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Why flowers are important to the history of philosophy

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In this paper, I intend to illustrate that a comparison with Darwin's studies in floral biology has provided the conceptual foundations for recognising a particular theoretical space in the historical dimension of philosophy. This space can serve to legitimise the interconnection between life sciences and philosophy, improve the historical understanding about topics and themes associated with the philosophy of biology, and create conceptual and dialectical tools to inform the current debates on ecology.

In the last 20 years of his life, Darwin published six botanical treatises and 75 articles in which he carried out an uninterrupted series of analytical studies on the finely articulated architecture of plants, their physiology, and the ecological dimensions of their existence[1].

All this contributed to introducing evolutionary biology to the heart of botanical studies.

The sobriety and humility that distinguished his character and scientific method made him decline the right to define himself as a professional botanist[2]; in fact, he did not intend to become a profound connoisseur of botanical taxonomy, nor did he intend to bind himself to the detailed description of plant biogeography or create a research station, laboratory, or a university-centred programme entirely dedicated to experimentation on plant physiology[3].

1 F. DARWIN, *The botanical work of Darwin*, «Annals of Botany», 13/1899, pp. ix-xix, http://darwin-online.org.uk/content/frameset?itemID=A261&viewtype=text&pageseq=1; P. AYERS, *The Aliveness of Plants: the Darwins at the Dawn of Plant Science*, Pickering & Chatto, London 2008.

2 From Darwin to Hooker, 12 December 1843, Darwin Correspondence Project.

3 S. DE CHADAREVIAN, *Laboratory science versus country-house experiments. The controversy between Julius Sachs and Charles Darwin*, «The British Journal for the History of

And yet, with the aim of defending and consolidating his most important theory, we can today define Darwin as an essential botanist for two primary reasons. The first is his in-depth knowledge of the phenomena of plant life, thanks to the value of his innovative studies whose originality contemporary and new generations of botanists drew from to direct their research in specific fields of plant science, and secondly, for the unbridled passion that led him to engage in the study and experimentation in the botanical field for such a long period of his life.

The garden made available to him by his father in the Mount in Shrewsbury was the stage for his first experiments in physiology, while the gradual approach to the Linnean sexual system began with the reading of *Botanic Garden*, inherited from his grandfather[4]. However, his academic studies of botany increased at Cambridge: Charles attended Henslow's lectures from 1829 to 1831 at Christ's College.

The passionate and dedicated teaching of this new master flowed through the reading of his innovative anatomical diagrams, embroidered with brief didactic compendiums, and in exploratory journeys with students that allowed him to always retrieve new fresh samples for dissection. Darwin soon became part of the intimate circle of students who actively participated in Henslow's research, and later the scientific collaboration turned into a confidential friendship on which the English naturalist could rely on to engage in a scientific cruise around the world aboard the Beagle.

During this fascinating and difficult adventure, his training focused on the works of Charles Lyell and Alexander von Humboldt, which led the author of *Origin of Species*[5] to establish an intimate relationship of familiarity and friendship with every flower and plant, always listening to how the vivid and direct voice of nature was able to address his feelings.

Soon the wonder and curiosity turned into an irresistible impulse to understand in detail the functioning of floral biomechanics as a function of pollination, and finally, after the publication of *Origin*, Darwin realised that the study of flower adaptations could effectively demonstrate the explanatory power of natural selection.

It was a fundamental decision that culminated in the publication of a treatise on the fertilisation of orchids[6].

Science», 29/1996, pp. 17-41.

[4] E. DARWIN, *The Botanic Garden. A poem in Two Parts; Containing The Economy of Vegetation and the Loves of the Plants*, Jones & Co., London 1825.

[5] C. DARWIN, *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*, John Murray, London 1859: from here on *Origin*.

[6] C. DARWIN, *On the Various Contrivances by Which British and Foreign Orchids Are Fertilised by Insects, and on the Good Effects of Intercrossing*, John Murray, London 1862: from

1. Darwinian network

Although the debate on the philosophy of nature underwent a profound renewal with the publication of *Origin*, in 1859, European botany was still dominated by a solid tradition of classificatory studies and remained anchored to the primacy of the observational phenomenon, understood as an event to be explained and reconstructed in terms of analysis and description. Attempts at speculative generalization from which to deduce new natural laws that explained the greater number of observed facts were of lesser importance.

Three years later, Darwin published a study which apparently seemed entirely dedicated to the interpretation of the morphology and biomechanics of the flowers of the orchid family, through a meticulous work of morphological analysis and devoid of metaphors and the more theoretical aspects contained in *Origin*.

However, in reality, this was a flank movement[7].

This small treatise, and other Darwinian publications on flowers, led to a close confrontation between different and opposing philosophies of nature, which implied, for those who adhered to them, a specific conception of the world that sometimes coexisted, but more often was in competition with, evolutionism in the attempt to interpret known and fresh plant phenomena.

This extraordinary and dynamic stage of scientific philosophical contention was also achieved thanks to the method and personality of the British naturalist, characterized by a multiplicity of interests that are not usual in a professional botanist and seemingly dispersive. However, it was precisely that multidisciplinary curiosity that led him to devour the treatises of horticulturists, to seek a fertile ground for comparison and to strengthen himself through daily correspondence with naturalists, geologists, botanists, physiologists, farmers, and hybridizers, who found in the author of *Orchids* the concrete capacity of amalgam and fusion: the theoretical focal point of an extensive process of protracted observations and experiments of crossing and dissections.

What seemed to converge towards a uniform traditional interpretation of the shape, colours, and smells of flowers coming from the sapiential patrimony of natural theology, in *Orchids* this well-established meaning shatters and disperses: some take possession of a philosophical-scientific aspect, others of another, and thus begin disputes on the correct interpretation of botanical case studies. The various meanings are radicalised, they enter conflict, they are

here on *Orchids*.

7 From Asa Gray to Darwin, 2-3 July 1862, Darwin Correspondence Project.

swallowed up into a clash of forces at times ideological, where new contrasts flourish or ancient arguments find space: chance or purpose? Spiritualism or materialism? Evolutionism or creationism? Speculative impetus or Victorian methodology? Amateur experiments or laboratory study? Descriptive or philosophical botany? Nature in balance or struggle for existence?

