywhere but in the fertile womb of man's imagination."[406]

This letter represents, in the conceptual synthesis of a great scientist, all the cultural fears and prejudices that were stirring in the minds of the cultured people who were committed to reading *The Origin of Species*.

Darwin did not expect a positive judgment from his elder teacher,[407] [408] and yet this, like many other subsequent criticisms, personally wounded him to the extent that they accused him of betraying the rigorous method of natural philosophy.

Sedgwick's attack did not hurt Darwin as far as *The Origin of Species*' content was concerned, however, which could be more or less questionable: instead it was the accusation of methodological heresy Darwin most strongly rejected.

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[406] Darwin Correspondence Project, from Sedgwick to Darwin, 24 November 1859.

[407] Despite this judgment we have to remember that Sedgwick loved his geological pupil and always spoked of him with cordiality and kindness.

In 1835, while Darwin was absent on board The Beagle, Sedgwick wrote to Dr Butler of Shrewsbury, "His [Dr Darwin's] son is doing admirable work in South America, and has already sent home a collection above all price. It was the best thing in the world for him that he went out on the voyage of discovery. There was some risk of his turning out an idle man, but his character will be now fixed, and if God spares his life he will have a great name among the Naturalists of Europe.", Quoted in Clark, J. W. and T. M. Hughes *The walking tour in North Wales. In The life and letters of the Reverend Adam Sedgwick*, Cambridge University Press, 1890, vol 1, p. 379–81.

[408] About the direct behaviour that characterized his geological master, Darwin wrote to professor T.M. Hughes in 24 May 1875: "[…] I find that I have kept only one letter from Professor Sedgwick, which he wrote after receiving a copy of my Origin of Species. His judgement naturally does not seem to me quite a fair one, but I think that the letter is characteristic of the man, and you are at liberty to publish it if you should so desire.", Quoted in Clark, J. W. and T. M. Hughes *The walking tour in North Wales. In The life and letters of the Reverend Adam Sedgwick*, Cambridge University Press, 1890, vol 1, p. 379–81.

It was a question he could not conceal from his old master and mentor, pointing out that he had followed the procedure that other scientists before him had accomplished in justifying their principles:

"In a letter to me & in the above notice he talks much about my departing from the spirit of inductive philosophy.— I wish, if you ever talk on subject to him, you would ask him whether it was not allowable (& a great step) to invent the undulatory theory of Light—ie hypothetical undulations in a hypothetical substance the ether. And if this be so, why may I not invent hypothesis of natural selection (which from analogy of domestic productions, & from what we know of the struggle of existence & of the variability of organic beings, is in some very slight degree in itself probable) & try whether this hypothesis of natural selection does not explain (as I think it does) a large number of facts in geographical distribution—geological succession—classification—morphology, embryology &c. &c.— I should really much like to know why such an hypothesis as the undulation of the ether may be invented, & why I may not invent (not that I did invent it, for I was led to it by studying domestic varieties) any hypothesis, such as natural selection. […]I can perfectly understand Sedgwick or any one saying that natural selection does not explain large classes of facts; but that is very different from saying that I depart from right principles of scientific investigation."[409]

The problem was that few naturalists in 1859 believed that a theological account of the origin of species was possible on the basis of a correct inductive practice: paradoxically, one could share the notion of a species birth by natural causes,[410] but few were willing to try to demonstrate such a thing. Rather than embarking on speculation about the origin of species, most naturalists passively maintained the position articulated by Hooker in the 1950s before he embraced Darwin's theory.[411] The immutability of species was not accepted dogmatically; rather, it was a methodological assumption maintained on a pragmatic basis and by virtue of the previous scientific authority.

11.5 The reasons of those who thought of it as did Sedgwick

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[409] From Darwin to John Stevens Henslow, 8 May 1860, Darwin Correspondence project.

[410] Secondary causes.

[411] A position we saw at the beginning of the dissertation.

Darwin did not accept the criticisms they established he had arrogantly distanced himself from the rigor of the inductive method. He knew that the role of inductive practice in Victorian science did not depend solely on adherence to methodological procedures, but also on the spirit with which such procedures were put into practice. Being a good philosopher of nature meant to correctly follow the inductive method, which implied the possession of virtues such as patience, attention, sagacity, and critical judgment. On the other hand, it was believed that the analyses of a mediocre philosopher were characterised by indifference and argumentative weakness. The scientist who forgot the correct use of the inductive method not only committed unacceptable errors, but engaged in sin by rejecting the common duty of every natural philosopher. This conception of scientific practice entails that scientists who proposed a new theory at the same time promoted it on the basis of a correct ethical conduct towards the inductive method. To those who were criticised was applied an incrimination behaviour that originated the new theory.

Transmutation allowed that species could arise from the continuous action of material causes, rather than direct divine control.

When the conclusions of science presented apparent difficulties because they ran contrary to religion, they sought to set up a patient inquiry, inspired by the sincere love of truth, in order to reject any conclusion that was not justified by direct physical evidence.

Nevertheless for many scientists, first of whom was the Reverend Adam Sedgwick, any attempt to understand the origin of the species through secondary causes could not be conducted through correct inductive practice, because it pushed the naturalists to base arguments on hypotheses that could not rationally lean on the sensory perception. Consequently, the transmutationist theories, hating religion, were not recognised as scientific because they lacked a devoted observance and obedience to physical evidence.

The relationship between transmutationism and induction was inconsistent: transmutationism is an outrageous idea, the result of scientific misconduct; but if inductive investigation destroys an outrageous idea, and it is so because is the antidote for scientific misconduct, then it is impossible to reach at transmutationism hypothesis or conclusion through induction.

Sedgwick's reaction to *The Origin of Species* was thus strong: it comprised rank materialism and the author had abandoned induction for unfettered speculation.

In spite of his opening in the first paragraph of *The Origin of Species*, stating that he had arrived at his theory after long years of patient and steady investigation,[412] he received accusations of inductive misconduct in the most decisive way possible: through original scientific research.
In 1859, a monstrous form of frigid Begonia appeared in Kew under little-known circumstances, just in the same period in which *The Origin of Species* appeared in Abemarle Street 26 among the papers of the publisher John Murray. This detail did not escape a professor of botany at Trinity College in Dublin: William Harvey,[413] who was part of Hooker's close friendships, attacked Darwin by claiming that his Darwinian theory was fatally undermined by a monstrous form exactly identical to the frigid Begonia. The criticism was developed in the *Gardeners Chronicle*, and what Harvey wanted to emphasise was that the facts of nature were far from the speculation of some authors who, like Darwin, intended to educate the practical readers of the English magazine.
In particular, Harvey pointed out, on Hooker's observation, the eggs were all fruitful and healthy: a gardener could sow and obtain flowers similar to those of Begonia. However, if this happened in the state of nature, botanists would have considered such a specimen the type of a new natural order. The Darwinian hypothesis does not allow this supposition, because the selection would require hundreds of generations, perhaps thousands, to create a new order. Begonia was therefore among the fatal counter-examples for the Darwinian theory because it showed the existence of a passage that was not at all gradual, a saltus that questioned the path of slow accumulation of small

[412] Darwin, 1859, p. 1.

[413] Harvey was a different matter: here was an experienced naturalist used to handling the same kind of evidence as Darwin himself, although he was described by Leonard Huxley as a systematist rather than a généraliser. William Henry Harvey (1811–1866) was a specialist in marine algae who had made extensive collections of plants in southern Africa while he was Colonial Treasurer in Cape Town from 1836 to 1842. He was appointed keeper of the herbarium at Trinity College Dublin in 1844 and professor of botany in 1856. He travelled extensively in Sri Lanka, Australia and the Pacific islands to collect plants and was on good terms with Joseph Hooker, who took him to visit Darwin at Down House in August 1858. Harvey was a deeply religious man and he seemed to have been willing to make some concessions to evolution theory, so long as he could preserve an element of creative design in the system. Darwin and Harvey exchanged a number of long letters, trying to thrash out the differences between them.

variations: a sudden change, not at all contemplated by Darwinian theory, capable of putting it in crisis, given the possibility for a horticulturist to produce fertile offspring of this monstrosity.[414]

Harvey's attacks did not stop: in February 1860, he sent a satirical condemnation to the zoological and botanical association of the University of Dublin, entitled "An Inquiry into the Probable Origin of the Human Animal, on the Principle of the Darwin's Theory of Natural Selection, and in Opposition to the Lamarckian Notion of a Monkey Parentage."

He respected Darwin, but he never supported a theory that seemed to him devoid of the sobriety typical of scientific discoveries.

Hooker publicly replied to Harvey's criticisms based on the discovery of the *Begonia frigida*.[415]

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[414] Harvey, W.H. Mr. Darwin on the Origin of Species, Gardener's Chronicle, Feb. 25, 1860."

[415] Hooker replied to Harvey in Gardener's Chronicle, 25 February 1860, affirming that to think to the saltus of *Begonia frigida* has not the importance that Harvey imagines. Indeed, the differences between the extreme forms of *Begonia* flowers are not in contrast with Darwin's hypotheses because

"Instead of this being a case which (according to Dr. Harvey) "was not contemplated by Mr. Darwin's hypothesis," it is one of a class which he had specially in view; it is a beautiful illustration of the truth and wisdom of his chapter on classification, in which he shows how false are often the standards by which we estimate the value of characters; how loaded by preconceived ideas is the balance in which we wigh them; how prone, in short, we are to assume that a change is in itself fundamental, because it shakes our systems to the foundation. The differences between the extreme forms of the *Begonia* flowers are in no way comparable to those between "an elephant and a rhinoceros;" nor do they lead us to imagine that the latter could ever be the progeny of the former. According to Darwin's hypothesis, the change from species to species must be slow, and is effected by the accumulation of small differences; this *Begonia*, assuming of how slow and partial such a change is at the commencement; for it is confined to one set of organs in a very few flowers of one sex only, is conducted with the least possible disturbance of the functions of the plant, and there are prodigious odds against its ultimate success. We cannot, indeed conceive the new form replacing the old till after the lapse of many generations, and a long course of that operation of natural selection which my friend thinks his forthcoming new type of Beegoniaceae has already dispensed with.", Hooker, J.D. The Monstrous *Begonia* frigida at Kew, in relation to Mr. Darwin's Theory of Natural Selection, Gardeners' Chronicle, Feb. 25, 1860. See on The The Annals and Magazine of

Harvey, like many others, started from the assumption that the natural laws acted only in the second measure, after the intervention of the Creator arranged to make everything happen in harmony. This finalistic control of the Creator was maintained and could not leave room for the case inherent in the variations that constituted the starting point of the selection.

Rather, the perfection of the adaptations showed the existence of a divine providence that had guided them in their realisation. In an issue of the *Edinburgh Review* in April 1860, he focused on the lack of logical connections in the arguments present in *The Origin of Species*, such as to frustrate the author's efforts in the search for an origin of the species and to invalidate all the most original contributions. Like the contribution present in Vestiges, and those of Lamarck, Buffon and his bold generalisations represented everything opposite sober and prudent research, capable of deluding the expectations of the scientific community with insufficient evidence and lack of rigor.

The book was so full of fanciful speculations that they were an insult to those who seriously and patiently and honestly dealt with natural history.[416]

Even Wilberforce did not refrain from attacking Darwin vehemently in the *0*'s issue of July: it was not a human possibility to verify Darwin's conclusions in *The Origin of Species*, for this he had betrayed the Baconian law of observation of the facts with speculative arrogance. Respect for the experimenter's discipline, confirmation of facts, and the elimination of fanciful hypotheses were only some of the most important shortcomings that characterised Darwin's work as devoid of honour. Darwin's work presented a danger to the intellect of the young naturalists, who had gained no learning insight from Darwinian speculation: the theoretical audacity, the lack of humility, and the infinite vision had completely compromised the sober philosophical of course that the author claimed to have scrupulously followed.[417] Even in Wilberforce's review, one could hear the echo of Sedgwick's methodological conception,[418] also mentioned by the bishop: in the end, Darwin hoped

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natural History: zoology, botany and geology at https://www.biodiversitylibrary.org/item/19558#page/394/mode/1up

[416] [Owen, Richard]. 1860. [Review of Origin & other works.] Edinburgh Review 111: 487–532.

[417] Wilberforce's note: "A Discourse on the Studies of the University, p. 149."

[418] "Analysis," says Professor Sedgwick, "consists in making experiments and observations, and in drawing general conclusions from them by induction, and admitting of no objections against the conclusions but such as are taken from experiments or other certain truths; for hypotheses are not to

for Lyell's intervention, specifically that as a teacher and friend of Darwin he could make it come to his senses and convert it, denying once for all the possibility of a transmutationist hypothesis.[419]

11.6 First attempts of defence of Darwinian method

As the situation worsened and the negative comments continued to accumulate, Huxley reacted by writing a series of reviews that stressed how Darwin's work was revealing a high scientific profile, while the skills of those who judged it insufficient or outrageous instead[420] belonged to the world of literature, pure mathematics, or theology; these critics, therefore, could not allow a full understanding of the methodology that led to determining a scientific fact by induction, starting from experiments or observations. Yet these critics, lacking scientific legitimacy, allowed themselves to discuss the relationship between Darwin and the Baconian or inductive method.[421] [422] Among the few others who defended Darwin by demonstrating his behaviour and tenacity as cautious and moderate in his observations, even if reduced to extremely difficult physical conditions, William Carpenter saw this as all the common reflections of another authoritative systematic botanist named George Bentham:

"the idea was at first cautiously entertained; it was gradually developed into a systematic form, and subjected to a great variety of tests; and when its author had satisfied himself of its soundness, he applied himself for several years, during such time at least as his feeble health permitted him to

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be regarded in experimental philosophy" (A Discourse on the Studies of the University, by A. Sedgwick, p. 102).

[419] [Samuel Wilberforce], "Darwin's Origin of Species," Quarterly Review, 1860, 108:225–264, on pp. 231, 239, 250, 261–262.

[420] And here he was referring above all to those who had written about it in the Westminster Review.

[421] Huxley, T. "Darwin on the Origin of Species," Westminster Review, 1860, 17:541–570, on pp. 542.

[422] Huxley, T. "Darwin on the Origin of Species," Westminster Review, 1860, 17:541–570, on pp. 566–567.

labour, to the preparation of a work which should contain not only an exposition of his views, but a full statement of the evidence on which they are based."[423]

In Darwin's response to Carpenter,[424] we also find an embryonic mention of Gray's flank movement, reinterpreted in this paper, even more significant because it is linked precisely to the figure of Bentham. However, a few years will pass before the publication of *On the Various Contrivances*.

Meanwhile the number of opponents to *The Origin of Species* increased, while Bentham, after reading *The Origin of Species* decided to listen to Hooker's words in defence of Darwin in the introduction to *Flora Tasmaniae*: his position, much to Hooker's regret, remained that of never wanting to deal with such issues again.

Hooker and Daubeny represented the possibility of a ransom for the defence of the theory contained in *The Origin of Species*, and in fact the director of the botanical garden of Kew dedicated the introduction to *Flora Tasmaniae* to demonstrate how he was fundamentally convinced of the possibility of a variation within species during his journey and how this could be appropriately explained with the application of Darwinian theories. His defence was powerful, and his contributions to botanical science were extraordinarily important, but only around 1862 did most botanists began to get excited about its introduction and to understand how much Hooker owed to Darwin.[425]

Finally, the holder of the botanical and rural economics chairs at Oxford Charles Daubeny was another illustrious botanist who, like Bentham, could mark a decisive point precisely when the debate about the Darwinian inductive malpractice had become very violent. Would he have accepted or refused *The Origin of Species*?

Reading by Owen and Wilberforce inspired his stance during the Oxford British Association's meeting. Unexpectedly, however, Daubeny distinguished himself in another way in the article "Remarks on the Final" with the particular reference to Darwin's work: in this paper Daubeny stresses that the debate that went wild around *The Origin of Species* publication could not be conducted on a moral or theological level. The scientific method did not benefit from the

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[423] Carpenter,W. B. "Darwin on the Origin of Species," National Review, 1860, 10:188–214.

[424] Quotation.

[425] Quotation.

interference of these two views, but more observations and problems were needed to clarify this delicate subject. Daubeny rejected the blind mechanism of adaptation by natural selection. He further believed that a study in terms of purely natural causes could not apply to humanity and argued that the weakness of the Darwinian analogy lay in the inability of artificial selection to create new species. However, he was convinced that the application of Darwin's method and discoveries could help a great deal in establishing a new definition of species and in resolving technical issues related to taxonomic classification:

"Dr. Daubeny remarked, that if we adopt in any degree the views of Mr. Darwin with respect to the origin of species by natural selection, the creation of sexual organs in plants might be regarded as intended to promote this specific object. Whilst, however, he gave his assent to the Darwinian hypothesis, as likely to aid us in reducing the number of existing species, he wished not to be considered as advocating it to the extent to which the author seems disposed to carry it. He rather desired to recommend to Naturalists the necessity of further inquiries, in order to fix the limits within which the doctrine proposed by Darwin may assist us in distinguishing varieties from species."[426]

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[426] Daubeny, C. G. B. 1861. Remarks on the final causes of the sexuality of plants, with particular reference to Mr Darwin's work "On the origin of species by natural selection". Report of the British Association for the Advancement of Science 30th meeting (1861), Transactions of the sections: 109-110.

12 THE CONVERSION OF BOTANISTS

Abstract

The problem was that most of Darwin's work appeared not to respect the methodological categories proposed by Whewell and Herschel. In the nineteenth century, in fact, the worth of a scientific discovery was determined by the works of the most important philosophers of science, who were concerned with defining the validity of inductive investigation. For the philosopher, it was a matter of establishing the boundary between theory and research, both from a philosophical and scientific point of view. The culture of Victorian England required the observance of precise methodological canons on the basis of which scientists could open up new areas of knowledge.

If this did not happen, a series of ethical judgments served to undermine the aura of scientificity that served as a dividing line between works by naturalists in the field and works by authors of surreal novels.

Consequently, although *Origin* presented a long chain of empirical evidence,[427] it was difficult to recognize the method that linked these data to the originality of *Origin*'s conclusions, and many scientists dismissed them as weak and fanciful speculations. Hence, the philosophical-scientific problem became philosophical-moral: if a theory is not able to correctly explain the phenomena, then the behavior of the theorist is incorrect: he is arrogant in his speculation, and devoid of respect for and recognition of the truth of the facts.

This depicted the author of these generalizations as a traitor to the moral virtues that formed the personality and method of a great man of science, such as patience, earnestness, discipline, humbleness, exactness, meticulousness, an indefatigable attitude towards work, and cautiousness.

Origin seemed to be a work without such virtues, and this was the greatest obstacle to the diffusion of the Darwinian revolution.

This chapter intends to demonstrate that the *Orchid* book became a scientific treatise capable of mending the wounds inflicted by *Origin*'s enemies. *Orchid* achieved this by describing the reactions of botanists, who absorbed one aspect or another of the flank movement into their daily work. Old- and new-generation botanists began to venerate the *Orchid* book and decided to take an active part in the international circle of adherents to the subspecialization of Darwinian botany that dealt with cross-fertilization by insects.

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[427] Which became increasingly detailed in the following editions.

Moreover, the *Orchid* book created an immense amount of interest, especially among botanists, and gave rise to a vast literature devoted to the biology of pollination. Among those who were led by the flank movement to help develop this field of knowledge, there were many botanists who decided to take up both evolution and natural selection.
Darwin's ultimate goal had been achieved.

12.1 Orchid Book
The *Orchid* book was presented as an object that produced and transmitted culture. In the endless proliferation of his observations, the author scrupulously balanced the opinions of British and foreign colleagues, constantly maintained comparisons with current reference points and the classics of the past in botanical science, and allowed field scientists all over the world to grow professionally in the continuity of a scientific and editorial project and in a variety of concrete experiences. In correspondence, the authors who wrote to Darwin revealed how the application of the theory of natural selection and the doctrine of homologies had allowed them to establish previously unimaginable connections and to create apparently anomalous but valuable logics to understand more deeply the reality of the living, both in its most evident and most hidden aspects. Although many of his adversaries deprecated his ability to create continuous short circuits in the explanation of *Origin* overturning the claims of natural theology in historical questions, the *Orchid* book showed that this practice was the fruit of the work of an untiring discoverer and suggester of conclusions, of a man who discovered new works on the subject and helped to translate them and publish them. This multiplied interventions and collaborations. Although his health granted him only a few hours of daily scientific work, he never stopped giving himself generously to the work and the resolution of the problems that his colleagues mentioned to him in correspondence.
The second edition of the *Orchid* book was the result of continuous updates and changes made over the years. Its pages without fear in recognizing personal doubts and uncertainties, which, discussing with the results of other botanists and naturalists opposed to his conclusions, almost never object directly. Rather, they answered in a dubious way, starting from the peripheral and lateral parts of the innumerable experiments and observations carried out on the behavior of insects, and then forcing readers to take a different point of view and use their ability to create case studies around themselves. The book contains pages of a mercurial intelligence, funabolic and unsettling, in which Darwin continuously shifts between his different souls of geologist, naturalist and botanist, and presents descriptions in which the talent of the talmudist reigns. The analysis of the anatomy of the

flowers became a way for Darwin to exercise the daily discipline of science. According to this discipline, one must never trust generalizations based on an insufficient number of observations for nothing protracted for a long time. One must always check if colleagues' articles and monographs coincide with the empirical facts, and if what is engraved in the illustrations coincides with what is written in the text. Microscopically exact stamens, pistils, columns, anthers, pollen masses, stigmata, seeds, ovaries, rostella, sepals, petals, labella and nectaries of each genus must be examined, as must the behavior of insects involved in pollination. The same meticulous attention must be paid to samples obtained by correspondence, comparisons with foreign genera, the homologies of the flowers, the consistency of the classifications in use, the logical status of hypotheses and Creationist critiques, and the overall balance of the theory behind the conclusions of the book. Yet, Darwin strove never to be intimidated by the alleged authoritativeness of his collaborators or botanical history, because the important thing was to ask questions about function and history. He did not even proceed calmly when his experiments seemed to run smoothly and the conclusion seemed at hand, because it is in the details that mistakes are hidden, and it is in the care and time dedicated to the details that he tried to transform the reception of *Origin* in the 1860s.

Through an enormous amount of evidence, experiments and observations, Darwin revolutionized the scientific understanding of the complex relationship between pollinating plants and insects as well as of the morphology of flowers and their sexuality. The moral virtues demanded by the philosophers of the vitreous science found in this work their most profound application, and no one could claim that the *Orchid* book was methodologically unsound. Thus, the *Orchid* book represents the vanguard of the line of defense that the author put in place to stem and reject the criticism directed at *Origin*, but this was not the only consequence. The amount of evidence and examples Darwin provided was incredible, so much so as to increase a new research area and create a new international network of correspondence between scientists involved in the field.

Cooperation with professional botanists and technicians involved in the orchid mania was fundamental. The exchange of samples and observations contributed to the involvement of an extended number of collaborators, and their contributions proved to be valuable in both the analysis and book dissemination phases. On the one hand, to describe these orchids, it was necessary to obtain anatomical parts that were not easy to find on the market. On the other, this type of collaboration fueled a positive and interested reception of Darwinian work internationally.

Hooker ensured that the nexus of exchange of notifications and maintenance of contacts remained the Gardeners' Chronicle: the articles, observations, requests and answers between Darwin and his readers were going to fill the columns of this newspaper that dealt mainly with orchids. In this way, the attention of experts, scholars and amateurs of that historical period contributed to different degrees and more or less directly to the debate and the development of evolutionary theories without becoming entangled in the most extreme philosophical consequences.

But Darwin insisted also on a highly descriptive and practical language, because his intent was to reach both the scientific community and the technical public, who used to inquire about the Gardeners' Chronicle. All these readers preferred technical language without metaphysical ambiguity. The technicians involved in botany outside the academy were actually large in number and, as we have seen, lived during a unique moment, when the passion for orchids, recognized as status symbols, was spreading. Darwin, who knew all of this in depth, tried to adapt the form and content of his manuscript to satisfy the curiosity and passion of an ever-growing number of readers. He succeeded because The Athenaeum, the Journal of Horticulture, Cottage Gardener and Country Gentleman, The Parthenon, Gardeners 'Chronicle and Agricultural Gazzette continued to present papers on orchids and on his little orchid book.

12.2 **Miles Joseph Berkeley**

Charles Darwin read the first review of his orchid book, 'Fertilisation of Orchids,' and was amazed. It was an anonymous review in the London Review and Weekly Journal of Politics, but Darwin felt the need to know the author's name so he wrote to Murray and Hooker.[428]

The author was Miles Joseph Berkeley, and his was a review completely devoid of a mixture of science and religion, which instead would be the prerogative of the reactions of many creationists. Berkeley favourably welcomed the scientific content of the book and the theories that derived from 'On the Origin of Species' that were beautifully applied in orchid book, so much so that he did not

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[428] Darwin read the review and wrote about it to Murray: "There is a superb, but I fear exaggerated, Review in "London Review". But I have not been a fool, as I thought I was, to publish; for Asa Gray, about the most competent judge in world, thinks almost as highly of book as does London Review.", from Darwin to Murray, 18 June 1862, Darwin Correspondence Project. About the same review he wrote to Hooker: "Did you see the review of my Orchis Book in London R. By Jove it was too strong & made me feel modest & that was a wonderful feeling. I wonder who wrote it. I have had several letters from Asa Gray, who seems about as much infatuated over orchids, as I have been.", From Darwin to Hooker, 23 June 1862, Darwin Correspondence Project.

oppose it by ridiculing the observational prediction that Darwin made in relation to the Angraecum sesquipedale pollinator.[429]

Berkeley was born in Biggin Hall in Northamptonshire on 1 April 1803; in 1868 he was appointed Vicar of Sibbertoft, where he died on 30 July 1889. He studied natural sciences at Cambridge University, becoming a passionate student of Henslow's lectures. He began to publish mainly on zoological subjects, but after meeting Dr Harvey in Dublin and Dr Greville in Edinburgh, he devoted himself to botanical studies, becoming a recognized teacher of systematic mycology, cryptogamic botany, and plant pathology. Berkeley collaborated with Hooker and Sir William Thiselton-Dyer, and as a result received many samples of exotic mushrooms from the royal garden of Kew. He then became one of the most important classifiers of this edible plant.

His reading of Darwin's orchid book convinced Berkeley to deal with the greatest observer of our age, crowning a completely mutual estimate that had begun during the years of study at Cambridge, where Berkeley was an undergraduate student from 1821 to 1825 and Darwin from 1828 to 1831.[430]

But it was not only the reading of 'Orchids' that made him recognize the greatness of the author of 'Origin': As J. Browne declares,[431] after Bentham's presidential address to the Linnean Society held in 1862 and in the following year, the president recognized Darwin to have explained in a specific way how the variation could take place, consequently the theories contained in 'Origin' represented an example of legitimate hypothesis in need of verification. As we will see to guide Bentham's words will not only be reading Mill,[432] but also 'Orchids': The fact is that after that endorsement by the president of the Linnean Society, Berkeley, Charles Naudin, Alphonse de Candolle, Jean Louis Quatrefages, and Charles Daubeny slowly began to re-evaluate Darwin's words in his writings on species.

Berkeley then enthusiastically embraced the contents of 'Orchids', but did not go so far as to rule on the philosophical implications underlying the results obtained in the small treatise on orchids.

12.3 **Joseph Hooker**

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[429] Arditti, Elliott, Kitching, Wasserthal 2012.

[430] From Darwin to Berkeley, 7 September 1868, Darwin Correspondence Project.

[431] Browne, 2003, p. 194.

[432] Mill, 1881.

The title of best physiological observer and experimenter that botany has ever had was also confirmed by the director of Kew Garden immediately after reading ‘Orchids’:[433] According to Hooker, ‘Orchids’ had illuminated the structure and function of the floral organs in this immense and anomalous plant family more than was ever done by other botanists before Darwin. This work also opened up new fields of research and led to the discovery of new and important principles that would have been applied to the entire plant kingdom.[434]

Even Hooker did not fail to express his regret that he had not studied Listera, of which he had published a paper in ‘Philosophical Transactions’. Darwin pointed out in the second edition, in terms of a devoted substitution, that the structure and anatomy had been perfectly described and analyzed, but the study of the relationship with pollinating insects was missing, an element that weakened the interpretation of the functions of the parts of the flower.[435]

What Hooker most admired about the book was the author’s ability to write observations and experiments not only in a systematically orderly and careful way, but also according to an intelligent method. In other words, observations to achieve results worthy of importance must be suggested from theories and ideas that precede and direct them and must be collected for two purposes: the support of these theories and their falsification. If they are ordered in this way, the observations can lead to the attainment of some truths or to the discovery of erroneous conclusions.

In ‘Orchids’, Darwin had presented some tests aimed at demonstrating not only the principle that no hermaphrodite is self-fertilized for infinite generations, but also of the common descent theory and natural selection. In the words of Hooker, the book represented the triumph of Darwin, who had described the contrivances in a way that demonstrated that ‘all our previews were wrong, and most of our observations were faulty’. In this he was referring to the previous fallacious interpretations of

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433 Darwin Correspondence Project, Hooker to Darwin, 28 June 1862.

434 Hooker, J.D. Report of the Thirty Eight Meeting of the British Association for the Advancement of Science held in Norwich in August 1868, Murray, London, 1869, p. LXVII.

435 Darwin in Orchid book at page 139 mentioned Hooker: “*Listera ovata or Tway-blade* – The structure and action of the rostellum of this Orchid has been the subject of highly remarkable paper in the Philosophical Transactions, by Dr. Hooker, who has described minutely, and of course correctly, its curious structure: he did not, however, attend to the part which insects play in the fertilisationof this flower.”

the phenomenon of self-fertilization that had dominated in the botanical field until the publication of 'Orchids'.

This result could be achieved thanks to a profound knowledge of the flowers of orchids, possible only for an expert botanist, able to explain the function of the rostellum to a generic public with a simple and engaging language, knowledge difficult to acquire even in a course of quarterly botanical like those ordinarily established in Europe.[436]

Hooker had directly contributed to the writing of the first—and, above all, of the second edition—with his advice and the sending of notifications and samples to Darwin. Following the publication of the book, the help also became political support. In fact, for Hooker, as it also was for Gray, the reviews and the articles that reflected a rhetorical and technical support of Darwin's book were not only the complacent help of a friend: They were a public form of support to Darwin's theories that were the target of the controversies and of the hatred that had been generated in those years in the debate around the acceptance or rejection of transmutationist theories. Although Hooker and Gray made no mention of common descent and natural selection, this kind of scientific support turned into political support that amplified the flank movement's scope: It was not about attacking those who did not accept the evolutionist hypothesis, but to defend Darwin from those who unjustly accused him of being guilty of inductive malpractice. This type of defence constituted the scientific support and the political basis for the subsequent Darwinian counterattack in support of natural selection with the subsequent editions of 'Origin'.

As for Hooker, this type of commitment involved him personally as president of the British Association for advancement of science: He introduced a prediction concerning Darwin's botany within the presidential speech read in 1868. Tying together rhetoric and politics, Hooker relaunched the role of Darwin's botanical works with these words: 'What are Faraday's findings on telegraphy, those of Darwin will certainly try to the rural economy.'[437]

12.4 **Charles Lyell**

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[436] Joseph Hooker, Review of *Orchids* by Charles Darwin, *Natural history review*, II, (1862), 371-6, https://babel.hathitrust.org/cgi/pt?id=hvd.32044106377336;view=1up;seq=483

[437] Hooker, 1869, LXVIII.

Lyell's opinion on the value of 'Orchids' considered within the post-'Origin' bibliographic production reaches us indirectly, through the words that the geologist John Wesley Judd wrote to Francis Darwin before the publication of 'Life and Letters':

"Lyell once told me that […] if Darwin's works on Orchids, on Climbing Plants, on Dimorphism &c had been published he thought it would have been quite otherwise. Next to the Origin of Species, Lyell considered the "Fertilization of Orchids" as the most valuable of all Darwin's works, and yet it was the only one which was considered by the publisher at the time as a failure"[438]

12.5 **Asa Gray**

Gray approved the contents of 'Orchids' from the first reading but wanted to test it with the comparative analysis of American orchids; the book passed the test and Gray did not falsify any of the Darwinian descriptions.[439] At this point, the American botanist decided to support Darwinian work, and his support developed in different directions—scientific, political, and editorial. As for this last Gray, even considering the difficult thing to do, he made every effort to have 'Orchids' published in the United States by Appleton.

Gray had asked Darwin to send him the 'Orchids' printed sheets so he could write a first review.[440] In April 1862, Darwin sent him the sheets of half of the book[441] and, shortly after the May 15 publication, a presentation copy, all of which led to Gray's review in the American Journal of Science.

We have already seen in the previous part of the dissertation how the most important Harvard botanist interpreted the flank movement achieved with 'Orchids'.

After reading Darwin's book, Gray pondered publishing an essay on the role of teleology in scientific explanation in botany but, given the publication of Müller and Darwin in which the answers to Delpino's finalist positions were contained, he decided to postpone. Instead, Gray

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[438] (DAR 112. B100) as quoted in Porter, D.M. and Graham P.W. Darwin's sciences, Wiley Blackwell, West Sussex, 2016.

[439] From Darwin to Oliver, before 11 June 1862, Darwin Correspondence Project.

[440] From Gray to Darwin, 31 December 1861, Darwin Correspondece Project.

[441] From Darwin to Gray, 21 April 1862, Darwin Correspondence Project.

collected essays to complete 'Darwiniana'[442] without directly addressing the subject of fertilization of flowers in the same collection.

Gray congratulated Darwin, defining his 'charming book', recognizing his great talent and genius for this kind of research, and admitting that he had learned more than he ever knew in one night of reading the introduction and the first chapter. Only thanks to Darwin's indications, Gray admitted, he would now be able to understand some adaptation when he had observed an orchid.[443]

Gray appreciated the book especially for the novelties contained in it. Most of the curious contrivances were made known to the public for the first time—the reciprocal relationship making flowers and insects essential to each other could no longer be underestimated as it had been until then.

Gray does not fail to recall the role of a design in the explication of adaptations and exquisite contrivances, trying to reconcile Darwin's work with that of natural theologians,[444] and yet his intention remains that of underlining the methodological character of the book regardless of the use of secondary laws or the intervention of the creator, who in any case can be reconciled in the words of the American botanist.

He recognizes the book as a faithful and rich record of scrupulously observed facts, complete with drawings that help to clarify the descriptions without the need for additional abstracts for each species treated, full of wonderful and illuminating experiments, and an irreplaceable guide for those wishing to explore the world of orchids.[445]

But Gray added a new review on the same periodical, after the previous one in July where he had mainly presented the first two chapters, and it is important to point out that he understood that Darwin's little treatise had opened a new era for botanical science. Hooker thanked Darwin for introducing the philosophia botanica; Gray thanks him for introducing teleological considerations into the morphological analysis, which can also be translated by introducing philosophical considerations into natural history. In fact, teleology must be considered as a philosophical

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[442] Gray, 1876a.

[443] From Gray to Darwin, 18 May 1862, Darwin Correspondence Project.

[444] See in teh chapter dedicated to teleology.

[445] Asa Gray, review of On the Various Contrivances by Which British and Foreign Orchids Are Fertilised by Insects, and on the Good Effects of Intercrossing, in *American Journal of Science and Arts*, vol. 34, p. 130-144, July, 1862. https://archive.org/details/mobot31753002152616/page/138

evaluation of the mechanisms and natural organs that can be attributed to a creator, a design, or secondary causes. Gray opts for the arguments of the second type, always in an attempt to reconcile Darwin with natural theology. But it is undeniable that there is a common independent result achieved by various scientists and that it consists in recognizing to Darwin the introduction of a novelty in botanical science: the search for meaning in the various forms and diversifications of organs, a search that does not stop at pure classification and description but requires explanatory principles that the botanist must explain and justify historically and philosophically. After 'Orchids', botany became a science that could not do without the philosophical considerations of natural history, and this entailed not only methodological and epistemological but also political consequences. Classifying plants now also meant taking sides for or against special creation, design intelligent, transmutation, and natural selection.[446]

But in 1882, Gray resumed the battle for teleology. In 'The Relation of Insects to Flowers',[447] he starts from 'Orchids' and focuses on the action of bees in making the gardens and fields neat and splendid, as Lubbock[448] had stated in his public speech. In the eyes of the American botanist, the usefulness of the bees' presence could be compared to the postman's function in delivering letters to us. It is not enough to reduce the complex effects of life to the unconscious choice made by some

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[446] "[…]"in his fascinating book of on the Fertilisation of Orchids, and in his paper explaining the meaning of dimorphism in hermaphrodite flowers, Mr. Darwin – who does not pretend to be a botanist – has given new eyes to botanists, and inaugurated a new era in the science. Hereafter teleology must go hand in hand with morphology, functions must be studied as well as forms, and useful ends presumed, whether ascertained or not, in every permanent modificttion of every organ. In all this we *faithfully* believe that both natural science and natural theology will richly gain, and equally gain, whether we view each varied form as original, or whether we come to conclude, with Mr. Darwin, that they are derived;-the grand and most important inference of *design in nature* being drawn from the same data, subject to similar difficulties, and enforced by nearly the same considerations, in the one case as in the other", from Asa Gray "Fertilization of orchids through the agency of insects", American journal of science and arts, 34, 1862, p. 420-9, p. 429, https://archive.org/details/mobot31753002152616/page/429

[447] Gray, 1882, p. 598-609.

[448] Lubbock, 1881. The scientist had stated that the beauty of the gardens and the sweetness of the fields were due to the presence of bees.

organisms such as bees; the beautiful results that we can contemplate in nature depend on a large number of biological laws and on a variety of life forms that are subject to unexplainable variations by Darwinians, me perfectly referable, according to the teleologists, to the maintenance of an orderly plan in nature.

12.6 **George Bentham**

Bentham's position reveals the most exemplary key to understanding the political aspect of the flank movement: From the outset he expressed a rejection of 'Origin', but after reading 'Orchids' he actively set out to agree to discuss Darwin's theories. However, the influence he exerted through his role in the Linnean Society reveals the importance of 'Orchids' in convincing the scientific community to accept common descent and natural selection.

As seen previously, Bentham was among the opponents of 'Origin' and used his role as president to silence the spread of this type of hypothesis. His opposition was not only realized in public life; even privately, Bentham displayed an aversion to initiating discussions on the consequences of Darwin's book on the origin of species.

He belonged to that conservative tradition that dated back to Thomas Bell in prohibiting any formal discussion about the theory of evolution within the Linnean Society.[449]

When Bentham received the little treatise on orchids, echoing the words written by Gray to Darwin, he hastened to write to the author of 'Origin' even before concluding the reading.

The curious reading of a few pages was enough to cause him not to listen to the call of the bed for two chapters and the introduction, although he was tired by his duties for the worldly counterpart organized by the president of the Royal Geographical Society. The next day, Bentham hastily wrote to Darwin, thanking him for the new field of natural observations he had officially opened, but above all for the tools he had endowed scientists with in seeking an explanation for phenomena that appeared indecipherable to the usual and ordinary methods of forecasting and analysis. President Bentham now believed that Darwinian observations were invaluable to the entire world:[450] It was not just a truce that served as a prelude to an alliance, the botanist decided to become a supporter of the Darwinian way to proceed in natural history.

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[449] The protocol envisaged by the Company was that of not considering as its own competence any theoretical argumentation without formal reports of new facts or original observations.

[450] From George Bentham to Darwin, 15 May 1862, Darwin Correspondence Project.

This change had profound political and scientific consequences. As president of the Linnean Society, Bentham delivered the society's anniversary address on 24 May 1862,[451] saying that if biology first meant a study closely related to the history of animal and plant life forms,[452] it now proved to be a field of comparative studies that revealed new and unexpected ways to explore. The Darwinian method presented itself as a successful explanation tool that was to stimulate other scholars to proceed in a similar way.[453] But then he hastened to specify:

"I do not refer to those speculations on the origin of species, which have excited so much controversy; for the discussion of that question, when considered only with reference to the comparative plausibility of opposite hypotheses, is beyond the province of our Society.... But we must all admire that patient study of the habits of life, with that great power of combining facts, which has revealed to us so much of surprising novelty in the economy of nature. The wonderful contrivances for the cross-fertilization of Orchids, so graphically detailed in Mr. Darwin's new work, and which rival all that had been previously observed in the singular economy of insect life, had been hitherto unsuspected even by those botanists who had specially devoted themselves to that family."

The scientific results of 'Orchids' represented a legacy sufficiently important to reach a formal report within the Linnean Society.

Now the shifting of the balance's needle was official: Bentham, who had turned out from the beginning 'greatly agitated' by 'Origin'; who believed that reading that book had caused him such a severe 'pain and disappointment'[454] at first to be urged repeatedly to personally discuss it with Hooker in a hasty and agitated manner;[455] who had initially left Darwin without support in the

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[451] Bentham 1862b.

[452] Bentham 1862b, p. lxviii.

[453] Bentam 1862b, p. lxxxi.

[454] From Bentham to Francis Darwin, 30 May 1882, (Dar 112).

[455] Bentham had at first been 'greatly agitated' by Origin: "I have had another talk with Bentham who is greatly agitated by your book— evidently the stern keen intellect is aroused & he finds that it is too late to halt between two opinions—how it will go we shall see. I am intensely interested in what he shall come to, & never broach the subject to him.", from Hooker to Darwin, 20 December

Linnean Society and fed to his critics; now the president himself and his ‘stern keen intellect’[456] became an admirer of Darwin’s work. In fact, Bentham suggested an opening towards a complete adoption of the theories and conclusions of the author of ‘Orchids’, an adoption that he publicly admitted in his presidential address of the 1863 Linnean Society.[457] In that address, the prohibition of discussion on Darwin’s evolutionary theories was removed, and ‘Origin’ became an example of scientifically correct and productive theoretical generalization. It was the first time after five years of prohibition; the public reading of the works of Darwin and Wallace on the species led to the launching of an era in which the formal reading of scientific papers dealing with related issues was no longer prohibited.

Patient research and acuteness of observation had overcome the opposition front: The president invited all members to read Darwin’s book, ‘Fertilisation of Orchids’.

What happened to Bentham represents the reaction that many botanists had when reading ‘Orchids’: Under the guise of floral biology in that investigated way, evolutionary hypotheses became more acceptable. The book constituted a reaction capable of neutralizing the crossfire of distrust, scepticism, and prejudice that had originated from the critical reception of ‘Origin’. The reading of the book on orchids by Bentham and many other scientists had broken the silence on the dangerous subject of evolution.

Bentham did not fully support the arguments of the two evolutionists; the conclusions reached were too extensive to be experimentally demonstrable. However, he praised the ethical-scientific value of the observations made. It was no longer possible, according to Bentham, to oppose scientific arguments and observations only on the basis of the philosophical, moral, and religious consequences that the works of the two authors involved. This type of sentimental and religious opposition had addressed effective criticism against the ambitious speculations of Lamarck and

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1859, Darwin Correspondence Project. However George Bentham in a letter dated 30 May 1882 wrote Francis Darwin of his support of Darwin’s views: ‘I have been throughout one of his most sincere admirers, and fully adopted his theories and conclusions, notwithstanding the severe pain and disappointment they at first occasioned me.’One year later his speech quoted above, in 1863, he publicly acknowledged his adoption of CD’s theory in his presidential address at the Linnean Society.

[456] From Hooker to Darwin, 20 Decemeber 1859, Darwin Correpondence Project.

[457] Bentham, 25 May, 1863.

Vestiges, but in the case of the two works in question, readers were faced with lucid and moderate generalization starting from phenomena that were scrupulously observed. A persevering obstinacy in this sense constituted an unjustified and gross obstinacy. The perspective introduced by Bentham's speech overturned the situation that had continued to open up from the reception of 'Origin' and in the anniversary of the birth of Carl Linneaus, after years of cultural embargo within one of the most influential cultural societies of the British scientific establishment.
After Bentham's 1863 speech, Darwin wrote to the president:

'I have been extremely much pleased & interested by your address, which you kindly sent me. It seems to me excellently done, with as much judicial calmness & impartiality as the Lord Chancellor could have shown. But whether the "immutable" gentlemen would agree with the impartiality may be doubted,—there is too much kindness shown towards me, Hooker & others, they might say. Moreover I verily believe that your address, written as it is, will do more to shake the unshaken & bring on those leaning to our side, than anything written directly in favour of transmutation.[458] […] You have done, I believe, a real good turn to the right side.'[459]

Although this small book on orchids had also been published for the general public—those not specialized in academic studies but involved in the orchid mania—through the use of a sometimes simple and direct language, it was precisely those who practiced science every day who remained invested in his extraordinary capacity for analysis and explanation.