In this way, starting from the 60s of the nineteenth century, Charles Darwin became the beating heart of an international research network dedicated to the study of the ecology of flower pollination, which included Fritz Müller, Federico Delpino, Asa Gray, Friedrich Hildebrand, Joseph Dalton Hooker, Severin Axell, Herman Crüger, and Herman Müller.

Although the members of this working group adhered to the different philosophical and religious orientations underlying their interpretations, all drew inspiration from the works of Darwin, who, as conductor, undertook a project of encouraging publications, financing the translation and dissemination of more deserving works, and implementing the discussion and circulation of original interpretations within the scientific community.

Over the years, Darwin assumed the role of a scientific catalyst by resolving to respond with subsequent publications and countless letters not only to accredited critics and scholars, but also to enthusiasts belonging to the periphery of the scientific community, without engaging directly on the philosophical level, but preferring the analysis of observations and experimental confirmation.

In resonance with the first edition of *Orchids,* many authors published a series of monographs[8] that Darwin read carefully and to which he replied with a second edition, fuelling a fruitful circle of progress in the evolutionary research of flowers that could then count on the other two Darwinian treatises[9] and other articles entirely dedicated to the study of fertilisation mechanisms and the relationship between these mechanisms and the incredible structural variety and biodiversity offered by floral morphology.

Subsequently, hundreds of botanists based their research methodology on the contents and analysis tools that Darwin had dedicated to these topics[10].

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8 C. DARWIN, *The Various Contrivances by Which British and Foreign Orchids Are Fertilised by Insects, and on the Good Effects of Intercrossing*, 2nd edition, D. Appleton & Co., New York 1877, pp. vii-xi.

9 C. DARWIN, *The Effects of Crossing and Self-Fertilisation in the Vegetable Kingdom*, John Murray, London 1876; C. DARWIN, *The Different Forms of Flowers on Plants of the Same Species*, John Murray, London 1877.

10 Hermann Müller reports at least 814 later works (H. MÜLLER, *The Fertilisation of Flowers*, translated and edited by D'Arcy W. Thompson, Macmillan & Co., London 1883), while Knuth's more complete bibliography included 3748 publications (P. KNUTH, *Handbook of Flower Pollination*, Clarendon Press, Oxford 1906).

Darwinian schools of botany were founded in Germany and Italy[11], and even today the most recent results of various specialisations of plant science reflect or start from the conclusions that the English naturalist reached in his publications[12].

2. Natural system and classification

Linnaeus' sexual system was the reference point of 19th century floral botany. The Linnean school naturalist, who aspired to speak the language of nature correctly, had to first write the lexicon: it was thus that in the 18th and 19th centuries, naming and classifying became the fundamental tasks in the career of every scholar of living forms. Following in the footsteps of Adam in an earthly paradise, the scholar assigned a name to things and then made a classification, and in this way the correct positioning of living forms became a privileged scientific activity: it meant disclosing the rational model that God had conceived and in agreement with which reality itself was structured.

The idea that the description of the wonders of creation constituted the heart for the demonstration of the existence of God had been inherited from the scientific literature of the seventeenth and eighteenth centuries.

The constitutive elements of this intellectual habit were many. Firstly, the unmeasurable quantity of natural forms created, known only by the Creator, was the proof of his unlimited abilities and the fruitfulness of his wisdom and power[13]; an extraordinary and immense variety of organisms, like the variety found in their structures, functions, and behaviours, to mark the extent of its infinite power[14]; furthermore, sophisticated reciprocal adaptations of living

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11 D. KOHN, *Darwin's Garden: An Evolutionary Adventure*, The New York Botanical Garden, New York 2008, p. 29.

12 G. CRISTOFOLINI, A. MANAGLIA (eds.), *Il giardino di Darwin, l'evoluzione delle piante*, Umberto Allemandi & Co., Torino 2009.

13 J. RAY, *Wisdom of God manifested in the works of Creation*, W. Innys, London 1743, pp. 17-19.

14 This correspondence between variety and divine power is illustrated also in Voltaire's Zadig: «But,» said Zadig, «what if there were only good and no evil at all?» «Then,» answered Jesrad, «this earth would be another world, the chain of events would be ordered by wisdom of another kind; and this order, which would be perfect, can only exist in the eternal abode of the Supreme Being, which evil cannot approach. He has created millions of worlds, not one of which can resemble another. This boundless variety is an attribute of His boundless power. There are not two leaves of a tree upon this earth, nor two globes in the infinite fields of heaven, which are alike, and everything that you see on this little atom where you have been born must fill its own place, and exist in its own fixed time, according to the immutable decrees of Him who embraces all». F. M. AROUET, *Zadig and other tales*, translated by R. B.

beings and organs to the functions that must be performed to guarantee the harmony of nature do not allow them to be reduced to an explanation that makes use of arid mechanism or chance, rather the finalism that they manifest legitimises the explicative recourse to a divine plan[15].

Darwin from the beginning distanced himself from this explanatory mode, which found a flourishing development in the Bridgewater Treatise[16]: he intended,

> 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 inter-position of the Creator[17].

The recourse to the study of natural causes for the study of the history of life on earth requires methodological independence and explanatory autonomy with respect to metaphysics and religion. In the naturalist's work, the groupings in which orchids were placed were no longer the result of continuous acts of separate creation, but rather the result of a slow and gradual evolution in which natural selection was the main causal process, but not the only one. The species existed in nature, and their study produced a genealogical tree able to illustrate the descendent relations of the degrees of kinship between the current orchid species, which represented the result of a slow and gradual diversification, starting from extinct monocotyledonous ancestors.

This new way of conceiving organisms according to genealogical affinity also made it possible to overcome the problems related to the artificiality of the Linnean classification system[18]. The classification thus came to rely first on the historical knowledge of organisms and their genealogical relationships. However, there were other Darwinian reasons according to which it was not possible to conceive species as separated and immutable creations.

Boswell, George Bell and Sons, London 1907, p. 151.

15 A. LA VERGATA, *L'evoluzione biologica: da Linneo a Darwin*, Loescher Editore, Torino 1979, p. 55.

16 This is a series of volumes financed by the Earl of Bridgewater and published between 1833 and 1836, in which some of the foremost scientists in the United Kingdom, including William Whewell, set out to demonstrate existence, infinite wisdom and goodness of God based on natural wonders.

17 C. DARWIN, *On the Various Contrivances by Which British and Foreign Orchids Are Fertilised by Insects, and on the Good Effects of Intercrossing*, cit., p. 2.

18 J. ENDERSBY, *Orchids, A Cultural History*, The University of Chicago Press, Chicago 2016; L. KOERNER, *Carl Linnaeus in His Time and Place*, in N. JARDINE, J. A. SECORD, E. SPARY (eds.), *Cultures of Natural History*, Cambridge University Press, Cambridge 1996.

In the eighth chapter of *Origin*, Darwin recognised how much importance naturalists had attached to the role of sterility in maintaining precise boundaries in the separation of species[19].

The principle of sterility of hybrids[20] supported a definition of species linked to the essentialist concept: species were real but had to be conceived as types and not as populations. Furthermore, the constancy and invariability of their characters closed the door to any explanation that proposed an evolutionary derivation of a species from a variety.

On the one hand, therefore, the fertility observable only in members of the same species, and on the other, the discontinuity found in nature between the species, led to the same result: the guarantee against the possibility of the derivation of an intermediate or entirely new essence in an offspring resulting from the hybridization of two distinct species.

The limits and conditions of sterility became the subject of Darwin's studies on plants, in particular on *Primula veris* and *Primula vulgaris*[21]. The flowers that Darwin analysed in his Down House garden, in his greenhouse but also in an open field and in a shady wood, led him to conclude that it was not a case of mere variability.

Despite the similar dimensions, the two forms of *Primula* exhibited considerable differences in the morphology of the stigma, pistils, stamens, corolla, and pollen grains, and, moreover, the author did not find any transitional grades between the two forms.

After experiments with a protective net and observing that all species secreted plenty of nectar, Darwin realised that *Primula veris* and *vulgaris* needed visits of insects for their fertilisation, but that one hermaphrodite form of *Primula*, to be perfectly fertile, must unite with the other hermaphrodite form.

If the meaning of the existence of two forms of *Primula*, with their contrivances and pollen adapted for reciprocal union, was to favour intercrossing and the fact that two individuals of the same species, when

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[19] C. DARWIN, *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*, cit., p. 245.

[20] According to Buffon the main criterion for discriminating the belonging of two organisms to distinct species was the recognition of the sterility of hybrids (G.-L. BUFFON, *Histoire naturelle*, IV: *Histoire des Quadrupèdes. L'âne*, in J. PIVETEAU (ed.), *Oeuvres Philosophiques*, Presses Universitaires de France, Paris 1954). The influence of this method will remain throughout the century and will flow into the next; however, it is good to remember not only that Buffon at the end of the eighteenth century had to recognise the existence of several exceptions, but also that his thinking is too complex to be defined as essentialist.

[21] C. DARWIN, *On the Two Forms, or Dimorphic Condition, in the Species of Primula, and on their Remarkable Sexual Relations*, «Journal of the proceedings of the Linnean Society (botany)», 6, 22/1862, pp. 77-96.

homomorphically united, remained sterile in the same way that many distinct species when crossed convinced Darwin that sterility could no longer be conceived as a characteristic assigned by the Creator to keep species separated and distinct from the moment of their creation: rather, this case of dimorphism showed that sterility was slowly acquired to support a gradual evolutionary transition of *Primula* from the state of hermaphrodite to two distinct sexual forms.

It seemed therefore that sterility was not strictly linked to the specific divergence, and this convinced the naturalist to recognise once again the inexistence of a clear dividing line between species and variety[22]: a shocking conclusion for the fixists of the time that left open the possibility of a reconciliation with the transformation of species.

Starting from this discovery, Darwin's research on heterostyly of *Linum*, *Lyhtrum*, and other genera became an integral part of a new monograph[23] with which Darwin definitively solved the evolutionary enigma of flower fertilisation, reaching one of the happiest moments of his scientific career[24].

3. Teleology

The field of botany that studied species in their ecological relationship was a field that had its origin in the studies of the second half of the 18th century[25]. This orientation of thought between organisms gave birth to the work of Christian Sprengel[26], rediscovered by Robert Brown and then passed into the hands of Charles Darwin, Federico Delpino, Herman Müller, and many other botanists.

Thus, it was found that the research on the fertilisation of flowers, which grafted onto the philosophical tradition that had long been concerned with the methodology of teleological explanation in the natural sciences as it had been handed down on the Kantian tradition from the end of the previous century, gave rise to a philosophical and theological debate on finalism,

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22 C. DARWIN, *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*, cit., p. 278.

23 C. DARWIN, *The Different Forms of Flowers in Plants of the Same Species,* cit.

24 F. DARWIN, *The Life and Letters of Charles Darwin, Including an Autobiographical Chapter*, John Murray, London 1887, p. 97.

25 The concept of Œconomia naturae studied and elaborated by Linnaeus and his school, spread among scholars and convinced them of the importance of studying the complexity of the relationships between the plant and animal kingdom as evidence of a finalistic order.

26 C. K. SPRENGEL, *Das entdeckte Geheimniss der Natur im Bau und der Befruchtung der Blumen*, Friedrich Vieweg, Berlin 1793.

which could now rely on the contribution of new scientific observations and conclusions, such as evolutionism[27].

Speaking of finality in botany in the nineteenth century meant interpreting the unfolding of the history of life as a progress in form and function in the direction of perfectibility attainable thanks to the teleological relations internal and external to organisms. By engaging in the interpretation of floral case studies, Darwin initiated an inescapable action of eroding the consensus of botanists on the finalist model that informed Sprengel's conclusions.

Darwinian evolution occurs according to two contingent series of causal coordinates: an internal one, that is to say, the causal chain that gives rise to individual variations that will be scrutinized by selection, and an external one given by the historical contingency of the environmental events in which the organisms find themselves surviving. The sum of these coordinates guarantees a succession of events that leave no room for a preordained direction of evolution[28].