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[458] In summing up the literature relating to Origin, Bentham suggested that the 'tide of opinion' among 'philosophical naturalists' was 'setting fast in favour of Mr. Darwin's hypothesis', and that few who really considered the subject could deny that new species had been produced from a common ancestor by natural selection (Bentham 1863, pp. xxi–xxii). He continued:
The great objections still urged are to the insufficiency of the data yet ascertained for the extension of the principle to all changes and to all species; and whilst many of Mr. Darwin's generalizations may be considered as adopted, there are others which many persons are disposed to refer for further proof, and many objects of research more or less relevant, indicated only by him, are still obscured from our view"

[459] Darwin to Bentham, 19 June 1863, Darwin Correspondence Project.

Bentham's conversion reveals that the true Darwinian intent had been successful and suggested that many others would follow the president of the Linnean Society.

At this point, even those who were not part of the close circle of friends of Darwin began to have a deep admiration for his studies on orchids.

12. 7 **Charles Giles Bridle Daubeny**

Daubeny became professor of chemistry at Oxford University in 1822 and, starting in 1834, held the chairs of botany and of rural economy at the same university.

In 1860, at the meeting of the British Association for Advancement of Science at Oxford, he read a paper titled 'Remarks on the Final Causes of the Sexuality of Plants' at the Natural History Section, where he attempted to prove that the Darwinian theory of the common descent presented weak meshes within the argumentative chain that supported its truth. And yet, Daubeny admitted a fact to which he drew the attention of all the critics: This theory had cast its author along a series of original discoveries both in the botanical and zoological fields. Daubeny respected Darwin's observational ability and believed that life forms should be studied through explanations that resorted to secondary causes, including human beings; no other consideration that did not belong to the field of pure science had to become part of the field of discussion.[460] This, too, was a point he had convinced himself by reading Darwin and which should not necessarily lead to contrast with the interpretations of the Holy Scriptures, once he admitted that God had infused life into the first monad of evolution.[461]

According to Daubeny, Darwinian theory had to be considered based on its scientific merits, without any metaphysical bias. Precisely in this field he had no intention of extending the evolutionist hypotheses to the conclusions reached by Darwin; indeed, he warned other naturalists to deepen their research to try to set limits to the suggestions that the Darwinian doctrine could inspire in terms of distinction between species and varieties.[462]

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[460] Daubeny, 1860, p. 26.

[461] Speech as President of Devonshire Association, p. 193

[462] Daubeny, C. J. B, Remarks on the Final Causes of teh Sexuality of Plants, with particular refeence to Mr. Darwin Work 'On the Origin of Species by Natural Selection', from Report of the Thirtieth Meeting of the British Association for the Advancement of Science, held at Oxford in June and July 1860, p. 109.

Moreover, Daubeny went so far as to set limits directly to the theory of natural selection,[463] on the basis of what the Duke of Argyll had reported on the inability of this explanation to account for the 'beauty' of nature.[464]

However, he maintained a deep and implicit debt with the British naturalist, a debt that was renewed whenever Daubeny mentioned the orchids in his speeches and in the lectures given at Oxford. The contrivances and mutual adaptations that made up the wonderful orchid flowers were a topic that the botanist loved from the first reading of the orchid book. This book had persuaded him to give up publishing his lecture on the subject because it '…contained little or nothing which has not been much better explained by yourself and other original investigators of the subject of orchids'.[465]

But this relationship was important because it was the first time that Darwin's work was again and publicly discussed in Oxford after the incident between the Archbishop of Oxford and Huxley.[466]

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[463] Idem p. 196

[464] Speech to the Royal Society of Edimburgh,

[465] From Charles Giles Bridle Daubeny to Darwin, 5 July 1862, Darwin Correspondence Project.

[466] During the meeting at Oxford of the British Association for the Advancement for Science held on June-July 1860, to which Darwin could not participate due to his poor health and that of his daughter, a ferocious exchange of words took place between Thomas Henry Huxley and Samuel Wilberforce, bishop of Oxford, at the round table of section D (zoology and botany-physiology). At that moment Daubeny held the chairs of botany and rural economy and witnessed what happened after reading his paper on plant sexuality. The paper was read on Thursday 28 June, but the following Saturday the public assembly met in the reading room of the natural history museum of Oxford. The rev. John Stevens Henslow took the chair. After reading a paper by John Draper of New York University on the intellectual development of Europe described according to the evolutionary perspective of Charles Darwin, Henslow opened the debate by allowing the word exclusively to those who had arguments to adduce and not mere statements. Wilberforce took the floor and, supporting the same arguments he had presented in an anonymous review of Origin on The Quarterly Review, attacked Darwin and insulted Huxley by involving him in a metaphor of the grandfather-ape and receiving numerous applauses. There are more versions that report the exchange of words, but in substance he came out strongly against a theory which holds it possible

Whenever Daubeny recalled the example of the contrivances of orchids against self-fertilization, he quoted directly and immediately Darwin's name, professing an intellectual debt to the English naturalist.[467] Daubeny did not know a more complete and accurate description than that given by the English naturalist regarding orchids: The only doubts, due to the dissolving which he always addressed to Darwin, concerned the coevolutionary relationships between insect species and pollinated orchid species.[468]

According to Richard Bellon, Daubeny never returned the theory of evolution with the love he instead dedicated to 'Orchids', a passion that led him to suggest to his colleagues to read Darwin's little treatise during the speech given at the British Association for the Advancement of Science at the 1862 meeting in Cambridge. This reveals the scientific-political influence of the orchid book; Daubeny delivered the suggestion to his colleagues by arguing that reading would defuse the methodological criticisms born, nurtured, and extended since 1859, demonstrating its baselessness.[469]

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that man may be descendent from an ape. If it did not seem to Huxley that it was important to establish for a man whether his grandfather was an ape or not, he would have to speak for himself and ask himself about the apelike origin of his ancestors. And yet Huxley answered: "I asserted, and I repeat, that a man has no reason to be ashamed of having an ape for a grandfather. If there were an ancestor whom I should feel shame in recalling, it would rather be a man, a man of restless and versatile intellect, who, not content with [...] success in his own sphere of activity, plunges into scientific questions with which he had no real acquaintance, only to obscure them by an aimless rhetoric, and distract the attention of his hearers from the real point at issue by eloquent digressions and skilled appeals to religious prejudice.", from a letter of John Richard Green to sir William Boyd Dawkins.

[467] Daubeny, C. Address delivered at Tiverton, in August, 1865, as President of the Devonshire Association for the Advancement of Scinece, Literature, and Art, p.198.

[468] From Charles Gile Bridle Daubeny to Darwin, 5 July 1862, Darwin Correspondence Project.

[469] Richard Bellon reports that the speech was held in 1862 at the Cambridge meeting of the British Association for Advancement of Science. However, 3 speeches by Daubeny that do not mention Darwin are recorded at that meeting: On flint implements from Abbeville and Amiens, p.71, On the last eruption of Vesuvius, p. 71 e Reply to the remarks of M.F. Marcet on the Power of Selection ascribed to the Roots of Plants, p. 141. Si tratta del Report for the British Association for the

12.8 **John Hutton Balfour**

In 1841, Balfour[470] began teaching botany in Glasgow and later at the University of Edinburgh, in addition to serving as Regius Keeper of the Royal Botanic Garden in the same city. He always nurtured a profound respect for Darwin as a person—they had attended the cultural circles of the Plinian Natural History Society[471]—but above all for the botanical production of the English naturalist, in the light of which he intended to examine specimens of the genus Primula present in the Edinburgh botanical garden.[472]

However, Balfour did not fully support the conclusions of the theories contained in 'Origin', above all for the new classification that, according to Huxley, had to consider in a single order men and apes. For Balfour, the moral qualities and human intellectual functions constituted a saltus that did not he could ignore.

After reading 'Orchids', Balfour was convinced that, unlike Darwin, orchids were really able to attract insects due to their shape, which reproduced animal forms.[473] This point was criticized by Darwin but re-evaluated by current botanical science.

Balfour remained convinced that the contrivances played a fundamental role in the fertilization of the orchids and accepted the Darwinian descriptions on the modalities of displacement of the pollens on the stigmatic faces. He took as an example three images of the flower of Parnassia palustris. He sought to prove one of the main theses of 'Orchids', namely that the contrivances have as their purpose the fertilization of a flower through the pollen of another flower and that in nature the self-fertilization is rare and cannot last to infinity. However, Balfour did not forget to mention that self-fertilization was observed in Ophrys apifera, not in controversy with Darwin but more as an indication for the reader to analyze any flower structures that were able to self-fertilize.[474]

Advacement of Science, 32nd meeting held at Cambridge in 1862, John Murray, London, 1863, https://www.biodiversitylibrary.org/item/93054#page/5/mode/1up

[470] Edimburgo, 15 settembre 1808 – Edimburgo, 11 febbraio 1884.

[471] From John Hutton Balfour to Darwin, 14 January 1862, Darwin Correspondence Project.

[472] From John Hutton Balfour to Darwin, 14 January 1862, Darwin Correspondence Project.

[473] Balfour, J. Outlines of botany, designed for school and colleges, 2nd edn, A. & C. Black, Edinburgh, 1862, 357.

[474] Balfour, J. 1862, 358.

Balfour was part of that generation of scientists who, once the validity of the Darwinian method in ‘Orchids’ was accepted, decided to embrace and develop the scientific results of Darwin’s book without going so far as to accept the ambitious theoretical generalizations and the philosophical consequences that the author presented. It was a reaction that became common and was also shared by P.H. Gosse and Miles Berkeley.

12.9 **Philip Henry Gosse**

Gosse’s relationship with orchids can be reconstructed mainly through correspondence with Darwin. He was first and foremost a zoologist but decided to devote himself to studying orchids in the following years. After the publication of ‘Orchids’, Gosse undertook a real collaboration with Darwin in the studies of the discipline which dealt with floral pollination and which was born with the publication of the orchid book.

Gosse defined the treatise as a ‘charming book’ on the basis of which he began the experiments of pollination on the orchids of his collection. He also started a scrupulous study of the structure of Vandeae and Stanhopea pollens dried up on the basis of the anatomical drawings contained in ‘Orchids’.[475] With this book, for the first time, the philological depictions of flowers appeared, and in the specific case of longitudinal sections revealing the structure of the column in Vandeae and of pollens depicted before and after the movement of depression.[476]

Darwin, writing about Ophrys apifera,[477] remained perplexed in observing that the flowers appeared to have elaborate contrivances for directly opposed objects, that is, adaptations for both cross- and self-fertilization. The problem arose because one of Darwin’s intentions in ‘Orchids’ was to demonstrate that cross-fertilization was the main object of the contrivances by which orchids were pollinated, and yet there were several species—among which O. apifera was the case most clear and widespread—which presented special and perfectly efficient contrivances for self-fertilization.[478] He considered his observations dedicated to establishing whether the pollinia were ever removed by

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[475] From P.H. Gosse to Darwin, 30 May 1863, Darwin Correspondence Project.

[476] Darwin 1862, p. 179 and p. 185.

[477] Orchid book, p. 63-72.

[478] Orchid book, 359.

insects in this species insufficient. Since Gosse lived at Babbacombe Bay, near Torquay, Devon,[479] where the author of 'Orchids' had made some of his observations,[480] Darwin intended to solve his 'greatest puzzle' at any cost, and he did not hesitate to kindly ask Gosse for further comments regarding the removal of pollen on O. apifera.[481]

After dispatching his 13-year-old son to search for some inflorescences of O. apifera, on 16 plants with 32 flowers, Gosse sent Darwin three specimens. One was from the lower flower with a pollen adhering to the stigma and the other partially removed, and from the upper flower with both pollens removed; a second specimen had an open flower revealing both pollen removed; and a third specimen had two open flowers and one pollen removed with the other adhering to the stigma. Although Gosse had not directly seen the pollination by insects, he opened the possibility that the wind might have been the agent of pollination: He had blown on more flowers watching the pollen come off from anther cells and go to settle on the stigma.[482]

In all likelihood, the considerations of Gosse directly contributed to the Darwinian conclusions on apifera in the second edition of the orchid book,[483] even if they were not directly quoted. In fact, Darwin observed, 'From what I had … seen of other Orchids, I was so much surprised at the self-fertilisation of this species, that I examined during many years, and asked others to examine, the state of the pollen-masses in many hundreds of flowers, collected in various parts of England.'[484]

'Orchids' had therefore established in Gosse, as in many other naturalists, active participation in the Darwinian network of botanists, which included theoretical notifications, sample exchanges, and discussions and interpretations around case studies that were addressed on the basis of different philosophical orientations. This happened for the interpretation of Stanhopea's self-pollination between Gosse and Darwin:[485] The latter found the interpretation of Gosse extremely curious and

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479 The zoologist Gosse was born the 6th of April 1810 in Worcester and died in Torquay the 23th August 1888.

480 Orchid book, p. 66.

481 From Darwin to P.H. Gosse, 2 June 1863, Darwin Correspondence Project.

482 From P.H. Gosse to Darwin, 13 July 1863, Darwin Correspondence Project.

483 Darwin, 1877, p. 52-9.

484 Darwin, 1877, p.55.

485 From P.H Gosse to Darwin, 4 June 1863, Darwin Correspondence Project.

quite new, but, among other counsels, asked him to wait for his further examination of another inflorescence.[486]

In the case of Gosse, he was a zoologist who, in pouring significant energy into a field different from his previous education, mainly took inspiration from the Darwinian writings on orchids, although he did not mention or take part directly in the speculations on evolutionary theory.

12.10 **William Henry Harvey**[487]

Harvey graduated in medicine in Dublin in 1844 and approached botany through passion; aware that he had not received a profound education in natural sciences, he called himself an amateur.[488] And yet it was precisely the passion for algae that first put him in contact with Sir William Jackson Hooker,[489] who allowed him to collaborate and publish in two of his most important texts.[490] Later, Harvey's study and classification activity became more intense in the years 1836-1842, when he wrote his work on Flora capiensis as colonial treasurer of Cape Town.[491] In Darwin's words, Harvey became a first-rate botanist;[492] with this work and with his return to his homeland he was assigned the nomination of Conservator of the Herbarium of Trinity College and finally the professorship of botany at Trinity in 1856.

Just as with Bentham and many others, Harvey severely attacked the methodological framework of 'Origin', but starting in the 1860s he began to modify his conclusions on Darwinian work.

The criticisms that Harvey had first developed were of a religious nature: Darwinian theories did not agree with the biblical account of Creation. In this respect, Gray's mediation, which was

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[486] From Darwin to P.H. Gosse, 5 June 1863, Darwin Correspondence Project.

[487] Summerville, 5 February 1811 – Torquay, 15 May 1866.

[488] From Hooker to Darwin, 8 June 1860, Darwin Correspondence Project.

[489] He was the Royal Professor of Botany in Glasgow.

[490] It was British Flora del 1833 and the Botany of Captain Beechy's Voyage del 1841, this latter written in collaboration with Frederick William Beechey (1796-1856) e George Walker Arnott (1799-1868).

[491] Harvey, W. H., Sonder, O. W. Flora capensis: being a systematic description of the plants of the Cape colony, Caffraria, & Port Natal (and neighbouring territories), Hodges, Smith and Co., Dublin, 1859-60.

[492] From Darwin to Lyell, 18-19 February 1860, Darwin Correspondence Project.

continually engaged in reconciling Darwinism with natural theology,[493] persuaded Harvey to relax the religious patina with which he had covered his criticisms of 'Origin'.[494] However, Harvey was convinced that Darwin's was and remained an ingenious dream but he appreciated the chapters on geographical distribution and the geological-geographical distribution successively through the ages.[495]

However, the suspicion marked Harvey's relationship with Darwin's writings for several more years.

His strongest attack on the Darwinian theory was direct, and was published in the Gardeners' Chronicle about the frigid begonia discovered at Kew.[496] Darwin had established that the

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[493] Gray 1860a

[494] From Darwin to Gray, 26 September 1860, Darwin Correspondence Project.

[495] "I have read your Darwin papers with great pleasure and profit. Almost thou persuade me to be a Grayite. I have no objetcion per se to a doctrine of derivative descent. Why should I? One mode of creation is a feasible to Almighty as another, and, as put by you, is very consonant to sound doctrine. I have had a short briefly correspondence with Darwin on the subject, but without much result one way or the other. I confess, however, since I have read the whole book, to a somewhat changed view. His latter chapters are those which have most impressed me, and particualrly that on geographical distribution, and the geological-geographical distribution successively through ages. Certainly there are many broad facts which can be read by a supposition of descent with variation. How broad those facts are, and how broad the limits of descent with variation may be, are questions which I do not think his theory affords answer to. It opens vistas vast, and so it evidently points whence, through time, light may come by which to see the objects in those vistas, but in my mind it does no more. When he passes his true deductive inference, and proceed to build further inductions on it, and to force all things to converge on one point, then I draw back, thinking with Hamlet, that there may be things in the scheme of creation which are not explained, although (they may be "dreamt of") in our philosophy. A good deal of Darwin reads to me like an ingenious dream", Harvey to Gray, 3 November 1860, in Memoirs of W. H. Harvey, M.D., F.R.S., ed. by Lydia Jane Fischer (London, 1869), 337–8, as quoted in Bellon.

[496] It was an intervention in the form of a letter that William Henry Harvey sent and was published in the Gardeners' Chronicle and Agricultural Gazette, 18 February 1860, pp. 145–6.

monstrosities could not give rise to new species,[497] however, according to Harvey, B. frigida represented just the case of a new species that had originated through the abnormal development of the existing form and could involve serious damage to the Darwinian theory.[498] But it was Hooker's response that convinced Harvey that he was wrong.[499]

This led Harvey to re-read 'Origin' carefully and to admit with Darwin himself that the common descent theory was a subject he could converge on and could be harmonized with Creation. This further change of perspective took place after he read the chapters that dealt with the succession of forms starting from geological eras, geographic distribution, embryology, and morphology.[500] However, Harvey suspended the judgment regarding the chapters concerning the link between variation and selection.

In the same year, Harvey and Darwin began to discuss evolutionary theory applied to the study of orchids,[501] and Darwin—recognizing Harvey's abilities and his disposition to study his theories without any prejudice—was convinced that he could provide important contributions to the network of botanists Darwin was building. Darwin was also convinced that to continue working with Harvey in this way would have led to his conversion.[502]

This conversion was once again the fruit of Darwinian floral biology. Darwin sent Harvey copies of his paper on a Primula and orchids presentation; never before had Harvey received explanations of the structure of flowers so sophisticated and comprehensive. Naturalists now possessed more effective means to classify species within the natural system, and after the publication of 'Orchids' their collaboration between them became constant. An example is certainly that of the orchids of genus Disa from southern Africa. After reading 'Orchids', Trimen sent Darwin a postal expedition with a manuscript and drafts that reproduced in detail observations and drawings made by studying

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[497] Darwin, Natural Selection, p. 318-321.

[498] Harvery, 1860, p.145.

[499] Hooker, Gardeners' Chronicle and Agricultural Gazette, 25 February 1860, p. 171: "Instead of this being a case which (according to Dr. Harvey) 'was not contemplated by Mr. Darwin's hypothesis,' it is one of a class which he had specially in view; it is a beautiful illustration of the truth and wisdom of his chapter on classification."

[500] Harvey to Darwin, 24 August 1860, Darwin Correspondence Project.

[501] From Harvey to Darwin, 8 October 1860, Darwin Correspondence Project.

[502] From Darwin to Hooker, 4 December 1860, Darwin Correspondence Project.

South African orchids.[503] Darwin decided to forward the material to Harvey to ask for the name and details of those orchids; the author of 'Orchids' knew of the internship that the botanist had performed in Cape Town. In answering, Harvey admitted his decision to study orchids from the point of view which he had developed in 'Orchids':

'Dear Darwin
I am right glad to find you have got so capital a worker on Cape Orchids, which I have been longing to have investigated on the spot, from your point of view. The Ophrydeæ there are almost endless in extraordinary modifications of parts and well worth study. The two now sent are comparatively simple in modifications. Both are of the large genus Disa, and I feel confident in calling them (Pl. V.) D. barbata and (Pl. VI) D. cornuta, both common near Capetown.
Tell Mr. Trimen to dry specimens of everything he draws, and to send the specimens with Nos corresponding to the drawing. Then if he finds any novelty, we shall make sure of it, and we shall also be able to name his sketches without guess. Nectariferous back sepals are quite frequent among Cape Orchids and correspondently depauperated labella. The labellum is often a mere little tongue.'[504]

At this point, the collaboration between Harvey and Darwin extended to increasingly specific botanical themes and involved a subsequent Darwinian scientific production—the one dedicated to climbing plants Ceropegia Bowkeri, C. sororia, and Ipomoea argyraeoides.[505] [506]

12.11 **James Anderson**[507]

Anderson was a Scottish gardener and orchid specialist who, after reading Darwin's orchid book, maintained a constant correspondence with the author. Recognizing Darwin's authority in the floral

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503 From Darwin to Roland Trimen, 31 January 1863, Darwin Corresponendence Project.

504 Darwin Correspondence Project, from Harvey to Darwin, 3 February 1863.

505 Harvey to Darwin, 10 November, 1864, CCD (ref.5), XII, 406.

506 Harvey to Darwin, 11 November, 1864, CCD (ref.5), XII, 406-10, this kind of considerations will be taken up by Darwin in Climbing Plants p. 24 to demonstrate how the climbing plants' ability to move may lie dormant for many generations and then reactivate in the appropriate conditions.

507 (1831/2-1899) Scottish gardener and orchid specialist.

field, Anderson—who at the time was a gardener in Uddingston, Scotland—asked Darwin for explanations about the flowers of Cattleya crispa and Dendrobium cretaceum, which had produced seed capsules without opening.[508] Darwin involved Dr Hermann Crüger, then director of the Botanical Garden in Trinidad, who had already informed him about the existence of native forms of Cattleya, Epidendrum, and Schomburghkia that had exhibited similar behaviour. According to Crüger, pollination took place by means of small ants that managed to penetrate the flower from the base of the sepals.[509] Darwin asked Crüger to carefully check whether the seeds were in good health and to send him samples. Darwin could hardly believe that the flowers remained constantly closed and the pollination took place only by means of ants. The contrivances of these orchids were manifestly adapted for pollination by means of insects, so it could be that it was a case analogous to that of violets, bluebells, and oxalis that produce at the same time flowers adapted to self-pollination and flowers that require the action of insects or other natural agents.[510] From the utilitarian point of view of Darwinian theory, if such means had also evolved in orchids, this meant that somehow they had to fulfil the task of cross-fertilization, although Crüger claimed to have observed that in some of these orchids with flowers closed Pollinche remaining in situ masses emitted pollen-tubes capable of reaching the stigma and causing fertilization.[511]

Anderson's observations also called into question the contribution of J. Scott who, working at the Botanical Garden of Edinburgh, was involved in the same phenomenon described by Crüger: Pollen-like masses that emitted pollen-tubes remaining on the orchid rostellum.[512]

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[508] From Darwin to Journal of Horticulture and Cottage Gardener, 17-24 March 1863, Darwin Correspondence Project.

[509] As we will see, Crüger will review this interpretation in a communicated paper to Linnean Society on 3 March 1864. Darwin, referring to orchids with unopened flowers or seeds intended to abort, will define Crüger's as "mere hypothesis" in From Darwin to John Scott, 24 March 1863, Darwin Correspondence Project.

[510] The phenomenon of cleistogamy had already affected Darwin in From Darwin to Daniel Oliver, 12 April 1862, Darwin Correspondence Project.

[511] Darwin 1862, p. 149.

[512] From Darwin to John Scott, 24 March 1863, Darwin Correspondence Project.

At this point, the collaboration between Anderson and Darwin became very close and had mutual influences on the development of the orchid book and on the subsequent research of the Scott. On the occasion of one of the many epistolary notifications with sample exchanges, Anderson wrote:

'Enclosed is one of the seed capsules of the Dendrobium cretacæum of which I wrote in the Journal for your inspection.[513] It has taken fully twelve months to mature. You may depend upon this act of fertilization being carried on within the floral envelope; and I should like to know the results of your investigation and opinion.' [514]

Anderson's scientific testimony regarding Cattleya now describes him as perfectly integrated into the network of Darwinian botanists, intent on involving other scholars, experimenting based on Darwin's indications, and waiting for his further interpretations from which to draw inspiration:

'I enclose for your inspection a few of the seeds of the abortive Cattleya crispa flower as well as a few of Lælia cinnabarina from a perfect flower without manipulation; both of which have been ripe for the last two months. The Den. Cretaceum pods are yet unripe but when they are so I shall submit a few of the seeds for your inspection for I look upon them with more interest having watched the anomalous proceeding with more interest than the Cattleya flower, some of the phases in the progress of which not being so closely watched, as it being the first instance of the kind that came under my cognisance I supposed it would be an entire failure. I have also sent pkts. to Mr Gosse and I hope you will "report progress".
I am exceedingly glad to embrace this opportunity of bearing testimony to your unwearied and painstaking abilities in going so minutely into what may appear at first a more difficult problem than what it really is.'[515]

12.12 **Charles Grant Blairfindie Allen**[516]

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[513] The reference is to a notice by Anderson in the Journal of Horticulture, 17 March 1863, pp. 206-208

[514] Darwin Correspondence Project, from Anderson to Darwin, 18 June 1863.

[515] Darwin Correspondence Project, from Anderson to Darwin, 1 April 1863.

The Canadian anthropologist and scientific writer was educated at Oxford beginning in 1876 and decided to extend Darwinian theories into two books: ‘Physiological Aesthetics’[517] and ‘The Colour Sense: its Origin and Development’.[518]

Allen read ‘Orchids’ thoroughly and called it wonderful and fascinating. He described it as the capillary work on every kind of detail; he praised the marvellous patience of which Darwin had become a great master and the depth of the research that characterized every aspect of his work. Allen said all of that convinced him to accept the explanation of natural selection with regard to fertilization through contrivances, adding, ‘These, and a hundred other similar instances, were all carefully considered and described by the great naturalist as the by-work with which he filled up one of the intervals between his greater and more comprehensive treatises’.[519]

The evolutionary relationships between insects and flowers contained in ‘Orchids’ had for Allen, above all, the function of responding to objections to the main theory contained in ‘Origin’. However, Allen, once converted, began to apply a Spencerian synthesis to the physiology of aesthestic feelings. In ‘Physiological Aesthetics’, he proposed an explanation based on natural selection and sexual selection for the origin of aesthetic judgments and feelings, which were then shared with other life forms[520] and described in materialistic terms.

In ‘The Colour Sense’, Allen also took up the theory of the common descent underlying the inheritance of the ability to discriminate colour from ancestors who ate fruit and, in turn, inherited this ability from insects and birds. From here, Allen extended a capacity that insects had initially developed to search for food, the explanation of which he had read in ‘Orchids’, to the development

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[516] February 24, 1848 in Kingston - October 25, 1899 in Hindhead: he taught at Brighton College between 1879 and 1871 and then moved to Jamaica to teach at Queen’s College. Returning to England in 1876, he devoted himself to publishing popular works, literature and scientific essays and articles on flowers and insect perception.

[517] Allen, 1877.

[518] Allen, 1879.

[519] Allen, 1885, p. 128.

[520] Allen 1877, p. 9.

of an aesthetic sense that called into question sexual selection,[521] [522] including after the reasoned reading of descent.

In this way, Allen reached the same philosophical conclusion as Darwin, namely that the colour of the flowers did not consist in a divine creation realized for the enjoyment of human beings, but through a forcing in the interpretation of the data provided by 'Orchids'. Colours, although the result of the action of natural selection[523] to respond to the reproductive needs of flowers and insect food, were self-generated.

It was a conversion that, starting from the same Darwinian axioms as the law of Darwin-Knight,[524] reached a completely original development. Therefore, Allen started from the botanics of Darwinian 'Orchids' and applied the absorbed conclusions to the aesthetic philosophy in a way that Darwin had not imagined. The author of 'Origin' had recognized the danger of a consideration of the beauty of plants in terms of natural theology:

'The foregoing remarks lead me to say a few words on the protest lately made by some naturalists against the utilitarian doctrine that every detail of structure has been produced for the good of its possessor. They believe that many structures have been created for the sake of beauty, to delight man or the Creator (but this latter point is beyond the scope of scientific discussion), or for the sake of mere variety, a view already discussed. Such doctrines, if true, would be absolutely fatal to my theory. I fully admit that many structures are now of no direct use to their possessors, and may never have been of any use to their progenitors; but this does not prove that they were formed solely for beauty or variety'.[525]

If Darwin did not feel like entering into the specific treatment of a utilitarian conception of beauty in the first edition of 'Origin' in 1859, that changed with the fourth edition in 1866. In fact, after research on man and sexual selection and support from the pollination research of 'Orchids' and of plant physiology, at this point he felt confident enough to affirm that the marvellous colours of

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[521] Allen 1879, p. 4-120-122.

[522] Allen 1877, p. 156-157; p. 181

[523] Allen 1877, p. 61.

[524] Allen 1877, p. 39.

[525] Darwin, 1859, p. 151.

flowers and fruits, in contrast with the constant colouring of the foliage, are an adaptation to allow insects and birds to see them,[526] visit them, fertilize them, and spread the seeds of the fruits. That conclusion was also supported by Wallace,[527] who, however, attacked the Darwinian theory of sexual selection, forcing Allen to a further interpretation of the same that avoided the difficulties highlighted by Wallace.[528]

12.13 **Daniel Oliver**[529]

During Hooker's work into classification and study of the Kew collection that grew each year thanks to the dispatch of numerous samples from all over the world, he asked Oliver to carry out a series of experiments on cross-fertilization in plants on the direct inspiration of the Darwinian research on orchids. Oliver succeeded in surprising Darwin not only for his experimental ability but also for his profound knowledge of botany. Their collaboration became even closer when it came to experimenting on climbing plants; it proved to be a valuable resource in terms of theoretical notifications and exchange of samples for the duration of their scientific production.

Precisely because of Oliver's extraordinary knowledge, sober and cautious experimentation, and for the mental discipline he manifested in the classification field, Darwin proposed him for the chair of botany then vacant at the University of London.[530]

In terms of floral morphology, Oliver recognized Darwin's deep ability to understand,[531] asking him for news and interpretations of insects' fertilization of flowers.

He had accepted the Darwinian theory of contrivances as adaptations to allow insects to fertilize, and since 1862 the two were working together on Catasetum.[532] Sprengel represented for both the starting and comparing point whenever it was a question of examining the genres that need insect fertilization competition.[533] What interested Oliver was, above all, the explanatory capacity of the

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[526] And Allen takes up these theses in Allen 1877, p. 124-146-147-157-

[527] Wallace, 1882, p. 38.

[528] Allen, 1877, p. 155-

[529] 1830-1916, keeper of the herbarium and library at Kew from 1864 till 1890.

[530] Dal 1860 rimase porfessore di botanica sino al 1888.

[531] From Oliver to Darwin, 14 April 1862, Darwin Correspondence Project.

[532] From Darwin to Oliver, 12 April 1862, Darwin Correspondence Project.

[533] From Darwin to Oliver, 15 April 1862, Darwin Correspondence Project.

doctrine of homologies[534] and the dimorphism in orchids. In the conclusion of his review for dimorphic condition in Primula,[535] Oliver revealed that he waited for a discussion of dimorphism based on the results obtained in 'Orchids'.

Darwin, for his part, involved Oliver in the analysis and in the new classification of the forms of Catasetum together with Crüger and in the fertilization modalities of Coryanthes, always with the descriptions of the director of the botanical garden of Trinidad.[536] Oliver therefore knew both the potential of the Darwinian theory in classification, and the role of the orchid book in the battle against teleology and creationism.

On the other hand, Oliver introduced Darwin to the position of von Mohl regarding homologies,[537] and their discussion of the evolutionary development of leaves continued for many years.[538]

Darwin's trust in Oliver was such that he was able to correct Fritz Müller's scientific literature on some climbing plants in his place. Although Darwin thought it worthy of being sent to the Linnean Society, he wanted the technical opinion of a botanist and saw that Hooker was ill and away from Kew; the only one with technical knowledge and sufficient capacity to deal with evolutionary arguments developed within the circle of Darwinian botanists turned out to be Oliver.[539]

Given the collaboration between the British naturalist and the botanist, Oliver's was a conversion that took place partially after 'Origin' and definitively with the reading of 'Orchids'.

12.14 **John Lubbock**[540]

Allen had already seen in Lubbock one of the most important continuators of Darwinian research on floral morphology according to the pollination relationships mediated by the presence of insects,[541] following in line with Müller, Delpino, Axel, and Hildebrand.

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[534] From Oliver to Darwin, 12 March 1864, Darwin Correspondence Project.

[535] Darwin, 1862.

[536] Fron Darwin to Oliver, 17 February 1864, Darwin correspondence Project.

[537] From Oliver to Darwin, 13 July 1864, Darwin correspondence Project.

[538] From Oliver to Darwin, 12 March 1864, Darwin correspondence Project.

[539] From Darwin to Oliver, 20 October 1865, Darwin correspondence Project.

[540] 1834 - 1913, first Baron Avebury, fourth baronet: besides being a scientist he was also involved in politics, archeology and was a philanthropist. In 1878 he became trustee of the British Museum and from 1888 to 1892 he was president of the London Chambers of Commerce.

Lubbock also absorbed and worked on the research indications that Darwin set in his botanical production. He was a friend of Darwin, and in the publication of his popular 'On British Wild Flowers Considered in Relation to Insects',[542] Lubbock recognized the precedence of other great masters such as Axel, Bennett, Delpino, Hildebrand, Hooker, and F. Müller. Above all, however, he acknowledged having achieved an inexhaustible debt with each of the pages written in the works of Darwin, Sprengel, and H. Müller.[543]

Lubbock appropriated the Darwinian style and illustrative method with the reproduction of the long-styled form diagram of Lythrum salicaria,[544] the labellum of Orchid mascula,[545] and the labellum of Catasetum saccatum.[546] After underlining the primacy of Sprengel in having spotted the relationship between the structure of the flower and the importance of insects in pollination, Lubbock recalled that Darwin deserved credit for having demonstrated that the shape and colours of wildflowers are due to a sort of unconscious selection made by insects.[547]

According to Lubbock, the importance of Darwin must be sought in the value of his observations: He was the only one to understand that the structure of the flower was an adaptation to attract insects,[548] that the visit of the insects was fundamental to transport the pollen from the stamens of one plant to the stigmatic surfaces of another,[549] that if a flower is fertilized with pollen from another plant the seeds will be stronger and more vigorous than they could be if the flower self-fertilized,[550] that if a plant is fertilized by the wind it will never reveal a gained-colour corolla,[551]

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[541] Allen, 1885, p. 161-162.

[542] Lubbock, 1882.

[543] Lubbock, 1882, p. VIII.

[544] Lubbock, 1882, p. 103.

[545] Lubbock, 1882, p. 171.

[546] Lubbock, 1882, p. 182.

[547] Lubbock, 1882, p. 2.

[548] Lubbock, 1882, p. 3.

[549] Lubbock, 1882, p. 4.

[550] Lubbock, 1882, p. 7.

[551] Lubbock, 1882, p. 8.

that irregular flowers almost always seem to be fertilized by insects,[552] that no plant invariably self-fertilizes itself,[553] and that there are three forms in Lythrum.[554]

Lubbock finds that the foundation of Darwin's genius rests in his inexhaustible ability to persevere in the search for meanings that adaptations covered within the flower economy;[555] in the infinite series of careful and elaborate experiments;[556] in the opening to scientific disputes that led him to repeat the experiments, observing the same phenomenon from renewed perspectives;[557] and in an effort not to limit himself to an anatomical description but to produce an account of all of the functions of the flower organs within ecological relationships.[558]

Lubbock received a copy of 'Fertilisation of Orchids' in the afternoon of 15 May 1862[559] and began to read it immediately. Later, he called it an admirable[560] and charming work.[561] Although he never went too far into the theory of natural selection in his botanical writings, Lubbock remained fully captured by Darwinian works on orchids and other plants, so much so that he continued to require inspiration and approval from the author of these works throughout his subsequent scientific production.

The moment of maximum public reverberation of the Darwinian influence through the conversion of Lubbock was the presidential address that the latter pronounced in 1881 for the British Association for the Advancement of Science. On this occasion, Lubbock did not forget to insist on the Darwinian interpretation of the role of the insects in the fertilization of flowers as well as the entire process that had caused to generate their form and their adaptations.[562]

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[552] Lubbock, 1882, p. 9.

[553] Lubbock, 1882, p. 29.

[554] Lubbock, 1882, p. 40.

[555] Lubbock, 1882, p. 39.

[556] Lubbock, 1882, p. 77.

[557] Lubbock, 1882, p. 91.

[558] Lubbock, 1882, p. 101.

[559] From Lubbock to Darwin, 15 May 1862, Darwin Correspondence Project.

[560] Lubbock, 1882, p. 170.

[561] Lubbock, 1882, p. 181.

[562] Lubbock, 1881.

12.15 **John Scott**[563]

Admiration for Darwin's work on orchids began with communications concerning Acropera;[564] the naturalist's interpretation allowed the botanist to correct his mistakes not only regarding the species in question but also regarding Catasetum.[565]

The gratitude, the pressing questions, and the passion with which Scott reciprocated the theoretical and descriptive notifications of Darwin configured their relationship as that between teacher and student. However, Scott always manifested the presence of strong objections to the theory of natural selection, without ever entering the particular.[566]

Despite the differences in views at the theoretical level, Darwin was interested in following Scott also from a formative point of view. He read Scott's papers and gave him advice not only in terms of content but also in style. Darwin attempted to present the corrections as a person with more experience provides a next-generation botanist to make his paper sentences more effective.[567]

Darwin highly esteemed Scott's observational ability and their collaboration was quite fruitful, both because he asked Scott to continually submit to him the criticisms he had about natural selection and because the work on orchids interested both. This shared interest was so great that Darwin asked Scott to engage in experiments on Gymnanedia tridentata to report useful conclusions on what had now become a case study that also involved Asa Gray.[568]

After the publication of 'Orchids', Scott increased his studies and experiments on orchids to the point of capturing support from Darwin, who recommended him to Hooker for a job at the Calcutta botanical garden. Although Balfour had offered him a place at the Cinchona plantation in India, Scott preferred to follow the path opened to him by Darwin where he would also find another important Darwinian botanist named Anderson.[569] From this moment on, Scott became a devoted

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[563] Scottish botanist (1836-1880) keeper of the Royal Botanic Garden of Edinburgh in 1859 and from 1864 manager of Calcutta botanical garden.

[564] It was a species that as we will see will become a case study involving also Delpino.

[565] From Scott to Darwin, 12 November 1862 and From Scott to Darwin, 15 November 1862, Darwin Correspondence Project.

[566] From Scott to Darwin, 20 November-2 December 1862, Darwin Corresponedence Project.

[567] From Darwin to Scott, 11 December 1862, Darwin Correspondence Project.

[568] From Darwin to Scott, 3 December 1862, Darwin Correspondence Project.

[569] From Scott to Darwin, 3 June 1863, Darwin Correspondence Project.

experimenter of all that Darwin needed to know about orchids in India. However, the conversion had already taken place with the orchids; Scott confidently admitted to Darwin that in the Edinburgh botanical garden his Darwinian positions sounded unpalatable. Despite this, '… I, having a strong conviction of its truthful teachings, would not on account of such dogmatic prejudices—for I cannot think they are aught else—sacrifice the "integrity of my own mind" '.[570]

The passion for orchids led Scott to write an abstract for a paper on the subject; he had it reviewed by Darwin and then published in the Gardeners' Chronicle on 13 June 1863.

After Darwin's corrections, Scott wrote the paper that was printed in June of the same year; he did not forget to thank Darwin for helping with the abstract and he was flattered by the expectations that the naturalist and Hooker had demonstrated to nurture in the comparisons of this publication.[571]

Both in the paper and in the abstract, Scott revealed that he shared Darwin's ideas on the sterility of orchids and the species issue. Since the paper was presented to the Edinburgh botanical society, the reaction to his Darwinian positions compromised a possible future career in that city. It was a conclusion that Hooker had anticipated and that prompted the director of Kew and Darwin to work together to locate a professional solution where Scott could continue his studies.[572]

From then on, Scott asked Darwin to review many botanical papers before their publication, and his interpretations of 'Orchids' and reviews on the small treatise continued.[573]

Their collaboration on orchids covered a significant period of time and involved several species: hybrid orchids, Catasetum,[574] Acropera,[575] and sterility.

Scott became a pupil and protégé of Darwin, and what the naturalist appreciated about him were precisely those characteristics that many of Darwin's critics saw missing in 'Origin': remarkable powers of observation, accuracy, indomitable perseverance, knowledge, modesty, and reliance on his own judgment.[576]

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[570] From Scott to Darwin, 3 June 1863, Darwin Correspondence Project.

[571] From Scott to Darwin, 16 June 1863, Darwin Correspondence Project.

[572] From Darwin to Scott, 11 June 1863, Darwin Correspondence Project.

[573] From Scott to Darwin, 3 March 1863, Darwin Correspondence Project.

[574] From Scott to Darwin, 1-11 April 1863, Darwin Correspondence Project.

[575] From Scott to Darwin, 18 February 1863, Darwin Correspondence Project.

[576] From Darwin to Scott, 10 June 1864, Darwin Correspondence Project.

Scott lost his job in Edinburgh due to his alignment with Darwinian conclusions,[577] and Darwin continued to offer him his support, not only political and scientific but also pecuniary.[578] After several hardships, on 21 July Scott wrote to Darwin that he had reached Calcutta for his new job.[579] At that point, the collaboration between the two became multipurpose, from the study of the pollination of orchids to the anthropological, cultural, and geographical descriptions of the new populations that Scott began to attend.

12.16 **John Traherne Moggridge**[580]

Despite his death at a young age, Moggridge was part of the new generation of botanists who had inherited and adopted the scientific baggage that Darwin had transmitted through his botanical works.

He was also an entomologist, arachnologist, and scientific illustrator. It was precisely in this capacity that he began an exchange of letters to Darwin, with drawings attached, that lasted until his premature death. The letters reveal how Darwin appreciated Moggridge's precision as well as the richness of his detailed explanations of the contrivances of orchids and insects involved in pollination.[581]

It is difficult to find a source of information more consulted by Darwin; he turned to Moggridge to learn about pollination methods in O. longibracteata, the convergence of pollen,[582] and the behaviour of X. Violacea in fertilizing it.[583] Darwin also sought information about the falling out of the pollen masses in Ophrys scolopax[584] and asked for an explanation of Moggridge's theory that Ophrys scolopax, aranifera, arachnites, and O. apifera were all varieties of the same species O.

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[577] From Scott to Darwin, 14 April 1864, Darwin Correspondence Project.

[578] Scott will not be the only one to whom Darwin will offer money: a similar thing had already happened with the captain of the Beagle Fitzroy.

[579] From Scott to Darwin, 21 July 1865, Darwin Correspondence Project.

[580] British botanist (1842-1874) fellow of the Linnean Society of London.

[581] From Darwin to John Traherne Moggridge, 19 June 1864, Darwin Correspondence Project.

[582] Fenomeno che Darwin riporta in Darwin 1862, p. 143 e Darwin 1877, p. 26-27.

[583] Fenomeno che Darwin riportò in Darwin, 1862, p. 143 e Darwin 1877, p. 27.

[584] What Moggridge wrote in Moggridge 1864 on this subject was reported in Darwin 1862 p. 145 and Darwin 1877 p. 52.

insectifera.[585] Darwin also continued to spur him on to present his drawings and descriptions to the Linnean Society for publication.[586]

For his part, Moggridge did not hide the inspirational debt he had accumulated while reading ‘Orchids’, a book he said had opened for him a ‘fresh and most delightful source of occupation.’[587] The two continued to exchange samples of orchids[588] and seeds,[589] notifications on cultivation methods,[590] and papers,[591] such that Darwin felt in scientific harmony with the young botanist who was eager to forward letters containing his various interpretations of the same phenomenon, as in the case of O. apifera.[592]

The scientific collaboration resulted in personal friendship,[593] and over the years, Moggridge increasingly demonstrated his mastery of the Darwinian investigative method in the description and study of orchids.[594] His contributions also proved important in evaluating the case studies that involved international botanists such as Delpino[595] in the case of Ophrys aranifera; consequently, the role of Moggridge proved to be fundamental both for the conclusions of the second edition of ‘Orchids’ and for the international diffusion of Darwinian theories.