The *Coryanthes macrantha* orchid offers a clear case of the methodological inapplicability of the finalistic explanations underlying an external causality[29]. The plant secretes a liquid similar to nectar, which is collected in a basin below the lip. The bees of the genus *Euglossa,* amid a confused gathering to feed on the cellular lining of the labellum, fall into the basin, involuntarily immersing themselves in the liquid that does not allow them to soar again in flight. Only by swimming a narrow passageway adjacent to the body of the flower can they come out and thus come into contact with the pollen masses that adhere to the insect's body. The insects thus freed can decide to get closer to the same labellum, then fall and this time release the mass on the stigma or fly towards a new flower[30].

If a fundamental event in the evolution of a species such as cross-fertilisation was based on a completely accidental bath, this strongly weakened the finalist concepts underlying the interpretations of many botanists such as Delpino[31], to whom random or unintentional events could not explain the origin of floral

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27 G. PANCALDI, *Teleologia e Darwinismo. La corrispondenza tra Charles Darwin e Federico Delpino*, CLUEB, Bologna 1984, p. 42.

28 D. PIEVANI, *Leggere* L'origine delle specie *di Darwin*, Ibis, Como 2015, pp. 76-77.

29 This is a case study presented by Hermann Crüger (1818-1864), German naturalist, correspondent of Darwin and since 1857 director of the botanical garden of Trinidad.

30 H. CRÜGER, *A few notes on the fecundation of orchids*, «Journal of the Linnean Society of London (Botany)», VIII/1864, pp. 127-135.

31 Delpino referred to the Kantian tradition of Naturphilosophie as it had been elaborated by Gottfried Reinhold Treviranus: consequently his finalistic conception of nature was based on an empirical research, on the use of a language, and on the reference to a theoretical basin in contrast with the Hegelian and Schellinghian currents of the philosophy of nature.

organs perfected for the performance of precise and sophisticated functions: in his view, the fertilisation process in *Coryanthes* could not depend on an accidental phenomenon, and the purpose of the liquid produced in the basin was not reducible to favouring the immersion of insects in an involuntary bath. Instead, Darwin, adopting Crüger's remarks, admitted:

> There cannot be the least doubt that the fertilisation of the flower absolutely depends on insects crawling out through the passage formed by the extremities of the labellum and the overarching column. If the large distal portion of the labellum or bucket had been dry, the bees could easily have escaped by flying away. Therefore, we must believe that the fluid is secreted by the appendages in such extraordinary quantities and is collected in the bucket, not as a palatable attraction for the bees, as these are known to gnaw the labellum, but for the sake of wetting their wings, and thus compelling them to crawl out through the passage[32].

From the perspective of the English naturalist, cross-fertilisation is not the result of an intentional act on the part of insects: they complete their visits because they are driven by the need to feed, while the origin of contrivances such as the secretion of the liquid, under the labellum, the channel that acts as a path to the insect, the pollen masses, etc., they were determined by coevolutionary events in which chance played a role, presenting itself in the form of an accidental bath.

The internal teleological relations, on the other hand, were closely linked to the concept of variation, which lent itself to granting margins of legitimacy to the arguments of the supporters of finalism: if in fact Darwin recognised the unknown factor of the causes of the variation, then precisely in that dimension of indeterminacy it was conceivable a plan preordained by the Creator or a rational principle that would act as a source of variations to unfold all wonderful harmonies that occur between organisms in the natural world.

Going back to this position, Asa Gray affirmed that adaptation remained the product of «streams of beneficent variation»[33]; the appearance of these variations was directed by a dynamic will that anticipated the selective mechanisms and gave an orientation to the evolutionary process[34].

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32 C. DARWIN, *The Various Contrivances by Which British and Foreign Orchids Are Fertilised by Insects, and on the Good Effects of Intercrossing*, cit., p. 176.

33 H. DUPREE, *Asa Gray: American botanist, friend of Darwin*, Johns Hopkins University Press, Baltimore 1988, p. 297.

34 This position was part of a series of attempts by the American botanist to reconcile natural selection with finalism by highlighting the relationship between orchid flowers and teleology. Delpino also tried to bring the reception of *Orchids* back into a finalistic horizon trying to

However, Darwin's studies on *Pisum sativum* and *Digitalis purpurea L.* convinced him of the existence of a close link between the hereditary characteristics of an organism and the environmental context where it develops, to the extent that «inherited variations arise because of differences in environment during the development of different individuals»[35].

According to Darwin, therefore, the origin of the hereditary variation was still subject to infiltration of external accidentality due to the causality of environmental factors.

However, reflection on the homology of the floral organs contained in *Orchids* offered Darwin new ideas on internal teleological connections. Already in *Origin,* the author observed how an organ, structure, substance, or behaviour could be gradually co-opted or converted to a completely different function and form than that originally possessed or at a stage in the past[36], but in studies on orchid flowers these cases are multiplied, described in detail, and closely connected to the evolutionary analysis of homologies and common descent.

One of the examples presented in *Orchids* is the peduncles of *Catasetum,* which, unlike the other species of *Vandeae*, are fixed in a curved position and, once released due to the bursting of the flaps of the disc into which they are inserted, they stretch with force to push the pollinia masses, the anther lodges, and the pollinium to a distance of two or three feet beyond the antennae. This is a case in which, according to Darwin, it is claimed that several modifications have been found in different species, changing structures and capabilities in a new species[37].

These phenomena defused the objections of design advocates that it is not possible to admit a gradual evolution of extraordinarily complex organs such as the vertebrate eye: how to justify a utility in terms of survival for the most primitive and partial evolutionary stages of a fully functional structure only in the final phase of its development? Yet, this Darwinian explanation of conversion allows us to conceive of the succession of several functions during the evolution of the same organ and determines a distinction between current utility and historical function. Darwinian co-optation guaranteed adaptation, a flexibility incompatible with the adaptationist fixism of the

bridge the methodological dissent that separated the two scientists (G. PANCALDI, *Darwin in Italia, Impresa scientifica e frontiere culturali*, il Mulino, Bologna 1983, p. 222).

35 P. R. BELL (ed.), *Darwin's biological work, Some Aspects Reconsidered*, John Wiley & Sons, New York 1964, p. 210.

36 C. DARWIN, *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*, cit., pp. 148-149.

37 C. DARWIN, *The Various Contrivances by Which British and Foreign Orchids Are Fertilised by Insects, and on the Good Effects of Intercrossing*, cit., pp. 179-180.

creationists, which in the perfection of creation did not allow room for further adjustments. However, neither could it be reconciled with a rational principle that intervened to direct the variation once and for all: conceiving evolution in these strict and flawless terms would not have allowed the floral organs the possibility of converting to new adaptive configurations which, in the case of changed environmental conditions, would have safeguarded the survival and reproductive capacity of a species[38].

Another characteristic of the study of homology in *Orchids* consists in recognising the evolution of structures that, starting from a rudimentary state, have been reused for a new function.

The existence of structures devoid of any function represents a poser for the finalist philosopher and for the supporters of design: if each organ is to serve a specific purpose in the internal organisation of the organism and is the result of the sharp work of a creative force infinitely wise, how does one justify the traces of useless or now disused organs, residues of a past too distant to decipher their usefulness?

Tracing vestiges and rudiments to an ideal and common *Bauplan* was the theoretical conviction on which it relied on the finalistic arrangement suggested by Severin Axell and those who saw in the adaptation of *Phanerogamae* the traces of an intelligent design guiding the progressive path towards the improvement of the floral organs. However, for Darwin, researching the basic floral model meant reconstructing the lineage from a common ancestor of orchids, along which it was possible to trace the immense variety of species that evolved from divergent specialisations mainly due to natural selection. Furthermore, the concept of common descent allowed the doctrine of homology in *Orchids* to open the field to the evolutionary interpretation of the vestigial organs[39], which, in Darwin's eyes, did not represent only the remains of an ancient genealogical heritage, but precious clues to reconstructing and deciphering the ancestral forms of ancestors and their environmental conditions. Specifically, the study of flowers demonstrated that these organs could be reused and acquire a new function, as in the case of *Malaxis paludosa,* where there is a cup clinandrum that protects the pollen mass, composed of two membranes representing

38 The Darwinian formulation was re-proposed by Mayr (E. MAYR, *The Growth of Biological Thought, Diversity, Evolution, and Inheritance*, The Belknap Press of Harvard University Press, London 1982, p. 562) and by Gould and Vrba (S. J. GOULD, E. S. VRBA, *Exaptation. Il bricolage dell'evoluzione*, Bollati Boringhieri, Torino 2008).

39 Vestiges are useless phenotypic features which, despite having lost their original adaptive function over time, many organisms inherit from their ancestors and which seem to exist as homologous counterparts functioning in other organisms.

the two upper anthers in the rudimentary state, therefore not working, but reused for a protection function[40].

Studies on flowers made it possible to reinterpret the useless parts of an organism, both in terms of usefulness for genealogical classification, and to understand the multiverse of evolution, where it was always possible to obtain a functional shift or a further adaptive refinement entirely unexpected or, more simply, a subtle link with history:

> At a period not far distant, naturalists will hear with surprise, perhaps with derision, that grave and learned men formerly maintained that such useless organs were not remnants retained by the principle of inheritance at corresponding periods of early growth, but were specially created and arranged in their proper places like dishes on a table (this is the comparison of a distinguished naturalist)[41] by an Omnipotent hand "to complete the scheme of nature"[42].

The opportunistic aspect of Darwinian nature, which self-evidently showed itself capable of reusing purposeless or rudimentary organs for a new function, as in *Malaxis*, demonstrated to supporters of intelligent design a concept of evolution that could do without new creations *ex novo* or adaptive processes necessarily aimed at perfecting all living structures.

These alternative functionalities could not be the result of the intervention of a rationality that dominated variation, because they could be reactivated by an unfolding of new environmental factors marked by historical contingencies[43].

Darwin did not destroy what, starting with Kant and Schopenhauer, philosophers called «internal finality» and which, referring to the Aristotelian concept of purpose, form, and power, they analogically linked to the concept of instruction or project contained in the DNA and placed as an internal and programmatic engine of individual ontogenesis[44].

The formation of the individual is not a topic on which Darwin methodologically argues in his writings on botany; however, Darwin's flowers

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40 C. DARWIN, *The Various Contrivances by Which British and Foreign Orchids Are Fertilised by Insects, and on the Good Effects of Intercrossing*, cit., pp. 131-132.

41 He refers to Augustin-Pyramus de Candolle (T. HOQUET, *Darwin teleologist? Design in the Orchids*, «Comptes Rendus Biologie», 333/2010, pp. 119-128).

42 C. DARWIN, *On the Various Contrivances by Which British and Foreign Orchids Are Fertilised by Insects, and on the Good Effects of Intercrossing*, cit., p. 244.

43 The case of *Malaxis* can be included in the so-called spandrels (S. J. GOULD, R. C. LEWONTIN, *The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme*, «Proc. R. Soc. Lond. B.», 205, 1161/1979, pp. 581-598).

44 A. LA VERGATA, *Darwin e la filosofia*, in «Atti della Società dei Naturalisti e Matematici di Modena», 147/2016, p. 313.

allow the disclosure of a methodological approach in radical opposition to the explanations that resort to finalism: the study of the variety of forms and physiology of orchids in terms of coevolutionary selective processes that can emerge in the heart of random events constitutes the fundamental Ariadne's thread that Darwin extends to the naturalists and philosophers of nature willing to follow him to the centre of the adaptive labyrinth of flowers.

To get out of this labyrinth, it is now necessary to conceive contrivances according to a new conceptual framework where randomness, co-optation, and rudiments entail the replacement of teleological reasoning with a probabilistic approach in nature where the hypotheses are tested through the study of homologies and selective dynamics.

4. Nature

The evolutionary perspective turned by Darwin to flower species and pollinator societies has opened new theoretical spaces in which to imagine and reconsider the meaning of the term nature. The heart of this new concept beats in the concept of adaptation, which in Darwin, in addition to denoting a phenotypic trait, intends above all to connote a way of understanding the relationship between organisms and the environment[45].

Contrivance indicated the complex adaptations of flowers, and starting in 1860, the author of *Orchids* distanced himself from the traditional semantic domain of the term developed by Paley and the natural theologians, who engraved the mark of divine creation that the naturalist had to recognise and connect to a static reality of essence and ideal types without defects[46]. The bright colours, scent, nectar, and countless floral biomechanisms now appeared to be adaptations to ensure cross-pollination by insects.