Even when the fruitful collaboration between the two shifted to themes concerning climbing plants, the passion for Darwin’s writings on orchids and notifications on these themes never failed.[596]

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585 Darwin, 1877, p. 58-59.

586 From Darwin to Moggridge, 19 June 1864, Darwin Correspondence Project.

587 Moggridge, 1864, p. 256.

588 From J.T. Moggridge to Darwin, 27 December 1865, from Moggridge to Darwin, 10 May 1866, from Moggridge to Darwin 21 May 1866, Darwin Correspondence Project.

589 From Darwin to Moggridge, 13 November 1866, from Moggridge to Darwin 3 August 1866, Darwin Correspondence Project.

590 From J.T. Moggridge to Darwin, 15 February 1862, Darwin Correspondence Project.

591 From Moggridge to Darwin, 12 July 1873, Darwin Corresponendence Project.

592 From Darwin to Moggridge, 13 October 1865, Darwin Correspondence Project.

593 From Moggridge to Darwin, 25 May 1866, Darwin Correspondence Project.

594 From Moggridge to Darwin, 22 April 1867, Darwin Correspondence Project.

595 From Moggridge to Darwin, 12 Decemeber 1869, Darwin Correspondence Project.

596 From Moggridge to Darwin, 16 September 1869, Darwin Correspondence Project.

12.17 **Mordecai Cubitt Cooke**[597]

Cooke was a botanist animated by a boundless passion for plants and the producer of an extraordinarily extensive bibliography, which allowed him to obtain a master of arts degree from St. Lawrence University,[598] a master of arts from Yale University,[599] and a doctorate from New York University. He also collaborated with the aforementioned 'Hardwicke's Science-Gossip: An Illustrated Medium of Interchange and Gossip for Students and Lovers of Nature'.[600]

In his 'Freaks and Marvels of Plant Life,[601] Cooke demonstrated that he had assimilated the Darwinian theory proposed and illustrated in all of his botanical publications. The capacities of patient observer and collector of facts from which to elaborate a theoretical generalization were recognized and praised as an example for all naturalists; once again, the observance of the ethical canons of the Victorian philosophy of science convinced the readers of Darwin!

In his analyses, Cooke accepted a survival function determined by the structures and behaviour of plants, and he also mentioned several times the importance of natural selection in guiding the development of structures and behaviours. And yet there are no defenders of this explanatory principle: Natural selection is still interpreted in teleological terms, as a divine design is always at work and Darwinian explanations do nothing but describe tools that the author of all of the botanical wonders succeed in putting in place thanks to its power and benevolence.[602]

In particular, Cooke focused on the explanations given by Darwin about the structure and function of the labellum,[603] which he accepted along with all other conclusions concerning climbing plants and insectivorous plants, always in terms of debt to the Darwinian experiments. In Cooke's words,

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[597] Horning, 12 July 1825-Southsea (Hants), 12 November 1914: in 1860 became Curator of Indian museum for the Indian office and was there till 1879. In same years made some lectures of natural history at Holy Trinity National School in Lambeth and in 1862 built the Society of Amateur Botanists. He got the Victorian Medal of Honour from the Royal Horticultural Society in 1902 and the Linnean Medal from the Linnean Society of London in 1903.

[598] In 1870 thanks to his work on mushrooms.

[599] In 1873.

[600] From 1865 to 1893.

[601] Cooke, 1882.

[602] Cooke, 1882, p. 21.

[603] Cooke, 1882, p. 237.

they had solved more than one mystery thanks to the discovery of details previously not considered. Cooke also recognized the Victorian tenacity of the author of 'Orchids' to carry out experiments even in the most adverse conditions,[604] day and night,[605] for the lucid and exciting narrative style.[606] Above all, Cooke explicitly embraced the utilitarian explanation for the function of the orchid's shape and structure by linking the need for such adaptations to the understanding that the reader may have if he possessed detailed depictions that actually took place in 'Orchids'.[607] He believed the reading of this book and the combination of images and descriptive captions could no longer leave doubts about the functions of the characteristics of the flowers which, for their extraordinary abilities, were called the 'monkeys of the vegetable kingdom'.

Although Cooke tended to expunge the case from the function of the adaptations and assign it a finalistic meaning, a careful analysis of Darwin's botanical works left their mark on him and on his publications. Although Cooke did not fully accept the philosophical consequences of Darwinian theories, he recognized the conclusions as original starting points to explore new realities in the light of new knowledge. Once again, the Darwinian method had reached the heart of another scientist.

12.18 **John Ellor Taylor**[608]

Taylor was a British botanist and geologist who worked in science education[609] and cultural formation.[610] He became a curator of Ipswich Museum from 1872 to 1893 where he gave an annual free lecture series in natural sciences.

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[604] Cooke, 1882, p. 143.

[605] Cooke, 1882, p. 154.

[606] Cooke, 1882, p. 165.

[607] Cooke, 1882, p. 268.

[608] September 21 1837- Spetember 28 1895.

[609] He became editor of the national popular science journal Hardwicke's Science Gossip Magazine, he gave lessons and published several important books like: *The Sagacity & Morality of Plants: A Sketch of the Life & Conduct of the Vegetable Kingdom* (Creative Media Partners, LLC, 2018) or *Half-Hours at the Seaside, Half-Hours in Green Lanes* (London, W.H. Allen & Co., 1884).

[610] He leaded the Ipswich Scientific Society in 1875 and founded the equivalent Society in Norwich in 1870 and was a co-founder of the Norfolk Geological Society.

Taylor's reaction was controversial: He fully accepted Hooker's definition of Darwin's botanical philosophy.[611] His 'Flowers: Their Origin, Shapes, Perfumes, and Colours',[612] dealing with Darwin's work on plant science, accepted the new Darwinian philosophy of flowers, which pointed out that flowers were created for their own survival. Despite this, Taylor finally interpreted the descriptions contained in the Darwinian botanical books as a tradition of natural theological understanding of nature. He believed that the treatment of botanical science exclusively in terms of secondary causes was insufficient; the teachings that should have been given to botanists and naturalists of the new generation regarding plants, flowers, and insects belonged to a higher spiritual level and required more respect and admiration for the wisdom of the Creator.

Even in 'The Sagacity and Morality of Plants',[613] Taylor forced the conclusions of 'Origin' by establishing that a description of the plant world in Darwinian terms, although correct, is not complete: It is not possible to underestimate or, even worse, forget the feeling of love and the infinite teleological wisdom underlying divine creations.

And despite this defence of the divine finality, Taylor authentically recognized the role of the Darwinian theory and wrote about it publicly, earning gratitude from Darwin.[614] 'Natural history has received a similar impetus under the Darwinian theory that astronomy did under the older Copernicus',[615] Taylor wrote in his article for Westminster Review regarding the distribution of plants and animals from a geological point of view.

Taylor's change in perspective can be defined as a half-conversion. The scientific methodology and the botanical results convinced him in full, as well as the need for a theoretical theorization that could provide an explanation able to link together a quantity of phenomena that at first sight were heterogeneous. However, Taylor was much less unanimous in pushing himself to the extreme consequences of the philosophical implications related to the theory of evolution; to the meaning of rudiments, vestiges, and reversions; and to the theory of natural selection. He feared an atheistic

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[611] From Hooker to Darwin, 11 April 1857, Darwin Correspondence Project.

[612] Taylor, J. E. 1885.

[613] Taylor, J. E. 1884, p. 303.

[614] From Darwin to Taylor, 13 January 1872, Darwin Correspondence Project.

[615] Taylor, 1872, p. 29.

drift of scientists and always fought to reconcile Darwinian theories with a 'clearer conception of Creational Power and Wisdom.'[616]

12.19 **Thomas Frederic Cheeseman**[617]

The influence of 'Orchids' in Cheeseman's analysis and interpretation work began when the New Zealand botanist sent Darwin a copy of his article 'On the Fertilization of the New Zealand Species of Pterostylis'.[618]

The latter recognized its value, but above all recognized in the explanation given by Cheeseman an analogy with a case he had dealt with in depth in 'Orchids'. The pollination of Pterostylis offered Darwin the opportunity to grasp a comparison with what was written on Cypripedium:[619] Small bees entered the top of the flower and, unable to escape by this route, were forced to exit via the small slits near the anthers and stigma. Darwin referred to his reinterpretation after reading the H. Müller monograph, but the British naturalist and New Zealand botanist were already working on orchids for some time and were exchanging opinions and experimental modalities in the wake of what was written in 'Orchids'.[620]

However, Cheeseman's paper revealed a deep bond with 'Orchids'. Inspired by Darwinian interpretations of those flowers, Cheeseman not only decided to devote time and study to orchids and to the description of Pterostylis contrivances, but also to explore the territories to which Darwin could not travel with profound scientific regret.

It was Darwin's claim that he could not observe any irritable labellum orchid[621] that prompted Cheeseman to describe in detail the pollination mechanism dependent on this irritability and send the model to Darwin himself. [622]

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[616] Taylor, 1885, p. viii.

[617] New Zeland botanist (1846-1923) dal 1874 secretary of Auckland Institute and Curator of the Auckland Museum.

[618] Cheeseman, 1872.

[619] Darwin, 1862, p. 271-5, although the author will adopt another explanation closer to H. Müller's interpretation (1873, p. 76) in 2nd ed. a p. 230-1.

[620] From Darwin to Cheeseman, 9 September 1873, Darwin Correspondence Project.

[621] Darwin, 1862, p. 172.

[622] From T.F. Cheeseman to Darwin, 27 June 1873, Darwin Correspondence Project.

Cheeseman asked Darwin to study and confirm his conclusions on Pterostylis trullifolia, which were then added by the British in the second edition of 'Orchids'.

It was a partnership that began and was fuelled over time by studies on orchids, as Cheeseman offered to send Darwin any knowledge in his possession on this topic.[623]

The correspondence between Darwin and Cheeseman lasted for more than six years and covered the fertilization of the orchids almost entirely. In the research, Cheeseman was often pushed to find confirmations of Knight-Darwin's law, and Darwin quoted in 'Orchids' his conclusions and findings on the role of insects in many of the New Zealand orchids.

Altogether, it is possible to state that Cheeseman contributed to and influenced in an important way the content of the second edition of 'Orchids'. The first edition of the book constituted a manual of experimental science that regulated all the experiments that the botanist carried out in his career dedicated to fertilization and floral morphology.

A relationship of mutual influence between the two was maintained and enriched thanks to correspondence. [624]

12.20 **Hermann Müller**

Müller emerged as the leading researcher on the fertilization of flowers through the competition of insects, and with the publication of his treatise[625] he demonstrated that he had developed in the most profound way the research approach that began with 'Orchids', intransigently rejecting Delpino's finalism. The treatise, which became a classic inspiration for many subsequent research studies, inherited not only the contents of 'Orchids' but also the patient and precise methodology[626] of listing all of the numerous visits of insects to plants.

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[623] From T.F. Cheeseman to Darwin, 27 June 1873, Darwin Correspondence Project.

[624] Mac Leod and Rehbock, 1994, p. 182.

[625] Müller, 1883.

[626] Delpino defined it a "precisione veramente germanica" from Delpino to Darwin, 18 Giugno 1873, Darwin Correspondence Project.

By December 1862, Hermann Müller had already accepted Darwin's main conclusions about evolution. The influence was exerted both by the reading of 'Origin' and by the publication of 'Orchids'.[627]

Müller and Darwin then maintained a regular correspondence relationship, sharing their observations on orchids. Müller's brother Fritz recognized that the researcher's understanding of the relationships between pollinators and flowers could provide new original contributions in the wake of Darwin, writing to him about 'a subject for which You would be particularly well qualified, having been as much occupied with entomology as with botany. For there is certainly still an immense amount to be discovered.'[628]

After reading Darwin's book on orchids, Müller remained focused on applying the Darwinian theory to his observations on flowers and pollinating insects,[629] and the result was published in 1869.[630] Müller's careful study of flower shapes as well as the behaviour and structure of insects proved that the Darwinian generalizations were correct.

Darwin was impressed by the amount of work that Müller had dedicated to his treatise. His admiration was not only for the many original observations contained therein, but also for the tireless ability of the German to describe insects at work in their countless visits to flowers and to note explanatory references. The British also appreciated one of the few historical introductions to the argument that he started from Sprengel and came to give an account of the major contributions offered by Darwinian botanists.[631] In it, Müller recalled that 'Orchids', 'freed from the fundamental flaw of Sprengel's theory and permeated by Darwin's acute reasoning and observation, was a model for the study of the forms of the flowers, and it gave a powerful impetus to further research based upon Sprengel's work.'[632]

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[627] Fritz Müller to Hermann Müller, 16 December 1862, *Briefe*:40-1. In this letter Fritz shows himself really delighted for the conversion of Hermann to Darwin's views.

[628] From Fritz Müller to Hermann Müller, 1 July 1866, West, 2003.

[629] From H.Müller to Darwin, 8 March 1870, Darwin Correspondence Project.

[630] Die Anwendung der Darwinschen Lehre auf Blumen und blumen-besuchende Insekten, H. Müller, 1869.

[631] From Darwin to H.Müller, 5 May 1873, Darwin Correspondence Project.

[632] Müller, 1883, p. 6-7.

According to Müller, the main lines of research that Darwin had developed were the demonstration of Knight-Darwin's law, the direct observation of the action of pollen from the same and from another flower, and the study of the dimorphic and trimorphic plants that shed light on the little-known question of hybridization.

In each of these three fields, Darwin had been successful, in the German botanist's opinion, and had inspired the work of other illustrious colleagues such as Hildebrand, Delpino, Axell, and Fritz Müller, who had discovered important new principles while walking in the footsteps of the British naturalist.[633]

The influence of 'Orchids' on Müller was decisive and can also be seen in the dispute between Darwin and Delpino on the interpretation of nectarless orchids. Darwin never directly attacked teleology, but aspects of his theory—such as his ecological conception of the struggle for survival, the utilitarianism of species, and the intelligence of insects—were assimilated and interpreted by the German as incompatible with finalism, so much so that the German supported Darwin and openly criticized teleology and Delpino.[634]

Despite the historical difficulties that Müller faced with the German government, Darwin never failed to lend his support.[635] Müller's research was so well-developed that the author of 'Orchids' decided to write the preface to the German botanist and entomologist's treatise. Darwin also chose it as a continuation of his research in Germany, preferring Müller to Haeckel.

12.21 **Friedrich Hildebrand**

After reading 'Orchids', Hildebrand offered to translate it into German.[636] His research on orchids that was started on a Darwinian inspiration led him in two directions—to publish an original paper and to test the Darwinian conclusions.

In the first case, he sent Darwin a paper that the British author greatly appreciated and sought to get published;[637] in the second, Hildebrand collaborated with Treviranus in applying the Darwinian theory to explain the structure of most German orchids.

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633 Müller, 1883, p. 11.

634 Müller, 1869, p. 140-159, 228-240 and 1883, p. 421-425.

635 Darwin tried to support in an economic way also Fritz Müller who lost much of his material and results due to natural causes.

636 From Hildebrand to Darwin, 14 July 1862, Darwin Correspondence Project.

The results of this second attempt[638] constituted the premise for one of Hildebrand's treatises, while the observations on Ophrys apifera, Catasetum, and Acropera induced Darwin to modify some of his results in the second edition of 'Orchids'.[639]

From that moment on, Hildebrand was a reference point for Darwin, not only for theoretical notifications but also for the exchange of samples and sending of papers.

Thanks to the influence of Darwin, Hildebrand was able to demonstrate that many contrivances that had been explained by Sprengel in terms of self-fertilization, such as Aristolochia clematitis,[640] were actually adaptations for cross-fertilization.[641] This type of analysis was applied from German to many species that Sprengel had not taken into consideration, while Darwin's experiments were applied to Primula sinensis, Pulmonaria officialis, and several species of Oxalis.[642] This concluded the validity of the Knight-Darwin principle and led to the discovery that artificial self-fertilization also means greater sterility.

But it was the experiments carried out on Corydalis cavea that demonstrated that self-fertilization, even in plants where it is widespread, does not provide any useful result minimally comparable to the results obtained through the fertilization of flowers belonging to separate plants. What until then represented a more-than-legitimate objection to Darwinian studies and the principle just mentioned was defused by Hildebrand, who in 1867, published his treatise 'Geschlechter Vertheilung bei den Pflanzen'. [643]

Another important result that the German achieved on the basis of the Darwinian observations on orchids looked at the pollination mechanism in Salvia. Hildebrand was able to demonstrate unequivocally that the cells of the anthers had gradually been transformed into mobile support bases thanks to the connective tissue,[644] which in the course of evolution had allowed various stages of

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[637] From Darwin to Hildebrand, 28 July 1863, Darwin Correspondence Project: si tratta di Hildebrand 1863.

[638] From Hildebrand to Darwin, 16 July 1863, Darwin Correspondence Project.

[639] Darwin, 1877, p. 153.

[640] Sprengel, 1793, p. 418-429.

[641] From Hildebrand to Darwin, 23 October 1866, Darwin Correspondence Project.

[642] H. Müller, 1883, p. 11.

[643] Hildebrand, 1867.

[644] The portion of the filament connecting the two lobes of the anther.

movement to anthers.[645] This result confirmed the Darwinian notion of conversion of organs to a new function that was born in 'Origin'[646] but was fully developed in 'Orchids'. Indeed, it was the Darwinian indications about the genus Catasetum that inspired Hildebrand's research, which carried on tests of what have been defined in previous chapters as a change of function over time and which is more commonly included in the concept of exaptation, the philosophical consequences of which have already been seen.

Hildebrand's contribution was therefore vital for the circle of Darwinian botanists; his confirmations and the widening of frontiers that his works allowed were able to transmit mature Darwinian principles and original young discoveries to successive generations of botanists.

12.22 **Federico Delpino**

Delpino loved 'Orchids' more than he liked 'Origin'. This was due to the fact that, while 'Origin' presented irreconcilable conclusions of the philosophy of biology with his conception of nature, in 'Orchids' he found a description of natural phenomena perfectly in agreement with and in harmony with his natural finalism.

In order to extend the study conducted by Darwin on orchids to other plant families, Delpino published 'Sugli apparecchi della fecondazione nelle piante antocarpe (fanerogame)',[647] which later spread to Germany thanks to Hildebrand.[648]

At the same time, Delpino undertook to interpret Darwin's theory in terms of a purposive conception of nature that neutralized the most materialistic aspects. This attempt materialized in 'Thoughts on Plant Biology', which addressed the taxonomic value of biological characters.[649]

Delpino attracted Darwin's attention thanks to his interpretation and criticism of the theory of Pangenesi,[650] and the two began a fruitful exchange of letters.

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[645] Hildebrand, On the fertilization of Salvias by insects (Pringsheim's Jahrb. wiss. Bot., I865, IV, p. 459, and P1. 33, figs. 8 and 9).

[646] Darwin, 1859, p. 179-194 e fourth ed. 229-231.

[647] Delpino, 1867a.

[648] Botanische Zeitung, XXV, 1867, p. 265-270, 273-278, 281-286.

[649] Delpino, 1867b.

[650] Pancaldi, 1984, p. 25-26.

Delpino's teleological conception led him to discuss with Darwin the nectar secreted by the Coryanthes mellifluous pebbles,[651] as well as Knight-Darwin's law, which Delpino accepted as a general principle capable of guiding his botanical[652] and naturalistic research in general,[653] and the evolutionary paradox of the persistence of homogamous fertilization in Hordeum distichum.[654]

The teleological interpretation was certainly a point of contrast that can be observed in the various case studies that opposed the two scholars: The most famous is that concerning the cases of fertilization of Ophrys apifera, an orchid that presented nectars without nectar. It was a thorny subject that had originated from an interpretation of Sprengel and also involved H. Müller. If for Sprengel we had to talk about the deception of nature imposed on insects, Darwin opposed his utilitarian conception and knowledge of the level of intelligence of the bees on which a series of new observations were supported on the walls of the nectars. Delpino gave up accepting the Darwinian explanation within the teleological framework of his observations, even when Müller agreed with the British naturalist. Given Darwin's esteem for Delpino, he made further observations; the new Darwinian and Müller conclusions did not in the end convince Delpino that he declared the victory of Sprengel's interpretation. And Darwin, while continuing his observations on the matter, did not directly attack the teleological conception of the Italian. Although this is a case in which the two authors confronted each other, we cannot limit ourselves to interpreting their complex relationship only as a function of a dispute between different philosophies of biology. Delpino had also absorbed the use of argumentation and metaphors from the field from Darwin, which often made the two scholars converge despite the various positions in the finalistic sphere.[655]

Delpino read in 'Orchids' a new teleology; the Italian botanist contrasted Darwin's work on orchids with Sprengel's teleology, Charles Bonnet and Bernardin de Saint Pierre, who recalled the divinity each time he wanted to explain how plants had developed sepals, petals, stamens, and stigmas. What in 'Orchids' appeared to Delpino as a teleology was in harmony with the facts and this led

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[651] From Delpino to Darwin, 1 Novembre 1869, Pancaldi 1984, p. 60.

[652] The Fertilisation of Winter-Flowering plants, Nature, 1, 85, 1869.

[653] From Darwin to Delpino, 14 October 1869; from Delpino to Darwin, 1 November 1869; from Delpino to Darwin, 7 January 1871, Pancaldi 1984, p. 60-63, 69-71.

[654] Delpino, 1867c.

[655] Pancaldi, 1984, p. 31.

him to affirm that 'la teleologia vera non poteva esistere prima di Darwin'.[656] As seen in the chapter on teleology, in 'Orchids' Darwin never attacked Delpino's philosophy directly, but he always discussed the examples proposed by Italian even in correspondence to subject them to criticism.

Delpino's conversion began with the variation theory contained in 'Origin' and settled definitively in 'Orchids';[657] he sought evidence for Knight-Darwin's law also in Asclepliadee and other plant families.[658]

Delpino wrote to Darwin to express profound gratitude for his observations on orchid fertilization in 'Orchids' and then for 'Origin', works without which he would not have been able to produce scientific investigation and would not have been able to realize a childhood dream of demonstrating the organic and behavioural harmony between plants and other beings.[659]

Despite the teleology that animated his conclusions, Delpino—unlike many other scientists who believed the transmutation of species was a hypothesis to be verified—came to define evolution as a truth of fact,[660] demonstrating that finalism did not conflict with change, especially over time.