The concept of nature also slipped through osmosis into the semantic conversion of the term contrivance. The organic nature of Linnaeus' scholars did not admit gaps or breakages in the balance: each of its parts, each of its corners unfolded a luxuriant and infinite catalogue of life forms according to a *Scala naturae* that could be travelled from inorganic to organic without interruption. There was a solid and eternal relationship between living beings in which every little detail had a profound meaning and was designed to guarantee and preserve a balance that was founded in the mind of the Creator.

45 A. LA VERGATA, *L'evoluzione biologica: da Linneo a Darwin*, cit., p. 191.

46 M. GHISELIN, *Foreword* to Charles Darwin's The Various Contrivances by Which Orchids Are Fertilised by Insects, The University of Chicago Press, Chicago 1984.

Along the path that leads Darwin to reelaborate the mechanisms of speciation, the complex concept of struggle for existence takes on ever more precise contours to determine a reinterpretation of the Linnean natural economy: if selection turns out to be the key process of Darwinian evolutionary theory, the concept of struggle for existence remains complementary, associated, and inextricably linked to that of natural selection[47].

In this formula, we find two main aspects: firstly, the apparent local balance between the forms of life emerges on a stage behind the scenes in which it lurks a story of extinction and destruction that projects a precarious future and ready to be disrupted again by new and fortuitous events. In this context, adaptation no longer appears as a gift bestowed by the Creator, but as a result to be won at the price of life.

However, that was not all, since the flowers exhibited a peculiar adaptation. In his works dedicated to flowers, Darwin reached the certainty that the ecological flower-pollinator relationship had reached a level of specialised interdependence due to small and gradual variations in the structure and physiology of the flower on the one hand and in the behaviour and anatomy of the pollinating insect on the other, which accumulated from selection along geological temporal dimensions brought about profound coevolutionary changes in species[48].

A selective mutualistic bond brings advantages to both parties and reveals the most important meaning of the struggle for existence: a set of ecological interdependencies between species, infinitely complex, variegated, hidden, and deep but complementary, an inextricable network of complex connections and reciprocal relationships among living beings that establishes constraints and balances of what we call ecosystem[49].

Through his studies on flowers and insects, Darwin has allowed posterity to interpret the natural economy in terms of networks of complex connections capable of connecting organisms belonging to distant and apparently unrelated kingdoms, thus opening a new phase in the history of ecological sensitivity where the relationships of the living form a dense hidden plot where the alteration of a minimal element can cause enormous ecosystemic imbalances.

This idea of nature contrasts with the organicistic image of nature, which from Plato's Timaeus is absorbed by the Renaissance and goes back through

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47 A. LA VERGATA, *L'equilibrio e la guerra della natura*, Morano Editore, Napoli 1990.

48 C. DARWIN, *The Various Contrivances by Which British and Foreign Orchids Are Fertilised by Insects, and on the Good Effects of Intercrossing*, cit., pp. 165-166.

49 C. DARWIN, *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*, cit., p. 84.

Naturphilosophie to today's New Age positions. However, it also differs from the mechanistic model that established itself in the scientific revolution of the seventeenth century and which is seen in the writings of Bacon, Galileo, Descartes, and Newton the foundation of a new way of understanding the relationship between man and nature.

The settings of various philosophical problems related to reflections on nature, even the most current perspectives with an ecological orientation, contract a speculative debt with Darwinian writings on flowers. If nature turns out to be an ecosystemic and articulated complex where the parts influence each other and the joints can prove to be more or less strong support elements because between necessity and chance, the conception of the harmony of nature created by the hands of God falls. And with this fall, a philosophical moral reflection is increasingly conditioned by an ambiguous and intricate image, not at all reassuring and unitary, of a nature of which human beings are part. Darwin's reader is prompted to interpret the lack of balance, now no longer guaranteed by the secular and unfathomable simplicity of a divine mind, as a state to be shared[50].

Darwin's flowers, once they leave the scene of the explanatory tradition of natural theology, also lose the providential meaning that creation had assigned them. There was good in the world if God was committed to designing the infinite variety and beauty of flowers and ingenious contrivances: this was the proof that God exists and that nature persisted in a rigid and continuous way in beatifying humanity, who contemplated it from the outside. The consolatory function of this conception did not escape the historians and philosophers of nature, who filled their descriptions with moral reflections. Moreover, through the traditional scientific transmission of floral adaptation, questioning oneself about the functions and beauty of creation also meant guaranteeing a moral and social substratum that not only directed the modalities of scientific research, but also built conceptual bridges and forms of cultural reflection that allowed a common and reciprocal understanding of the argumentative formulas even for those who were not directly concerned with classification, such as poets, theologians, or amateurs. Darwin's floral works thus help to erode this substratum, and amid the loss of the usual cultural connecting points, philosophers are forced to construct new cultural coordinates and new tools for reflection to reach

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[50] P. ROSSI, *L'uomo di fronte alla natura: signoria o servitù*, in L. BATTAGLIA (ed.), *Filosofia ed Ecologia*, Abelardo Editrice, Tor san Lorenzo - Ardea 1994, pp. 19-38.

an overall reformulation of the theodicy[51] and the relation between science and philosophy in their historical dimensions[52].

There are other aspects of the struggle for life that are irreducible to a series of antagonistic behaviours and which form the basis of ecological insight[53]. In all those scenes of plant and animal life that occurred under Darwin's eyes and that he paints with precision in *Orchids* and other publications where he gives advice to botanists, plant breeders, general readers, and horticulturists, it is possible to find cultural modalities through which to regain the relationship with environmental forces and ecosystem[54]. The concept of coevolution, which Darwin explores through the understanding of orchids and pollinating insects' coadaptations, becomes a cultural tool to recognise our environmental interdependence and relationality and is repeatedly taken up and developed differently to address the ecological relationships we have with ourselves and other nonhuman subjects in the Anthropocene[55].

Finally, Darwinian floral contrivances have also been interpreted as signaling tools that guide insects to establish a cooperative relationship with plants[56]: a modality of ecological interaction between plants and ecosystems no less complex and fascinating than animal adaptations. The definitions of intelligence provided by different disciplines throughout the history of philosophy have often presupposed the presence of a nervous system as a premise to a wide range of activities ranging from perception to conceptual knowledge, to the faculty of judgment, and so on.