Despite the differences over Corianthes and the nectarless orchids, Delpino continued to study meticulously what came out of the pen and the mind of the man considered the greatest naturalist of the century.[661] Likewise, Darwin attempted to direct Delpino's research with reading suggestions and experiments, demonstrating the awareness that the attention he paid to the questions he received from this circle of Darwinian botanists was growing all over the world.[662]

Beginning in the 1870s, contacts between the two scholars began to develop on topics such as the origin of man and the definitive conclusions on the Pangenese. However, the passion for plants—and the exchange of specimens, articles, and book—never flagged. Thanks to the connection that

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[656] Delpino, 1978, p. 203.

[657] From Delpino to Darwin, 5 September 1867, Darwin Correspondence Project.

[658] It was a principle that had been revealed by Sprengel (1793) and perfected by Darwin (1877), as he demonstrated that insects favor cross-reproduction even for hermaphrodite individuals. Delpino, who deeply appreciated all of Darwin's conclusions, continued research in other areas by stimulating all Darwinian botanists.

[659] From Delpino to Darwin, 5 Dicembre 1871, Darwin Correspondence Project.

[660] From Delpino to Darwin, 22 Agosto 1869, Darwin Correspondence Project.

[661] From Delpino to Darwin, 9 Ottobre 1869, Darwin Correspondence Project.

[662] From Darwin to Delpino, 14 Ottobre 1869, Darwin Correspondence Project.

Delpino nurtured with his studies on the fertilization of orchids, his change of philosophical perspective on the species was mentioned in one of his last letters:

'[…] Mi onoro di spedirle l'ultima parte delle mie osservazioni sulla Dicogamia. Ella vedrà che quasi ad ogni pagina figura il suo nome; nome che tanta orma ha lasciato in questo genere di ricerche. Nella conclusione del lavoro, a p. 336, dichiaro la mia piena adesione alla teoria transformista [sic] propugnata dal primo naturalista del secolo.'[663]

12.23 **Fritz Müller**

The collaboration between Fritz Müller and Charles Darwin was extraordinarily important from both a scientific and a personal point of view. With these words, Francis Darwin demonstrates how much his father valued the relationship with the German naturalist:

'My father's correspondence with Fritz Müller was, in its bearing on his work, second in importance only to that with Hooker. He had for Müller a stronger personal regard than that which bound him to his other unseen friends. Müller's letters were vividly interesting, with their constant stream of new observation on many biological subjects. Moreover, there was, by an unformulated arrangement, a certain community of research on many subjects. For instance, on orchid-fertilization, self-sterility, heterostylism, and climbing plants the facts supplied by Müller were important contributions to the building up and extending of Darwin's theories.'[664]

When Fritz Müller read 'Orchids', he was already converted to Darwin's views on transmutation but he thought that natural history was now more interesting because the book had changed his entire concept of nature.[665]

Darwin defined Müller as the 'prince of observer'[666] and considered him among those whose opinions he valued at a higher grade.

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[663] From delpino to Darwin, 8 April 1875, Darwin Correspondence Project.

[664] Darwin F. 1899, XIII-XIV

[665] From Fritz Müller to Darwin, 5 November 1865, Darwin Correspondence Project.

[666] West, 2003.

Müller became a defender of Darwin's theories after he read 'Origin' in 1861; he continued to believe in descent with modification and natural selection as the agent of evolution until his death in 1897.

However, in spite of having read 'Origin', Müller needed una prova decisiva: questa poteva essere soltanto the application without constraint to quite specific scientific circumstances in order to bring clarity and order to an apparent chaos.[667]

Moreover, he applied these theories to all of the subjects he studied: orchids, climbing plants, crustaceans, caddis fly cases, stingless honeybees, and so on. All of his research about ecology, inheritance, development, and behaviour were developed in an evolutionary framework.[668] His most significant correspondents about evolution were Haeckel, Agassiz, Hermann Müller, and August Weismann, with whom he shared observations, criticisms, and conclusions.

In the spring of 1841, Müller entered the university of Berlin. This university had been founded by Wilhelm von Humboldt,[669] Johann Gottlieb Fichte,[670] and Friedrich Schleiermacher.[671] These neo-humanists were intent on educating the whole man through the pre-eminence of philosophical studies as distinct from the three professional subjects then dominant in German universities—theology, law, and medicine.

In his acceptance of Darwinism, Müller was influenced by Ludwig Feuerbach's arguments in the religious sphere. He read Feuerbach's 'Essence of Christianity' (1841), which was considered the conceptual point of departure for scientific materialism in Germany,[672] and these readings led Müller to renounce the church in 1846 and to name a genus of orchid after Feuerbach 20 years later.

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[667] Fritz Müller to Max Schultze, 13 March 1864, *Briefe*:51-2.

[668] In the same year of the first publication of Orchid book, Müller was working overall on Crustacea under the light of Darwin's theory: "I have been almost exclusively occupied with Crustacea this past summer, particularly with the development of shrimp, which throws an entirely new light on the relationships of crustaceans and on the whole morphology of the arthropods, and i hope will provide important evidence in favor of Darwin's theory of the origin of animal and plant species.", Fritz Müller to Hermann Müller, 5 April 1862, Leben 87-8, as quoted in West, D. 2003.

[669] W. Humboldt (1767-1835) was brother of the great naturalist Alexander.

[670] J. G. Fichte (1762-1814) philosopher.

[671] F. Schleiermacher (1769-1834) theologian and philosopher.

[672] Gregory 1992: 46.

In 1856, Müller was offered a position teaching mathematics at a secondary school in Desterro,[673] and in this way he found the time to study marine invertebrates and to read 'Origin' a few years later. That led him to produce his first major work, a defence of Darwinism.

Actually, it was Max Schultze, his most important correspondent, who gave him a German edition of 'Origin' in 1861.

In September 1863, Müller finished a manuscript titled 'Für Darwin' and by February 1864 he had sent the last revisions and additions to Schultze. Finally, in the middle of the year, the book was published by Engelmann in Leipzig.

It is not known if Darwin read the manuscript directly or if he first became aware of the book through a letter from Ernst Haeckel.[674] What is known is that he employed a translator for all German works by Fritz Müller.[675]

The opinion of Darwin about the defensive work built up by Müller can be pointed out in a letter the British naturalist sent to the German zoologist:[676]

'I have been for a long time so ill that I have only just finished hearing read aloud your work on species. And now you must permit me to thank you cordially for the great interest with which I have read it. You have done admirable service in the cause in which we both believe. Many of your arguments seem to me excellent, & many of your facts wonderful. […] Permit me again to thank you cordially for the pleasure which I have derived from your work & to express my sincere admiration for your valuable researches. Believe me | Dear Sir with sincere respect | yours very faithfully | Ch. Darwin

P.S. I do not know whether you care at all about plants but if so I shd much like to send you my little work on the Fertilization of Orchids & I think I have a German Copy.'[677]

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[673] Now Florianópolis.

[674] Hackel to Darwin 26 October 1864

[675] Darwin to Haeckel 21 November 1864

[676] Darwin to Fritz Müller 10 August 1865

[677] The firt edition of Orchid book was translated in German by Heinrich Georg Bronn, a German palaentologist and geologist, in 1865.

Starting from that posting, the collaboration between Darwin and Müller on orchids became their main topic of discussion until the publication of the second edition of ‘Orchids’. However, the commitment to have the German naturalist’s work translated into English never failed: at first with a home-made translation of ‘Für Darwin’ commissioned from Camilla Ludwig[678] and in 1869 with the publication of a translation by William Sweetland Dallas.[679]

It was not the first exchange of correspondence between them: Darwin sent reprints of ‘On the Movements and Habits of Climbing Plants’ around this time. Müller received Darwin’s letter on 8 October and responded the next day with a preference for the English version of ‘Orchids’ instead of the German one Darwin had sent to him.

In early 1868, W.S. Dallas[680] offered himself to translate ‘Für Darwin’ to English and Darwin—after having written to Hooker that the book was one of the most important works in supporting his theories[681]—decided to pursue the translation.

Firstly, he wrote to Hermann Müller[682] about the decision to endorse a publication of the English version of ‘Für Darwin’, and after Hermann’s answer[683] he wrote to Fritz that John Murray would bring out a translation for commission.[684] In mid-March 1868, Murray published 1,000 copies.

Fritz Müller instead wished to publish a book about orchids, since he devoted years of work to studying those flowers. He continued to share the results of his research through regular letters to Darwin and his brother Hermann.

It was in response to Darwin’s publications and letters that Fritz expanded his interests into botany. At the end of 1865, when he was still in Desterro, the correspondence with Darwin was active. He received from the British naturalist a copy of ‘Orchids’ as well as articles on dimorphic plants[685] and climbing plants.[686] That was the first edition of ‘Orchids’[687] but the answers from Fritz Müller

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[678] Housekeeper in Down House tra il 1860 e il 1863.

[679] William Sweetland Dallas (1824-1890) British zoologist.

[680] Dallas to Darwin 22 february1868

[681] Darwin to hooker 31 may 1866

[682] Darwin to Hermann Müller 23 February 1868

[683] Herman Müller to Darwin after 23 February 1868

[684] From Darwin to F. Müller, 16 March 1868, Darwin Correspondence Project.

[685] From Fritz Müller to Max Schultze, 12 December 1865.

[686] From Fritz Müller to Darwin, 12 Augurst 1865.

and several papers by Darwin about the forms of flowers comprising this correspondence were the basis of the second edition in 1877.[688]

With the receipt of the book on orchid pollination, which Fritz Müller obtained in Brazil before leaving Desterro, the German scientist followed the directions in which Darwin pointed to the conclusions made in the studies on orchids.

However, his studies were helped by Darwin not only in orchids, but in a number of botanical subjects, most of all the mechanism of pollination of plants. One of the best known was that of Posoqueria, a shrub adorned by white flowers with a mechanism for avoiding self-pollination that Darwin defined as wonderful as that of the most wonderful orchid.[689] [690]

In general, the answer written by Müller illustrated a wide-ranging wealth of observation and experimental results, with images by pencil or watercolour,[691] or with samples of enclosing pressed flowers or butterfly wings.

It was a strict scientific relation full of passion and reciprocal trust. Müller wrote to Darwin about his new discoveries before publishing and often offered them to Darwin for publication, who published in the same way original observations coming from Hermann Müller and Friedrich Hildebrand. At the same time, Darwin queried Müller on his subtropical experience and often asked his opinion about new theories or ideas, opinions that the British naturalist considered more highly than that of almost anyone.[692]

Beginning in 1867, Müller was in Itajaí, Brazil, and began to communicate regularly with J.D. Hooker,[693] exchanging seeds and sending 483 sample of new plants to the Royal Botanic Gardens of Kew asking for their identification.[694]

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[687] Darwin, 1862.

[688] Darwin, 1877.

[689] Darwin to Fritz Müller, 9 and 15 April 1866

[690] We can find the description of the mechanism in these words written in Darwin 1878, p. 5.

[691] The letter from Müller to Darwin of 1 April 1867 contains attached watercolor of crab and the letter From Müller to Darwin of 2 June 1867 has attached watercolor and pencil illustrations of an orchid flower.

[692] Darwin to Fritz Müller 3 June 1868.

[693] Fritz Müller to Darwin, 5 November 1865.

[694] Herbarium Plant List, Royal Botanic Gardens, Kew, vol. 10: 73-8, 80-1, 83-4.

Late in 1865 he received the first edition of 'Orchids' and Darwin's papers on heterostyly in Lythrum and Linum.[695] That was the moment when he decided to study pollination in local orchids and the phenomenon of heterostyly.

Desterro represented the ecological framework that saw him involved in the study of orchids and in a passionate episodical exchange with his brother Hermann and Hildebrand about his discoveries on pollination and other aspects of orchid biology.

Müller's collection of orchids was left to Desterro when, in 1867, he decided to return to Itajaí. However, he soon began to build another one so as to create an enormous mass of works on orchids, including drawings and sketches, some of which he sent to correspondents and others that were found after his death.

According to David E. West, the care and commitment made in making observations, analyses, arguments, drawings, and notes reveal the intention to publish a book on the subject, an idea inspired by the reading of 'Orchids' and on which even his brother Hermann counted.[696] The studies carried out on the epiphytic orchids in South America by Müller were among the first to be developed; in this field he also influenced the Darwinian considerations.[697]

This type of experiment was carried out by Müller and repeated continuously and on other epiphytic orchid species, leading to the elaboration of a new conclusion on the pollen movements on the stigma of Oncidium flexuosum and in general on many other self-fertilizing orchids.[698] These considerations were recorded by the British naturalist in 'Variation'[699] and then Müller himself communicated them to Hildebrand.[700] These excerpts—as well as the letters that Fritz sent to his brother Hermann and again to Hildebrand and which appeared in Botanische Zeitung[701]—were used by Darwin as important information resources for the second edition of 'Orchids' and for 'Variation'.

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695 Darwin 1864; 1865.

696 West, 2003, p. 162.

697 Darwin 1875, 114-115.

698 From F. Müller to Darwin, 1 January 1867, Darwin Correspondence Project.

699 Darwin 1875, 115.

700 Müller 1868a, but these are extracts that can be found in a letter of 1867 sent by Fritz to Hildebrand.

701 Müller 1868c, 1869c, 1870a.

One of the most important examples of reciprocal influences after the first edition of 'Orchids' that fuelled the birth of the second edition was the observation that Fritz Müller made regarding the capacity of natural selection to modify an ancestral character of Epidendrum.[702] This was then taken up and developed by Hildebrand, prompting Darwin to use them as an example of a conversion of function of the organs.

The work inspired by Darwin continued to occupy Fritz Müller's observations for a considerable time, touching on themes such as extrafloral nectaries in orchids, relations between insect pollinators and flowering time, floral morphology, and scent and nectar production.[703]

His active role within the international circle of Darwinian botanists is not only witnessed by the epistolary exchange of books, samples, and observations with Darwin, Hildebrand, and his brother Hermann. Müller was a great connoisseur of Delpino's works and the theoretical comparison was particularly useful in the study of the function of the colour change of flowers in relation to the pollination performed by the lepidopterans.

The meaning of the versicoloured flowers had not yet been explained by sufficient observations; Müller himself complained about the lack of an exhaustive treatment in botanical manuals.[704] Delpino represented the exception that Müller did not forget to mention. According to the Italian botanist and entomologist, the change of colour in plants with versicoloured flowers was causally connected with the insects that were dedicated to their pollination and indicated the appropriate time for a visit for the cause of fertilization.

Within his collection, Fritz Müller carefully observed a Lantana; the observations lasted for three weeks during the spring of 1877. Müller noticed that moths belonging to a dozen different species visited the plant during the days when the flowers changed colour; they passed from the yellow of the first day to the orange of the second, and during the third day they reached a violet colour. However, in the stage of the last two colours, the flowers remained free of nectar. Müller noticed that the butterflies, with very few exceptions, approached only the yellow inflorescences, which, in fact, contained the nectar on which they fed.

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[702] Müller 1869b, 1870a

[703] Fm to Hermann Müller 8 December 1868

[704] Müller, 1877e

His studies concerned the behaviour of insects in relation to pollination and perception of colour, and in this respect he analyzed the strategy of a pierid butterfly,[705] which confirmed Delpino's conclusions. It was not an innate and inherited instinct: According to Müller, every single individual of the pollinating species had to learn through a personal experience that yellow flowers reward with sweet nectar, an essential mechanism to attract insects and allow pollen to be transferred from a flower. But Müller went further; he suggested that the permanence of the orange and purplish colour on flowers that no longer had reproductive functions reinforced the attractiveness of the inflorescence as a whole in the eyes of pollinators. All of this was experimentally proven in 1999.[706]

12.24 **Roland Trimen**[707]

Unfortunately, some letters from Trimen, his drawings, and his monograph on African orchids have been lost. However, it is reported from indirect sources that[708] Trimen told Darwin, on the first occasion they met and talked, that he had been told he was facing the most dangerous man in England.

After their first meeting they began to exchange theoretical notifications and drawings on orchids, and after a short time of scientific attendance, Darwin wrote to him: 'I am very glad to hear that you do not now think me so dangerous a person! You will gradually, I can see, become as depraved, as I am.— I believe, or am inclined to believe, in one or very few primordial forms, from community of structure & early embryonic resemblances in each great class.'[709]

On 4 June 4 1863, Trimen published a paper titled 'On the Fertilization of Disa Grandiflora'. In the application of a comparative analysis with British orchids, he adopted the vision and descriptions offered by Darwin in the first edition of 'Orchids' in toto as regards the mechanism that regulated the movement of pollen and the analogy with the phenomenon of pollination concerning Ophrys muscifera.

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[705] Müller 1877e

[706] Jones and Cruzan 1999.

[707] British-South African naturalist (1840-1916) son of the famous botanist Henry Trimen e curator of the South-African Museum from 1876 till 1895.

[708] Poulton's anniversary addresses, 1909, p. 213-215.

[709] From Darwin to Roland Trimen, 31 January 1863, Darwin Correspondence Project.

But it was not just a technical debt; the botanist realized that the more theoretical than systematic approach that Darwin had elaborated in 'Orchids' had allowed him to better understand the profound nature of the phenomena he was observing: '[…] You are pleased to be very complimentary on my performances, but I hereby declare that whatever merit they may possess is wholly due to your elaborate book, which opened up a terra incognita to me.'[710]

Trimen had absorbed the contents of 'Orchids' and had engaged in a close confrontation with the author in deepening even more the origin and structure of the contrivances. Eventually, Darwin had to ask him to limit the sending of samples; there were too many and he would not have found the time to analyze them. [711]

One of the chapters that Trimen studied most deeply was Cypripedium, so much so that Darwin involved him in the studies that Gray was carrying out regarding the fertilization that took place by means of small insects.[712]

Darwin's orchids had struck again: Trimen's drawings and his descriptions of African orchids left the British naturalist astonished, because the anatomical differences and the new contrivances discovered by the botanist were such as to push the two scientists to a deeper study of the evolution of these forms.[713]

The conversion of Trimen was experienced as a natural fact for those who were endowed with a scientific spirit. He himself reported to Darwin that it was interesting to observe how one after another, the most gifted naturalists with an observational spirit were obliged to admit the species mutability.[714]

Darwin and Trimen developed a personal friendship[715] and their collaboration on orchids went on until the second edition of 'Orchids', investing topics such as the structure of Acropera and Disa

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[710] From R. Trimen to Darwin, 16-17-19 July 1863, Darwin Correspondence Project.

[711] From Darwin to R. Trimen, 27 August 1863, Darwin Correspondence Project.

[712] Gray, 1862b e Darwin, 1877, p. 229-231.

[713] From Darwin to Roland Trimen, 31 January 1863. Moreover Trimen's drawings were analized and commented also by Harvey, from Trimen to Darwin, 16-17-19, July Darwin Correspondence Project.

[714] From R. Trimen to Darwin, 16-17-17 July 1863, Darwin Correspondence Project.

[715] From Darwin to R. Trimen, 24 December 1867, Darwin Correspondence Project.

Grandiflora[716] and then moving on to more general questions such as human evolution, [717] the latest edition of 'Origin',[718] and the shapes of flowers.[719]

[716] From R. Trimen to Darwin, 23 May 1863, Darwin Correspondence Project.

[717] From R. trimen to Darwin, 17-18 April 1871, Darwin Correspondence Project.

[718] From R. Trimen to Darwin, 13 April 1872, Darwin Correspondence Project.

[719] From R. Trimen to Darwin, 2 September 1877, Darwin Correspondence Project.

13 Conclusion

What the thesis proposed to portray is, therefore, that the flank movement consists of an intentional conversion of the members of the scientific community with the theories of *The Origin of Species,* obtained by Darwin through the publication of a small treatise that is recognised as an example of tirelessly profuse commitment in the field of natural history and a demonstration of the ability of Darwinian theories to solve old problems and obtain original results when applied to the new fields of botanical research.

It is an introduction to the interdisciplinary study of the darwinian flank movement, stressing the importance of both philosophical aspect (including theoretical generalizations about the relationships between darwinian evolutionary account for orchids and biological classification, teleology, scientific explanation, coevolution, natural theology, scientific ethics, aesthetics) and the historical aspect (including social and cultural context, political consequences for the publication of a book about orchids, with the birth of a new botanical discipline linking scientists from around the world).

The central assumption of my approach is that flank movement must be viewed as a composite process, made up of many partially separable philosophical and historical components. Many of these components regard the Victorian philosophy of science, others are tied to historical development of botanical sciences, others to social status of orchids and others to different philosophies of biology that were fighting for describing and explaining at their best the phenomena of natural history, but almost all them were simply regarding the human and cultural skills of the author to maintain alive the network of botanists and horticulturists he built.

We can consider the flank movement as a bag of tricks the author made use for reaching the most number of botanists and convince them that his theory was able to explain, praedict and connect phenomena before left alone or misteorious: To the extent that this historical and philosophical multi-component perspective is correct, any attempt to single out just one aspect of flank movement as "core" or "central" is a mistake. Darwin won this challenge because each botanist was now convinced by this now from the other aspect of the flank movement that was most compatible with the method and the personal results of each individual scientist or cultivator: in the book on orchids each of the scholars has grasped some darwinian truth evolution but none of these truths was complete in itself. If there is any element that may have struck most readers, these are the maniacal attitude that characterized his detailed descriptions and the predictability his theory gave to botanical generalizations.

The first element represented a fundamental ingredient for the Victorian methodology: not the pure innate talent but the patient and inexhaustible capacity for concentration and analysis distinguished the genius!

The second was instead an element of novelty for the botanist involved in the field: the classificatory activity was no longer passive observational description because now he had the tools to conceive structures and anatomies of organisms that had existed or existed even if they had not yet been observed . The theoretical generalizations on phenomena took on a broader scope, but they engaged scholars in the search for facts that could falsify their conclusions and that had to be compared with each other. In this way Darwin opened the path of philosophy to professional botany.

BIBLIOGRAPHY

ALLEN, DAVID ELLISTON

2001 *Naturalists and society. The culture of natural history in Britain, 1700-1900*, Variorum Collected Studies Series, Ashgate/Variorum, University of California.

ALLEN, GRANT

1877 *Physiological Aesthetics*, Henry S. King & Co. London,

1879 *The Colour Sense: its Origin and Development, An Essay in Comparative Psychology*, Houghton Ogood and Company, Boston.

1885 *Charles Darwin*, Longmans, Green and Company, London.

ALLAN, MEA

1977 *Darwin and His Flowers: The Keys to Natural Selection*, Taplinger Publishing Co., New York, USA.

ARDITTI, JOSEPH, JOHN ELLIOTT, IAN J. KITCHING and LUTZ T. WASSERTHAL

2012 'Good Heavens what insect can suck it' – Charles Darwin, Angraecum sesquipedale and Xanthopan morganii praedicta, in *Botanical Journal of the Linnean Society*, 169, 403–432.

AYALA, FRANCISCO

2009 Darwin and the scientific method, PNAS June 16, vol. 106 suppl. 1, 10033-10039.

2012 *Le grandi domande, Evoluzione*, edizioni Dedalo, Bari.

AYERS, PETER

2008 The Aliveness of Plants: the Darwins at the Dawn of Plant Science. London: Pickering & Chatto.

BAKER, HERBERT

1965 *Charles Darwin and the perennial flax- a controversy and its implication*, in Huntia, A Yearbook of botanical and horticultural bibliography, vol. 2, 15 October, The Hunt Botanical Library.

1979 *Anthecology: Old Testament, New Testament, Apocrypha*, New Zealand journal of botany, xvii, 431–40.

1983 *An Outline of the History of Anthecology, or Pollination Biology*, in Pollination Biology , chapter 2, pages 7-28, Academic Press, London.

BALFOUR, JOHN HUTTON
1862 Outlines of botany, designed for school and colleges, 2nd edn, A. & C. Black, Edinburgh.

BARLOW, NORA (editor)
1967 *Darwin and Henslow: The Growth of an Idea*, *Letters 1830-1860*, John Murry, London, England.

BARSANTI, GIULIO
1979 *Dalla Storia Naturale alla Storia della Natura, Saggio su Lamarck*, Giangiacomo Feltrinelli Editore, Milano.

BARRETT, PAUL, PETER, GAUTREY, SANDRA, HERBERT, DAVID KOHN, SYDNEY SMITH, (Edited by)
1987 *Charles Darwin's Notebooks, 1836-1844, Geology, Transmutation of Species, Metaphysical Enquiries*, Cornell University Press, New York.

BELL, P.R.(edited)
1959 *Darwin's Biological Works, Some Aspects Reconsidered*, Cambridge University Press, Cambridge.

BELLON, RICHARD

2003 *“The great question in agitation”: George Bentham and the origin of species*, in Archives of natural history 30 (2): 282–297.

2006 *Joseph Hooker Takes a ‘‘Fixed Post’’: Transmutation and the ‘‘Present Unsatisfactory State of Systematic Botany’’, 1844–1860*, Journal of the History of Biology 39: 1–39, Springer.

2009 *Charles Darwin Solves the ‘Riddle of the Flower’; or, Why Don’t Historians of Biology Know about the Birds and Bees?*, History of Science, 47, (2009): 373-406

2011 *The Moral Dignity if Inductive Method and the Reconciliatio of Science and Faith in Adam Sedgwick’s Discourse*, Springer Science+Business Media B.V. 2011.

2011 *Inspiration in the harness of daily labor: Darwin, Botany, and the Triumph of Evolution*. In: Isis 102(3), 2011: 393-420.

BENTHAM, GEORGE
1867 *Note on the Stigmatic Apparatus of Goodeaoviece*, Esq., F.R.S., Pres. L.S., [Read December19]

BERKELEY, MILES JOSEPH
1862 *Fertilization of orchids*, in London review and weekly journal of politics, arts and sciences, iv.

BERNHARDT, PETER
1989 *Wily Violets and Underground Orchids: Revelations of a Botanist*, William Morrow and CO., New York, USA.

BERTANI, STEFANO
2015 *Il letterato Darwin, La scrittura dell’evoluzione*, Editori University Press, Roma.

BONIOLO, GIOVANNI, STEFANO, GIAIMO (edited by)

2008 *Filosofia e scienze della vita, un'analisi dei fondamenti della biologia e della biomedicina*, Pearson Paravia Bruno Mondadori, Milano.

BOULTER, MICHAEL

2008 *Darwin's Garden: Down House and the Origin of Species*, Constable and Robinson, London, England.

BOWLER, PETER

2009 *In retrospect: Charles Darwin and his Dublin critics: Samuel Haughton and William Henry Harvey*, Proceedings of the Royal Irish Academy: Archaeology, Culture, History, Literature, Vol. 109C, pp. 409-420.

BOYLE, FREDERICK

1893 *About Orchids–A Chat*, Chapman and Hall, London, England.

BREWSTER, DAVID

1841 Flouren's Eloge Historique de Baron Cuvier, North British Review, I, 1-41.

BROWN, ROBERT

1833 *On the organs and mode of fecundation in Orchideae and Asclepiadeae*, in Transactions of the Linnean Society of London, xvi, 685–745.

BROWNE, JANET

2003 *Charles Darwin: The power of place*. Princeton: Princeton University Press.

2010a *Making Darwin: Biography and the Changing Representations of Charles Darwin*, The Journal of Interdisciplinary History, vol. 40, No. 3, Biography and History: Inextricably Interwoven, pp. 347-373, The MIT Press, Stable URL: http://www.jstor.org/stable/20685510

2010b *Asa Gray and Charles Darwin: Corresponding naturalists*, Harvard Papers in Botany 15(2): 209- 220.

BURKHARDT, FREDERICK

1996 Charles Darwin’s Letters, A Selection 1825-1859, Cambridge University Press.

CANBY, WILLIAM MARRIOTT

1874 *Observations on Drosera filiformis*, in *The American Naturalist*, 8.

CANDOLLE, ALPHONSE DE

1882 *Darwin considere au point de vue des causes des son succes et de l’importance de ses travaux*, Genève:H. Georg, 2. éd., rev. et augm.

CANDOLLE, AUGUSTE-PYRAMID DE

1819 *Théorie élémentaire de la botanique*, second ed., Déterville, Paris.

CANTOR, GEOFFREY, GOWAN, DAWSON, GRAEME, GOODAY, RICHARD, NOAKES, SALLY, SHUTTLEWORTH, AND JONATHAN R. TOPHAM

2004 *Science in the Nineteenth-Century Periodical: Reading the Magazine of Nature*, Cambridge University Press, Cambridge.

CAPANNA, ERNESTO, TELMO PIEVANI, CARLO ALBERTO REDI

2006 *Chi ha paura di Darwin*, Ibis, Como-Pavia, 2006.

CAVALLI-SFORZA, LUIGI LUCA

1996 *Geni, popoli e lingue*, Adelphi Edizioni, Milano.

CHADAREVIAN, SORAYA DE

1996 *Laboratory science versus country-house experiment: The controversy between Julius Sachs and Charles Darwin*, The British journal for the history of science, xxix, 17–41.

CECI, CHIARA,

2013 *Emma Wedgwood Darwin, Ritratto di una vita, evoleuzione di un’epoca*,
Sironi Editore, 2016.

CLARK, JOHN WILLIS, THOMAS MCKENNY HUGHES

1890 *The life and letters of the Reverend Adam Sedgwick (Vol. 2)*, Cambridge: Cambridge University Press.

CLARIDGE, MICHAEL, HASSAN, DAWAH, MICHAEL, WILSON

1997 *Species, the units, of biodiversity*, Chapman & Hall, Chapman & Hall, London.

COATS, PETER

1970 *Flowers in History*, Viking Press, New York, USA.

COOKE, MORDECAI CUBITT

1882 *Freaks and Marvels of Plant life*, Society for Promoting Christian Knowledge, London.

COCCIA, PAOLO

2003 *Un secolo di evoluzionismo in italia*, bibliografia 1859-1959, Partner-Ship, Prato.

CORSI, PIETRO

1988 *Science and religion: Baden Powell and the Anglican debate, 1800–1860*. Cambridge: Cambridge University Press.

2005 *Before Darwin: Transformist Concepts in European Natural History*, Journal of the History of Biology, 38: 67-83, Springer.

COSANS, CHRISTOPHER

2009 *Owen' s ape and Darwin' s bulldog: Beyond Darwinism and creationism*, Bloomington.

CRÜGER, HERMANN

1864 A few notes on the fecundation of orchids, Journal of the Linnean Society of London (Botany), VIII, p. 127-135.

WHIPPO, CRAIG, ROGER, HANGARTER,

2009 *The Sensational Power of Movement in Plants: A Darwinian System for Studying the Evolution of Behavior*, American Journal of Botany, 96: 2015-2017.

CRISTOFOLINI, GIOVANNI, ANNALISA, MANAGLIA (a cura di)
2009 *Il giardino di Darwin, l'evoluzione delle piante*, Umberto Allemandi & C., Torino, Coordinamento redazionale Lina Ocarino, videoimpaginazione Elisabetta Paduano, fotolito chiaroscuro, Torino, finito di stampare nel mese di marzo 2009 presso Tipo Stampa, Moncalieri (Torino).

CROMBIE, ALISTAR CAMERON
2006 *Some reflections on the history of science and its conception of nature*, Annals of Science, 6:1, 54-75.

CURTIS, RONALD
1987 *Darwin as an Epistemologist*, Annals of Science, 44, 379-408.

DARWIN, CHARLES
1841 *Humble-bees*, Gardeners' chronicle, 21 August, 550.

1845 *Journal of Researches into the Natural History and Geology of the Countries Visited during the Voyage of HMS Beagle round the World, under the Command of Capt. Fitz Roy RN*, 2nd edition, John Murray, London, England.

1859a *On the Origin of species by means of natural selection, or the preservation of facoured races in the struggle for life*, Murray:1th ed., London.

1859b *The origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*, Murray, London.

1862a *On the Two Forms, or Dimorphic Condition, in the Species of Primula, and on their remarkable Sexual Relations*, in Journal of the proceedings of the Linnean Society (botany), volume 6, issue 22, pages 77-96 [Read November 21, 1861]

1862b On the three remarkable sexual forms of Catasetum tridentatum, an orchid in the possession of the Linnean Society, in Journal of the proceedings of the Linnean Society (botany), vi, 151–7.

1862c On the Various Contrivances by Which British and Foreign Orchids Are Fertilised by Insects, and on the Good Effects of Intercrossing, John Murray, London, England.

1862d *Recollections of Professor Henslow*, in Jenyns, L., Memoir of the Rev. John Stevens Henslow M.A., F.L.S., F.G.S., F.C.P.S., late Rector of Hitcham and Professor of Botany in the University of Cambridge, London.

1863 On the existence of two forms, and on their reciprocal sexual relation in several species of the genus Linum, Journal of the Proceedings of the Linnean Society, Botany 7: 69-83.

1864 *On the sexual relations of the three forms of Lythrum salicaria*, Journal of the Proceedings of the Linnean Society, Botany 8: 169-196.

1865 On the movements and Habit of Climbing Plants, in Journal of the Linnean Society (Botany), IX, 1-118, 1865.

1868a The Variations of Animals and Plants under Domestication, John Murray, London, England.

1868b *The Variations of Animals and Plants under Domestication*, 1st American Edition with a preface by Professor Asa Gray, Orange Judd and Company, New York, USA.

1869 Notes on the fertilization of orchids, in Annals and Magazine of Natural History 4 (series 4): 141-159.

1872 On the Origin of Species by Means of Natural Selection, or the Preservation of favoured Races in the Struggle for Life, London: Murray. 6th ed., 1872, italian translation edited by Luciana Fratini, *L'Origine delle Specie*, Bollati Boringhieri, 1967, ristampa giugno 1999.

1874 Memoranda on Drosera filiformis, in Canby W.M.M. Observations on Drosera filiformis, in The American Naturalist, 8, July, 1874, p. 396.

1875a *Insectivorous Plant*, John Murray, London, England.

1875b The Variations of Animals and Plants under Domestication, 2nd edition, John Murray, London, England.

1875c *Insectivorous Plant*, 1st American edition, D. Appleton and Company, New York.

1875d *The Movements and Habits of Climbing Plants*, 2nd edition, John Murray, London.

1876a The Effects of Crossing and Self-Fertilisation in the Vegetable Kingdom, John Murray, London, England.

1876b *The Movements and Habits of Climbing Plants*, 2nd edition revised, D. Appleton and Company, New York, USA.

1877a The different forms of flowers in plant of the same species, 1st edition, John Murray, London, England.

1877b The Effects of Crossing and Self-Fertilisation in the Vegetable Kingdom, 1st American edition, D. Appleton and Company, New York, USA.

1877c The Various Contrivances by Which Brithish and Foreign Orchids Are Fertilised by Insects, and on the Good Effects of Intercrossing, 2nd edition, D. Appleton and Company, New York, USA.

1877d *The different forms of flowers in plant of the same species*, 1st american edition, D. Appleton and Company, New York, USA.

1877e *The Various Contrivances by Which Orchids Are Fertilized by Insects*, 2nd edition, revised with a new foreword by M. Ghiselin, University of Chicago Press, Chicago, IL, USA, 1984.

1878 The Effects of Crossing and Self-Fertilisation in the Vegetable Kingdom, 2nd edition, John Murray, London, England.

1880 *The Power of Movement in Plants*, John Murray, London, England.

1881 *The Power of Movement in Plants*, 1st american edition, D. Appleton and Company.

1882 *The Movements and Habits of Climbing Plants*, Final Text, John Murray, London, England.

1883 Prefatory notice in Müller, H. *The fertilisation of flowers*, translated and edited by D'Arcy W. Thompson, MacMillan and Company, London, England.

1884 The different forms of flowers in plant of the same species, 2st edition, John Murray, London, England.

1888 *Insectivorous Plant*, 2nd edition revised by Francis Darwin, John Murray, London, England.

1897 *Insectivorous Plant*, 2nd American edition, D. Appleton and Company, New York, USA.

1967 The autobiography of Charles Darwin, Journal of Researches into the Natural History and Geology of the countries visited during the voyage of H.M.S. Beagle round the world under the command of Capt. FitZroy R.N., More Letters of Charles Darwin, Life and Letters of Charles Darwin, introduction and edited by Pietro Omodeo, Viaggio di un naturalista intorno al mondo, Autobiografia, Lettere (1831-1836), edited by Pietro Omodeo, translation by Pietro Omodeo for Autobiografia e le Lettere, translation by Maria Vegni Talluri for Viaggio di un naturalista intorno al mondo (translation published in agreement with The Cambridge University Press, England), First edition 10 November 1967, Second edition March 1980, Giacomo Feltrinelli Editore, Milano.

1982 *Diario 1838-1881 e scritti autobiografici del 1837-38*, edited by Cesare Cesati, Edizioni Theoria, Roma.

1987 *Charles Darwin's Notebook, 1836-1844, Geology, Transmutation of Species, Metaphysical Enquiries*, transcribed and edited by Paul H. Barrett (Michigan State University), Peter J. Gautrey (Cambridge University Library), Sandra Herbert (University of Maryland – Baltimore County), David Kohn (Drew University), Sidney Smith (St Catharine's College Cambridge), The Trustees of the british Museum, Italian translation edited by Isabella C. Blum, italian edition edited by Telmo Pievani, Taccuini 1836-1844 (Taccuino Rosso, Taccuino B, Taccuino E), Editori Laterza, Bari, 2008.

DARWIN, FRANCIS (editor)
1880 Über das Wachstum negativ heliotropischer Wurzeln, in *Arbeiten des Botanischen Instituts in Würzburg*, vol. II, 3.

1887a *The Life and Letters of Charles Darwin, including an Autobiographical Chapter*, vol. 3, 12, John Murray, London, England.

1887b *The Life and Letters of Charles Darwin, including an Autobiographical Chapter*, Appleton and Company, New York, USA, 1896.

1909 Darwin's work on the movements of plants, in Darwin and modern science, ed. by Seward, A. C., Cambridge, 385–400.

DASTON, LORRAINE, PETER, GALISON
2010 Objectivity, Zone Books, New York.

DAUBENY, CHARLES
1860 *On the final causes of the sexuality of plants, with particular reference to Mr. Darwin's work on the origin of species*, Oxford.

1865 *The president's address, Reports and transactions of the Devonshire Association for the Advancement of Science*, Literature and Art, iv, 1–29.

DELL’AVERSANO, CARMEN, ALESSANDRO, GRILLI

2005 *La scrittura argomentativa, dal saggio breve alla tesi di dottorato*, Felice Le Monnier, Firenze, 2009.

DENNETT, DANIEL CLEMENT

1995 *Darwin’s Dangerous Idea, Evolution and The Meanings of Life*, Penguins Book, USA,

DELPINO, FEDERICO

1867a Sugli apparecchi della fecondazione nelle piante antocarpe, M. Cellini, Firenze.

1867b Pensieri sulla biologia vegetale, sulla tassonomia sul valore tassonomico dei caratteri biologici, e proposta di un genere nuovo della famiglia delle labiate, in Nuovo Cimento 25, 321–398.

1867c Sull’opera “La distribuzione dei essi nelle pnate e la legee che osta alla perennit della fecondazione consanguinea” del prof. Federico Hildebrand, Milano, Bernardoni, p. 30.

1978 Difesa della dottrina dicogamica, “nuovo giornale botanico italinao”, X.

DESMOND, ADRIAN

1989 *The politics of evolution: Morphology, medicine, and reform in radical London*, Simon and Schuster, Chicago: University of Chicago Press.

DESMOND, ADRIAN, JAMES MOORE,

1991 *Darwin*, Michael Joseph Editor, London.

DRESSLER, ROBERT LOUIS

1981 *The Orchids: Natural History and Classification*, Harvard University Press, Cambridge, MA, USA.

DRESSLER, ROBERT LOUIS, CALAWAY HOMER, DODSON

1960 *Classification and phylogeny in the Orchidiaceae*, Annals of the Missouri Botanical Garden 47:25–68.

DUPREE, HUNTER

1988 *Asa Gray: American botanist, friend of Darwin*, Johns Hopkins University Press, Baltimore.

DUTROCHET, HENRI-JOAQUIM

1828 *Nouvelles recherches sur l'endosmose et l'exosmose*, Wenthworth Press 2018.

1837 *Mémoires pour servir à l'histoire anatomique et physiologique des végétaux et des animaux*, J.B. Bailliere, Paris.

EBENSTEIN, WILLIAM

2006 *The early reception of the doctrine of evolution in the United States*, Annals of Science, 4:3, 306-318.

EGERTON, FRANK

2011 *Darwin's Evolutionary Ecology*, in Bulletin of the Ecological Society of America, vol. 92, issue 4.

EISELEY, LOREN

1958 *Darwin's Century, Eovlution and the men Who Discovered It*, Doubleday & Company - Il secolo di Darwin, *L'evoluzione e gli uomini che la scoprirono*, trad. Libero Sosio, Giacomo Feltrinelli Editore, Milano, 1975

ELLEGÅRD, ALVAR

1990 Darwin and the general reader. The reception of Darwin's theory of evolution in The British periodical press, 1859-1872, with a new foreword by D. L. Hull, Chicago and London, The University of Chicago Press.

ENDERSBY, JIM

2008 *Imperial Nature, Joseph Hooker and the Practice of Victorian Science*, The University of Chicago Press, Chicago, 2010.

2009a *Lumpers and Splitters: Darwin, Hooker, and the Search for Order*, Science 326, 1496, 2009b *Sympathetic Science: Charles Darwin, Joseph Hooker, and the Passions of Victorian Naturalists*, in Victorian Studies, Volume 51, Number 2, pp. 299-320, Indiana University Press.

2016a *Orchids, A cultural History*, The university of Chicago Press, Chicago and London.

2016b *Deceived by orchids: sex, science, fiction and Darwin*, BJHS 49(2): 205–229, June 2016.

FARBER, PAUL LAWRENCE
2000 *Finding Order in Nature, The Naturalist Tradition from Linneaus to E. O. Wilson*, The John Hopkins University Press, Baltimore and London.

FRANCIS, KEITH
2007 *Charles Darwin and The Origin of Species*, Greenwood Press, London.

FYFE, AILEEN, BERNARD, LIGHTMAN
2007 *Science in the Marketplace: Nineteenth Century Sites and Experiences*, Chicago University Press, Chicago.

GHISELIN, MICHAEL
1981 The triumph of the Darwinian method, University of California Press, Berkeley.
1984 *Foreword*, in C. Darwin, C., *The various contrivances by which orchids are fertilised by insects*, second ed., University of Chicago Press.

1994 Darwin's language may seem teleological, but his thinking is another matter, Biology and philosophy 9, 489–492.

GILMARTIN, PHILIP
2015 *On the Origins of Observations of Heterostyly in Primula*, in New Phytologist, Volume 208, Issue 1.

GLICK, THOMAS
1974 *The Comparative Reception of Darwinism*, The Chicago University Press, 1988

GLICK, THOMAS, DAVID, KOHN

1996 *Charles Darwin, On Evolution, The Development of the Theory of Natural Selection*, Hackett Publishing Company, Indianapolis, 2007.

GOULD, STEPHEN JAY

1978 *The Panda's peculiar thumb*, Natural History 87:105-108.

1982 *Exaptation. A missing term in the science of form*, Paleobiology 8, 4–15.

1994 *Hen's Teeth and Horse's Toes*, New York: W. W. Norton & Company, 1994.

1999 *Individuality and adaptation across levels of selection: How shall we name and generalize the unit of Darwinism?,* PNAS, October 12, vol. 96, no. 21, 11904-11909.

2002 *La struttura della teoria della evoluzione*. Codice Edizioni, Torino, 2003.

GRABO, CARL

2006 *Science and the Romantic Movement*, Annals of Science, 4:2, 191-205.

GRAY, ASA

1862a *Fertilization of orchids through the agency of insects*, American Journal of Sciences, series 2, 34:420–429.

1862b *Review of Orchids by Charles Darwin*, American journal of science and arts, xxxiv, 138–44.

1862c *Review of Orchids by Charles Darwin, Fertilization of orchids through the agency of insects*, American journal of science and arts, xxxiv.

1876a *Darwiniana, Essays and reviews pertaining to darwinism*, Cambridge University Press, 2009.

1876b *Natural selection not inconsistent with natural theology* [originally published in the Atlantic Monthly (1860)], in *Darwiniana: Essays and reviews pertaining to Darwinism*, New York: Appleton and Company, pp. 87–177.

1876c *The attitude of working naturalists towards natural selection* [originally published in The Nation (1873)], in *Darwiniana: Essays and reviews pertaining to Darwinism*, New York: Appleton and Company, pp. 236–251.