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51 A. LA VERGATA, *L'equilibrio e la guerra della natura*, cit.

52 L. KRUGER, *Why does history matter to philosophy and science?*, Selected Essays edited by T. Sturm, W. Carl and L. Daston, Walter de Gruyter, Berlin 2005.

53 J. JUSTUS, *Darwin's Evolutionary Ecology*, in M. RUSE (ed.), *The Cambridge Encyclopedia of Darwin and Evolutionary Thought*, Cambridge University Press, New York 2013, pp. 383-390.

54 C. DARWIN, *Humble-bees*, «Gardeners' Chronicle», 34/1841, p. 550; N. ELDREDGE, *Extinction and Evolution*, Firefly Books Ltd., Richmond Hill 2014; D. QUAMMEN, *Spillover, Animal Infections and the Next Human Pandemic*, Norton & Co., New York 2012.

55 Cf. the mutual aid or reciprocal advantage developed by Kropotkin (P. KROPOTKIN, *Mutual Aid, A Factor of Evolution*, Eleuthera, Milano 2020), and in position against Haeckel and Nietzsche's interpretation of struggle for existence. But also the most current readings of the coevolution between the plant world and human beings in the writings of Stefano Mancuso (S. MANCUSO, *Plant Revolution*, Giunti, Iolo 2017), and above all the literature relating to our interdependence and environmental fragility in relation to the spillover of zoonotic viruses (D. QUAMMEN, *Spillover, Animal Infections and the Next Human Pandemic*, Norton & Co., New York 2012) due to anthropic pressures as fragmented deforestation, which is closely related to the bushmeat and wildlife trade and air pollution.

56 S. MANCUSO, *Plant Revolution*, cit., pp. 115-118.

However, from an evolutionary point of view, the nonexistence of a brain in plants is not a lack, but rather a strategic alternative for adaptation and survival. The intelligence of floral plants then becomes a subtle and flexible ability to interact with other organisms living in the same ecosystem context, through the evolutionary refinement of their morphological and physiological traits according to the dynamics of Darwinian explanatory pluralism and as a function of an adaptive resolution of complex and unprecedented problems related to reproduction and survival.

This gave way to the new physiological research of the psychological principles that govern the botanical world, of which exponents are Stefano Mancuso[57] and Umberto Castiello[58], which can help philosophy to clarify the meaning of intelligence.

Conclusion

The choice of flowers and the significance of evolutionary floral works for the history of philosophy still echoes in the words of the naturalist who wrote: «I am quite convinced (Hooker & Huxley took the same view some months ago) that a philosophic view of nature can solely be driven into naturalists by treating special subjects»[59].

The birth of evolutionary floral morphology remains an event closely connected to the historical philosophical developments that affected the speculations of botanists, natural philosophers, and theologians of the nineteenth century all over the world: it inherited the logical and metaphysical roots of ancient and medieval philosophy linked to the definition and classification of species, it became the battlefield for the philosophies of the XVIII and XIX centuries from whose clash methods and tools emerge to turn reflections on nature into the scientific branches of learning; it determined some conceptual coordinates that influenced the reformulation of the theoretical-practical connections between philosophy and science.

The founding act of this discipline constitutes at the same time a Darwinian strategy: in demonstrating the ability of natural selection to explain the evolution of sophisticated floral contrivances, there is also a formidable attack on creationism and teleology and the formulation of a concept of

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57 E. BRENNER, R. STAHLBERG, S. MANCUSO, J. VIVANCO, F. BALUSKA, E. VAN VOLKENBURGH, *Plant neurobiology: an integrated view of plant signaling*, «Trends Plant Sci.», 11(8)/2006, pp. 413-419.

58 U. CASTIELLO, *La Mente delle Piante*, *Introduzione alla Psicologia Vegetale,* Il Mulino, Bologna 2019.

59 From Darwin to Henry Walter Bates, 3 December 1861, Darwin correspondence Project.

coevolution and nature intended as a turning point for the foundation of a new ecological sensitivity that no longer neglects the relationship with rationality of plants.

References

F. M. AROUET, *Zadig and other tales*, translated by R. B. Boswell, George Bell and Sons, London 1907

P. AYERS, *The Aliveness of Plants: the Darwins at the Dawn of Plant Science*, Pickering & Chatto, London 2008

N. BARLOW (ed.), *The autobiography of Charles Darwin*, Collins, London 1958

P. R. BELL (ed.), *Darwin's Biological Work, Some Aspects Reconsidered*, John Wiley & Sons, New York 1964

R. BELLON, *The Great Question in Agitation: George Bentham and the Origin of Species*, «Archives of Natural History», 30, 2/2003, pp. 282-297

R. BELLON, *Charles Darwin Solves the 'Riddle of the Flower'; or Why Don't Historian of Biology Know about the Birds and Bees?*, «History of Science», 47, 4/2009, pp. 373-406

R. BELLON, *Inspiration in the Harness of Daily Labor: Darwin, Botany and the Triumph of Evolution, 1859-1868*, «Isis», 102, 3/2011, pp. 392-420

E. BRENNER, R. STAHLBERG, S. MANCUSO, J. VIVANCO, F. BALUSKA, E. VAN VOLKENBURGH, *Plant neurobiology: an integrated view of plant signaling*, «Trends Plant Sci.», 11(8)/2006, pp. 413-419

G.-L. BUFFON, *Histoire naturelle*, IV: *Histoire des Quadrupèdes. L'âne*, in J. PIVETEAU (ed.), *Oeuvres philosophiques*, Presses Universitaires de France, Paris 1954

U. CASTIELLO, *La Mente delle Piante*, *Introduzione alla Psicologia Vegetale*, Il Mulino, Bologna 2019

S. de CHADAREVIAN, *Laboratory science versus country-house experiments. The controversy between Julius Sachs and Charles Darwin*, «The British Journal for the History of Science», 29/1996, pp. 17-41

G. CRISTOFOLINI, A. MANAGLIA (eds.), *Il giardino di Darwin, l'evoluzione delle piante*, Umberto Allemandi & Co., Torino 2009

H. CRÜGER, *A few notes on the fecundation of orchids*, «Journal of the Linnean Society of London (Botany)», VIII/1864, pp. 127-135

C. DARWIN, *Humble-bees*, «Gardeners' Chronicle», 34/1841, p. 550

C. DARWIN, *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*, John Murray, London 1859

C. DARWIN, *On the Two Forms, or Dimorphic Condition, in the Species of Primula, and on their remarkable Sexual Relations*, «Journal of the proceedings of the Linnean Society (botany)», 6, 22/1862, pp. 77-96

C. DARWIN, *On the three remarkable sexual forms of Catasetum tridentatum, an orchid in the possession of the Linnean Society*, «Journal of the proceedings of the Linnean Society (botany)», 6, 24/1862, pp. 151-157

C. DARWIN, *On the Various Contrivances by Which British and Foreign Orchids Are Fertilised by Insects, and on the Good Effects of Intercrossing*, John Murray, London 1862

C. DARWIN, *The Effects of Crossing and Self-Fertilisation in the Vegetable Kingdom*, John Murray, London 1876

C. DARWIN, *The Various Contrivances by Which British and Foreign Orchids Are Fertilised by Insects, and on the Good Effects of Intercrossing*, 2nd edition, D. Appleton & Co., New York 1877

C. DARWIN, *The Different Forms of Flowers in Plant of the Same Species,* John Murray, London 1877

E. DARWIN, *The Botanic Garden. A poem in Two Parts; Containing The Economy of Vegetation and the Loves of the Plants*, Jones & Co., London 1825

F. DARWIN, *The Life and Letters of Charles Darwin, Including an Autobiographical Chapter*, John Murray, London 1887

F. DARWIN, *The botanical work of Darwin*, Annals of Botany, 13/1899, pp. ix-xix, http://darwin-online.org.uk/content/frameset?itemID=A261&viewtype=text&pageseq=1

F. DELPINO, *Ulteriori Osservazioni sulla Dicogamia nel Regno Vegetale*, Tipografia Giuseppe Bernardoni, Milano 1870

J. DIAMOND, *Collapse: How societies choose to fail or succeed*, Penguin Putnam Inc., London 2004

H. DUPREE, *Asa Gray: American botanist, friend of Darwin*, Johns Hopkins University Press, Baltimore 1988

N. ELDREDGE, *Extinction and Evolution*, Firefly Books Ltd., Richmond Hill 2014

J. ENDERSBY, *Orchids, A Cultural History*, The University of Chicago Press, Chicago 2016

M. GHISELIN, *Foreword* to Charles Darwin's The Various Contrivances by Which Orchids Are Fertilised by Insects, The University of Chicago Press, Chicago 1984

S. J. GOULD, R. LEWONTIN, *The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme*, «Proc. R. Soc. Lond. B.», 205, 1161/1979, pp. 581-598

S. J. GOULD, E. S. VRBA, *Exaptation. Il bricolage dell'evoluzione*, Bollati Boringhieri, Torino 2008

A. GRAY, *Review of Fertilisation of Orchids*, «American Journal of Science and Arts», 2, 34/1862, pp. 138-144

J. JUSTUS, *Darwin's evolutionary ecology*, in M. RUSE (ed.), *The Cambridge Encyclopedia of Darwin and Evolutionary Thought*, University of Cambridge Press, Cambridge 2013, pp. 383-390

P. KNUTH, *Handbook of Flower Pollination*, Clarendon Press, Oxford 1906

L. KOERNER, *Carl Linnaeus in His Time and Place*, in N. JARDINE, J. A. SECORD, E. SPARY (eds.), *Cultures of Natural History*, Cambridge University Press, Cambridge 1996

D. KOHN, *Darwin's Garden: An Evolutionary Adventure*, The New York Botanical Garden, New York 2008

P. KROPOTKIN, *Mutual Aid, A Factor of Evolution*, Eleuthera, Milano 2020

L. KRUGER, *Why does history matter to philosophy and science?*, Selected Essays edited by T. Sturm, W. Carl and L. Daston, Walter de Gruyter, Berlin 2005

A. LA VERGATA, *L'evoluzione biologica: da Linneo a Darwin*, Loescher Editore, Torino 1979

A. LA VERGATA, *L'equilibrio e la guerra della natura*, Morano Editore, Napoli 1990

A. LA VERGATA, *Darwin e la filosofia*, «Atti della Società dei Naturalisti e Matematici di Modena», 147/2016, pp. 309-333

C. LINNEAUS, *Species Plantarum*, L. Salvius, Stockholm 1753

S. MANCUSO, *Plant Revolution*, Giunti, Iolo 2017

H. MÜLLER, *The Fertilisation of Flowers*, translated and edited by D'Arcy W. Thompson, Macmillan & Co., London 1883

G. PANCALDI, *Darwin in Italia, Impresa scientifica e frontiere culturali*, il Mulino, Bologna 1983

G. PANCALDI, *Teleologia e Darwinismo. La corrispondenza tra Charles Darwin e Federico Delpino*, CLUEB, Bologna 1984

D. PIEVANI, *Leggere* L'origine delle specie *di Darwin*, Ibis, Como 2015

D. QUAMMEN, *Spillover, Animal Infections and the Next Human Pandemic*, Norton & Co., New York 2012

J. RAY, *Wisdom of God manifested in the works of Creation*, W. Innys, London 1743

R. RICHARDS, *The Romantic Conception of Life. Science and Philosophy in the Age of Goethe*, The University of Chicago Press, Chicago 2002

P. ROSSI, *L'uomo di fronte alla natura: signoria o servitù*, in L. BATTAGLIA (ed.), *Filosofia ed Ecologia*, Abelardo Editrice, Tor san Lorenzo - Ardea 1994, pp. 19-38

M. RUSE (ed.), *The Cambridge Encyclopedia of Darwin and Evolutionary Thought*, Cambridge University Press, New York 2013

C. K. SPRENGEL, *Das entdeckte Geheimniss der Natur im Bau und der Befruchtung der Blumen*, Friedrich Vieweg, Berlin 1793

W. T. THISELTON DYER, *Work in Botany*, «Nature Series: Charles Darwin, Memorial Notice», MacMillan & Co., London 1882, pp. 29-45