1882 The Relation o fInsects to Flowers, The contemporary review, XLI.

GRIFFITHS, DEVIN
2015 *Flattening the World: Natural Theology and the Ecology of Darwin's Orchids*, Nineteenth-Century Contexts, 37:5, 431-452.

HALDANE, JOHN BURDON SANDERSON
1932 *The causes of evolution*, Longmans, Green and co., London.

1959 *An indian perspective of Darwin*, "Central Review of Arts and Science of Michigan State University", Michigan State University Press, vol. 3, n. 4.

HARDER, LAWRENCE, STEVEN, JOHNSON
2009 *Darwin's beautiful contrivances: evolutionary and functional evidence for floral adaptation*, New Phytologist 183:530-545.

HARDER, LAWRENCE, SPENCER, BARRETT (edited)
2006 Ecology and Evolution of Flowers, Oxford University Press, New York.

HARVEY, WILLIAM HENRY
1860a *An inquiry into the probable origin of the human animal, on the principle of Mr. Darwin's theory of natural selection, and in opposition to the Lamarckian notion of a monkey parentage*, Dublin 6, 10, Gardeners' Chronicle.

1860b *Darwin on the origin of species*, Gardeners' chronicle, 18 February.

HENSLOW, JOHN STEVENS
1830 *On the specific identity of the primrose, oxlip, cowslip, and polyanthus*, Magazine of natural history, iii.

HERSCHEL, JOHN
1830 *Preliminary Discourse on the Study of Natural Philosophy*, Longman, Rees, Orme, Brown and Green, London.

HILDEBRAND, FRIEDRICH
1863 Die Fruchtbildung der Orchideen, ein Beweis für die doppelte Wirkung des Pollen, Botanische Zeitung.

1864 *Experimente über den Dimorphismus von Linum perenne und Primula sinensis*, in *Botanische Zeitung*, 22.

1865 *Experimente über den Dimorphismus von Linum perenne und Primula sinensis*, in *Botanische Zeitung*, 23.

1867 Die Geschlecht-vereilung bei den Pflanzen und das Gesetz der Vermiedenen und unvortheilhaften stetigen Selbstbefruchtung, Leipzig.

HOLMES, RICHARD
2008 *The age of wonder*, Vintage Books, new York, 2010.

HOOKER, JOSEPH DALTON
1860 *The Botany of the Antarctic Voyage of HM Discovery Ships Erebus and Terror in the Years 1839-1843*, Volume 1, Flora Antarctica, part 2, Botany of Fuegia,The Falklands, Kerguelen's Land etc. Reeve Brothers, London, England.

1862a Review of Orchids by Charles Darwin, Natural history review, ii, 371–6.

1862b Review of Orchids by Charles Darwin, Gardeners' chronicle.

1868 Presidential address, in Report of the thirty-eighth meeting of the British Association for the Advancement of Science; held at Norwich in August, London, 1869.

HOQUET, THIERRY
2010 *Darwin teleologist? Design in the Orchids*, in Comptes Rendus Biologie, 333, 119-128.
2018 *Revisting The Origin Of Species*, Routledge, Abingdon, Oxon.

HULL, DAVID
1973 *Darwin and his critics, The Receptionof Darwin's Theory of Evolution by the Scientific Community*, The University of Chicago Press, Chicago.

HUXLEY, LEONARD (edited by)
1918 Life and letters of Joseph Dalton Hooker, Cambridge University Press, Cambridge, 2011.

IRVINE, WILLIAM
1955 *Apes, Angels, and Victorians: The story of Darwin, Huxley, and evolution*, Lanham, MD.

JANSSEN, MICHAEL
2002 COI Stories: Explanation and Evidence in the History of Scince, Perspectives on Science, vol. 10, no.4, The Massachusetts Institute of Technology Press, 2003.

JUNKER, THOMAS
1989 Darwinismus und Botanik: Rezeption, Kritik und theoretische Alternativen im Deutschland des 19. Jahrhunderts, Stuttgart, 138–50, 261–87.

KELLY, ALFRED
1981 *The descent of darwin, The popularization of Darwinism in Germany*, 1860-1914, The university of North Carolina Press, Chapel Hill.

KITCHER, PHILIP

2007 *Living with Darwin*, Oxford University Press, New York.

KOHN, DAVID

1986 *The Darwinian Heritage*, Princeton: Princeton University Press.

1989 *Darwin's ambiguity: the secularization of biological meaning*, in The British Journal for the History of Science 22, 215–239.

2008 *Darwin' s garden: An evolutionary adventure*, (New York, 2008).

KOHN DAVID, GINA MURRELL, JOHN PARKER AND MARK WHITEHORN

2005 *What Henslow taught Darwin*, Nature, cdxxxvi.

KELLY, ALFRED

1981 The descent of Darwin: The popularization of Darwinism in Germany, 1860–1914, Chapel Hill.

KELLY, AODHAN

The Darwin debate in Dublin, 1859-1908,

KNUTH, PAUL

1906 *Handbook of Flower Pollination*, based upon Hermann Müller's work "The Fertilisation of Flowers by Insects," translated by J. R. Ainsworth Davis, Oxgord Clarendon Press.

KREBS, JOHN, NICHOLAS, DAVIES

1993 An Introduction to Behavioural Ecology, 3th Edition Blackwell Science Ltd, Oxford, 2012.

LA VERGATA, ANTONELLO

1979 *L'evoluzione biologica: da Linneo a Darwin*, Loescher Editore, Torino.

1990 L'equilibrio e la guerra della natura, Morano Editore, Napoli.

LEIFCHILD, JOHN

1862 Review of Orchids by Charles Darwin, The Athenaeum, no. 1804, 683–5.

LENNOX, JAMES

1993 *Darwin was a Teleologist*, Biology and Philosophy, 8: 409-421, Kluwer Academic Publishers, Printed in the Netherlands.

1994 *Teleology by another name: a reply to Ghiselin*, Biology and philosophy 9, 493–495.

1995 *Teleology*, in Keywords in evolutionary biology, ed. by Evelyn Fox Keller and Elisabeth A. Lloyd, Cambridge, MA, 324–33.

LEWENS, TIM

2007 *Darwin*, Routledge Taylor & Francis Group , Abingdon, Oxon.

LIDDON, HENRY PARRY

1882 *The Recovery of St. Thomas: A Sermon Preached in St. Paul's Cathedral on the Second Sunday After Easter, April 23, 1882*, With a Prefatory Note on the Late Mr. Darwin, Forgotten Books, Classic reprint.

LIGHTMAN, BERNARD

2007 *Victorian Populazers of Science: Designing Nature for New Audiences*, University of Chicago Press, Chicago.

LINDLEY, JOHN

1846 *The Vegetable Kingdom; or the Structure, Classification and Uses of Plants Illustrated upon the Natural System*, Bradbury an Evans, London, England.

LINNEAUS, CAROLUS

1753 *Species Plantarum*, L. Salvius, Stockholm, Sweden.

1737 *Genera Plantarum*, C.Wishoff, Leiden, Sweden.

LYNCH, JOHN (edited)

2012 *Science and Education, Thematic Issue Popularizing and Policing "Darwinism," 1859-1900*, vol. 21, number 7, Springer Science+Business Media.

LONGO, CLAUDIO

1997 *Biologia vegetale, forme e funzioni*, Unione Tipografico-Editrice Torinese, Torino.

LONGO, CLAUDIO, GIOVANNA, MARZIANI

2005 *Biologia delle piante, forme e funzioni elementari*, UTET S.p.A. Divisione Scienze Mediche, Lungo Dora Colletta, Torino, 2008.

LUBBOCK, JOHN

1881 *Presidential address*, in British Association for the Advancement of Science, Report, York.

1882 *British Wild Flowers Considered in Relaton to Insects*, Macmillan, London.

MACLEOD, ROY, PHILIP, REHBOCK

1994 *Evolutionary Theory and Natural History in the Pacific*, Darwin's laboratory, University of Hawai'i Press, Honolulu, 1999.

MALTHUS, THOMAS

1798 *An Essay on the Principle of Population*, An Essay on the Principle of Population, as it Affects the Future Improvement of Society with Remarks on the Speculations of Mr. Godwin, M. Condorcet, and Other Writers, Printed for J. Johnson, in St. Paul's Church-Yard, London.

MANCUSO, STEFANO, ALESSANDRA, VIOLA

2015 *Verde Brillante, Sensibilità e intelligenza nel mondo vegetale*, Giunti eidtore, Firenze.

MAYR, ERNST

1964 *Introduction*, in Darwin, C., *On the Origin of species*, A facsimile of the first edition, Harvard University Press, Cambridge (Mass), 1964.

1982 *The Growth of Biological Thought, Diversity, Evolution, and Inheritance*, The Belknap Press of Harvard University Press Cambridge (Mass.), London – Storia del pensiero biologico, diversità, evoluzione, eredità, ediz. It. a cura di Pietro Corsi, trad. it. di Barbara Continenza [pp. 245-575, 674-805, 816-29, 832-35], Paolo Ghisleni [pp. 629-73, 807-09, 831-32, 837-40], Massimo Stanzione [pp. 577-628, 829-31], Riccardo Valla [pp. XI-XIII, 3-22. 83-95], Alessandro Zucchi [pp. 23-81, 97-243, 809-16], Revisione di Paolo Ghisleni, Bollati Boringhieri, Torino, 1990.

1983 The Concept of finality in Darwin and after Darwin, "Scientia", LXXVII, p. 97-117.

1985 *Darwin's five theories of evolution*, in Kohn, D., The *Darwinian heritage*, Princeton University Press, pp. 755–772.

1988 *Toward a New Philosophy of Biology, Observations of an Evolutionist*, Harvard University Press.

1991 *One Long Argument, Charles Darwin and the Genesis of Modern Evolutionary Thought*, Harvard University Press, Cambridge (Massachusetts), italian translation edited by Fiamma Bianca Bandinelli, *Un Lungo Ragionamento, Genesi e sviluppo del pensiero darwiniano*, Bollati Boringhieri, Torino, 1994.

1997 *This is Biology – The Science of the Living World*, The Belknap Press of Harvard University Press, italian translation edited by Antonella Vezzaro, *Il Modello Biologico*, McGraw-Hill Libri Italia srl, Milano, 1998.

2005 *L'unicità della Biologia*, Raffaello Cortina editore, Milano.

MEADOWS, JACK
2004 *The Victorian Scientist: The Growth of a Profession*, London: British Library, 2004

MICHENEAU, CLAIRE, STEVEN JOHNSON, MICHAEL FAY

2009 *Orchid pollination: from Darwin to the present day*, in Botanical Journal of the Linnean Society 161:1–19.

MILL, JOHN STUART

1881 A system of logic ratiocinative and inductive, 8th ed. Harper and brother ed., New York.

MILLER, GEOFFREY

2002 Uomini, donne e code di pavone, trad. it. Giuseppe Barbiero, Giulio Einaudi Editore.

MOORE, JAMES

1979 The post-Darwinian controversies, Cambridge University Press, Cambridge.

1991 *Deconstructing Darwinism: The Politics of Evolution in the 1860s*, in Journal of the History of Biology, vol. 24, no. 3, pp. 353-408, Kluwer Academic Publishers, Printed in the Netherlands.

MORREL JACK, ARNOLD THACKRAY

1981 Gentlemen of Science: Early Years of the British Association for the Advancement of Science, Oxford University Press, Oxford.

MÜLLER, JOHANN FRIEDRICH THEODOR

1863 *Facts and Arguments for Darwin*, translated from the german by Dallas, W. S., John Murray, London, 1869.

1866 *Notes on some of the Climbing-Plants near Desterro, in South Brazil*, in a Letter to C. Darwin, Botanical Journal of the Linnean Society, Volume 9, Issue 38, 1 November, Pages 344–349. [Read December 7, 1865]

1871 *Application of the Darwinian theory to flowers and the insects which visit them*, American Naturalist 5: 271-297.

MÜLLER, HERMANN

1883 *The Fertilisation of Flowers*, translated and edited by D'Arcy W. Thompson, with a preface by Charles Darwin, Macmillan and CO., London, England.

MURRAY, JOHN (edited by)
1869 Report of the Thirty-Eight Meeting of the British Association for the Advancemente of Science, held at Norwich in August 1868, Forgotten Books, London.

NICHOLSON CHARLES, JAMES BALES, JOYCE PALMER-FORTUNE, AND ROBERT NICHOLSON
2008 *Darwin's bee-trap The kinetics of Catasetum, a new world orchid*, Plant Signaling & Behavior 3:1, 19-23, Landes Bioscience.

NORDENSKIÖLD, ERIK
1928 *The History of Biology*, translated by the Swedish by Leonard Bucknall Eyre, Bjorck and Börjesson, Stockholm, 1936.

OMDUFF, R.
1984 Darwin's botany, in "Taxon", vol. 33, n. 1, 39-47.

OSPOVAT, DOV
1981 The Development of Darwin's theory. Natural history, natural theology and natural selection, Cambridge University Press, 1995.

OTTEN, CHARLOTTE FENNEMA
1979 *Ophelia's "long purples" or "dead men's fingers*," Shakespeare Quarterly 30:397–402.

OWEN, RICHARD
1860 *Darwin on the origin of species*, Edinburgh Review, 111, 487–532.

PANCALDI, GIULIANO

1984 *Teleologia e Darwinismo. La corrispondenza tra Charles Darwin e Federico Delpino*, CLUEB, Bologna.

1991 *Darwin in Italy: Science across cultural frontiers*, transl. by Ruey Brodine Morelli, Bloomington,107–36.

PASQUA, GABRIELLA, GIOVANNI, ABBATE, CINZIA FORNI
2015 *Botanica e diversità generale*, III ed., Piccin Nuova Libraria, Padova.

PETER CRAIG, STEVEN, JOHNSON
2006 *Doing the twist: a test of Darwin's cross-pollination hypothesis for pollination reconfiguration*, Biology Letters 2:65–68.

PIEVANI, TELMO
2012 Introduzione a Darwin, Editori Laterza, Roma-Bari.

2008 *Charles Darwin, Taccuini* (a cura di T. Pievani). Roma-Bari, Laterza.

2014 *Evoluti e Abbandonati*, Giulio Einaudi Editore, s. p. a., Torino.

PROCTOR MICHAEL, PETER YEO, ANDREW LACK
1996 *The Natural History of Pollination*, Timber Press Inc., Portland, OR, USA.

PUPILLO, PAOLO, ARIANE DRÖSCHER
2017 *Scienze botaniche e scienze della vita nel secolo XIX*, in Natura e Montagna, anno LXIV, n. 1/2017, Pàtron Editore, Bologna.

QUAMMEN, DAVID
2006 *The Reclutant Mr. Darwin: An Intimate Portrait of Charles Darwin and the Making of His Theory of Evolution*, Great Discoveries, WW Norton and Co., New York, USA.

REDI, CARLO ALBERTO (a cura di)
2009 *La lezione di Darwin*, Ibis, Como-Pavia.

REIDY, MICHAEL,
2008 *Tides of History, Oecan Science and Her Majesty's Navy*, The University of Chicago Press, Chicago.

RICHARDS, ROBERT
1992 *The Meaning of Evolution. The Morphological Construction and Ideological Reconstruction of Darwin's Theory*, Chicago: The University of Chicago Press.
2002 *The Romantic Conception of Life. Science and Philosophy in the Age of Goethe*, Chicago: The University of Chicago Press.
2008 The *tragic sense of life: Ernst Haeckel and the struggle over evolutionary thought*, The University of Chicago Press, Chicago.
Rosa D
1908 *Delle leggi che reggono la variabilità filogenetica*, in Rivista di Scienza "Scientia", 4:331-340.

RUSE, MICHAEL
2003 *Darwin and Design. Does evolution have a purpose?,* Harvard University Press, Cambridge (MA).

RUSE, MICHAEL, ROBERT, RICHARDS
2009 *The Cambridge Companion to the Origin or Species*, Cambridge University Press, Cambridge.

RUSSEL WALLACE, ALFRED
1858 *On the Tendency of Varieties to Depart Indefinitely from the Original Type*, written at Ternate, February, 1858, Instability of Varieties supposed to prove the permanent distinctness of Species.

RUPKE, NICOLAAS

1994 Richard Owen: Victorian naturalist, NewHaven.

SCOURSE, NICOLETTE

1983 *The Victorians and Their Flowers*, Timber Press, Portland, OR, USA.

SCHNECKENBURGER, STEFAN

2009 *Darwin und die Blütenbiologie*, in Darwin und die Botanik, ed. by Jürg Stöcklin and Ekkehard Höxtermann, 76–101.

SECORD, JAMES

2004 *Knowledge in Transit*, Source: Isis, Vol. 95, No. 4, pp. 654-672, The University of Chicago Press.

SEDGWICK, ADAM

1826–1832a *Presidential address*, in *Proceedings of the Geological Society of London*, 3rd series, Vol. 1, pp. 187–212, 1830.
https://www.biodiversitylibrary.org/page/33920379#page/197/mode/1up

1833 *A discourse on the studies of the university* (4th ed.). London: John Parker, Cambridge: J.J. Deighton, 1835.
https://archive.org/stream/adiscourseonstu04sedggoog#page/n4

SIEGEL, CAROL

2011 *Darwin and his love affair with orchids*, Orchid Digest 75:60-71.

SMITH, JONATHAN

2006 *Charles Darwin and Victorian Visual Culture*, Cambridge University Press.

SOBER, ELLIOTT

2000 *Philosophy of Biology*, Westviev Press.

2009 *Did Darwin write the Origin backwards?*, PNAS, June 16, vol. 106, suppl. 1, 10048-10055.

SOLLEREDER, BETHANY

2010 The Darwin–Gray Exchange, Theology and Science, 8:4, 417-432.

SEWARD, ALBERT CHARLES

1909 Darwin and Modern Science, Essays in Commemoration of the Centenary of the Birth of Charles Darwin and of the Fiftieth Anniversary of the Publication of The Origin of Species, Cambridge University Press, 2009.

SMITH, JONATHAN

2006 *Charles Darwin and Victorian Visual Culture*, Cambridge University Press, Cambridge.

SMOCOVITIS, BETTY VASSILIKI

2009 *Darwin's botany in the Origin of species*, in The Cambridge Companion to the "Origin of species", ed. by Michael Ruse and Robert J. Richards, Cambridge, 216–36.

SPRENGEL, CHRISTIAN KONRAD

1793 *Das entdeckte Geheimniss der Natur im Bau und der Befruchtung der Blumen*, Friedrich Vieweg, Berlin, Germany; Discovery of the secret of nature in the structure and fertilization of flowers, translated by Peter Haase, pages 3-43 in D.G. Lloyd e S.C.H. Barrett, editors, *Floral Biology: Studies on Floral Evolution in Animal-Pollinated Plants*, Chapman & Hall, New York, 1996.

STAMOS, DAVID

2007 *Darwin and the Nature of Species*, State of New York Press, Albany.

TAYLOR, JOHN ELLOR

1872 *The geographical distribution of animals and plants, geologically considered*, Westminster Review, January 1872.

1878 *Flowers: Their Origin, Shapes, Perfumes, and Colours*, 3rd edn., London: Bogue, 1885

1884 *The Sagacity and Morality of Plants*, London: Chatto & Windus, 1884.

TAIZ, LINCOLN, EDUARDO, ZEIGER

2010 *Plant Physiology*, V ed., Sinauer Associates, Edited by Massimo Maffei, *Elementi di fisiologia vegetale*, Piccin Nuova Libraria S.p.A., Padova, 2013.

TYLER-WHITTLE, MICHAEL

1970 *The plant Hunters*, Chilton Book Co., Philadelphia, PA, USA.

TREAT, MARY

1873 *Observations on the sundew*, in *The American Naturalist*, 7.

TREVIRANUS, GOTTFRIEB REINHOLD

1818 Biologie oder Philosophie der lebenden Natur, Johan Friedrich Röwer, Gottingen.

1831-33 Die Erscheinungen und Gesetze des organischen Lebens, J.G. Heyse, Bremen.

TREVIRANUS, LUDOLPH CHRISTIAN

1861 *The botany of the Antarctic voyage etc. by Joh. Dalton Hooker*, Botanische Zeitung, xix .

1863a Ueber Dichogamie nach C. C. Sprengel und Ch. Darwin, Botanische Zeitung, xxi.

1863b On the existence of two forms, and on their reciprocal sexual relations, in several species of the genus Linum by Charles Darwin, Botanische Zeitung, xxi.

VOGEL, STEFAN

1996 *Christian Konrad Sprengel's Theory of the Flower: The Cradle of Floral Ecology*, in Floral Biology, edited by David G. Lloyd and Spencer C.H. Barrett, Chapman and Hall, p. 44-63.

WALLACE, ALFRED RUSSELL

1882 Review of Vignettes from Nature, by Grant Allen, Nature 25.

WHEWELL, WILLIAM

1837 History of the Inductive Science, John W. Parker, London.

1847 Philosophy of the Inductive Sciences, John W. Parker, London.

WHITEHOUSE, HAROLD LESLIE KEER

1959 *Cross- and self-fertilization in plants*, in *Darwin' s biological work: Some aspects reconsidered*, ed. by P. R. Bell, P. R., New York, 207–61.

WHITTLE, TYLER

1997 *The Plant Hunters, Tales of the Botanist-Explorers Who Enriched Our Gardens*, Lyons & Burford Publishers, New York.

WILBERFORCE, SAMUEL

1860 *Darwin's origin of species*, in Quarterly Review, 108, 225–264.

1847 *Pride a Hindrance to True Knowledge: A Sermon, Preached in the Church of St. Mary the Virgin*, *Oxford, before the University*, on Sunday, June 27th, 1847, London: Francis & John Rivington. pp. 17–18.

J.S. Wilkie B.Sc. Ph.D. (1956) The idea of evolution in the writings of Buffon.—II, Annals of Science, 12:3, 212-227

WILSON, BEN

2007 The Making of Victorian Values: Decency and Dissent in Britain, 1789-1837, Penguin, New York.

WENTERSDORF, KARL

1978 *Hamlet: Ophelia's long purples*, Shakespeare Quarterly 29:413-417.

WEST, DAVID

2003 *Fritz Müller: A Naturalist in Brazil*, Blacksburg: Pocahontas Press.

WILBERFORCE, SAMUEL

1860 *Darwin's origin of species*, Quarterly review, cviii, 225–64.

WOODS, MAY, ARTE SWARTZ, WARREN

1988 *Glasshouses: A History of Greenhouses, Orangeries and Conservatories*, Aurum Press, London, England.