

DAVIDE WEIBLE

Exaptation: towards a semiotic account
of a biological phenomenon



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TABLE OF CONTENTS

| | |
|---|-----|
| Acknowledgements | 7 |
| Publications included in the dissertation | 8 |
| Introduction | 9 |
| 1. Before exaptation: preadaptation and Chauncey Wright..... | 11 |
| 2. Wright and Peirce on pragmatism and evolution | 17 |
| 3. Peirce’s evolutionism: the role of continuity and iconic abduction | 22 |
| 4. Abduction and exaptation..... | 32 |
| 5. The iconic and exaptive logic of technological development | 39 |
| 6. The origin of bloodsucking: a case of evolutionary abduction?..... | 45 |
| 7. Concluding remarks on the case study..... | 58 |
| 8. General conclusions | 62 |
| 9. References | 64 |
| Overviews of articles..... | 71 |
| Summary | 73 |
| Summary in Estonian | 74 |
| Publications | 75 |
| Curriculum vitae..... | 139 |
| Elulookirjeldus | 140 |

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INTRODUCTION

The objective of my thesis is to develop a description of the evolutionary phenomenon of *exaptation* — new usages of previous existing biological traits, whether they be already functional or not — within the modeling framework of C. S. Peirce's theory of signs. At the same time, in line with the approach of the coiners of the term, reference is made to modes of evolution complementary to the formulation based on genetic mutations, natural selection and adaptation; specifically, attention is paid to the role of lifetime behavioral changes able to modify the organism's ecological setting and, as a consequence, to start different evolutionary pathways. Perception is emphasized as the common element linking such view with Peirce's phenomenology and a generalized conception of hypothetical inference is provided to accomplish the modeling.

The term and the concept of exaptation were first introduced in Gould and Vrba (1982) and further developed in Vrba and Gould (1986): it refers to “such characters, evolved for other usages (or for no function at all), and later “coopted” for their current role [...]. They owe their fitness to features present for other reasons, and are therefore fit (aptus) by reason of (ex) their form, or ex aptus” (Gould, Vrba 1982: 6). One of the best analysis and operational application has been provided by Arnold (1994), while Gould (2002) dwells extensively on the topic. The casuistry of exaptive phenomena is wide: useful reviews are Coddington (1988); Buss et al. (1998); Gregory (2008); McLennan (2008); Thanukos (2009). A list of Gould's essays and articles dealing with different kind of exaptations can be found in Pievani (2008).

The concept has been proved fecund in the field of molecular evolution too (Gould 2002: 1234–1246), in the context of evolutionary innovations (Wagner 2012: 106; Barve, Wagner 2013) and it is central in the framework of evolutionary developmental biology (Carroll 2005); besides, it has been used to describe some crucial turns in the evolution of hominids and *Homo sapiens* (Tattersall 1998, 2002; Linde-Medina 2011). The human brain is considered a particular “field of exaptations” (Pievani 2003: 78-89; Gould 2002; Anderson 2007), along with consciousness (Gould 1984; Pievani 2002: 327; Humphrey 1986; 1992), language (Traugott 2004; Hauser *et al.* 2002; Deacon 1997) and many other areas of human culture: religion (Gould 1984), morality (Chapman *et al.* 2009), sociality (Brown, Feldman 2009; MacDonald, Leary 2005), technology (Cattani 2005; Arthur 2009; Allen, Andriani 2007) and economics (Dew *et al.* 2004).

In linguistics, exaptation has been used to account for the change whereby lexical terms and constructions come in certain contexts to serve grammatical functions or to develop new ones: Lass (1990; 1997), Traugott (2004), Fanego (2004) and Narrog (2007). Within semiotics, Sebeok (1984; 1985a; 1985b, 1991) was one of the first proponents to introduce the term; in biosemiotics, it has been used for instance by Stjernfelt (2007), Vehkavaara (2002), Maran and Kleisner (2010), Artmann (2004).

The aim of this introductory section is to show how the three papers constituting the research project, however heterogeneous and dealing with different topics, are in fact animated by a common design that has come to assume progressively a more clearly defined profile. At the same time, new insights and knowledge have been collected since the last publication, so that their integration makes the introduction as such to stand out as an autonomous piece of work.

The method adopted is the same as in the papers: on one hand, a selective review of the scientific, semiotic and philosophical literature focusing both on exaptation and connected fields of inquiry; on the other hand, personal elaborations on that material. In addition, a case study is included, so as to allow the overall speculative styling to be paralleled by a more strictly empirical dimension, especially through the proposal of possible laboratory experimentations capable of testing the suggested hypothesis.

1. BEFORE EXAPTATION: PREADAPTATION AND CHAUNCEY WRIGHT

The first article (Weible 2012b) has established the basic setup within which later investigations have been carried on. Firstly, it stresses (also Gould, Lewontin 1979) the necessity to take into account possible alternative evolutionary trajectories and explanations leading to the property of a biological trait to promote fitness, whether it be an organ, a physiological process or a behavior. In this respect, along with the process of progressive genes-driven refinement towards optimality and attunement to relatively stable environmental conditions, there appears evident another key factor enhancing survival, namely the potential of morphological, behavioral and biochemical features to be applied to new usages.

Since absolute, *ex novo* functional recruitments are rather rare, peculiar relevance assumes that subset of situations where “a character, previously shaped by natural selection for a particular function (an adaptation), is coopted for a new use” (Gould, Vrba 1982: 5). This is the specific type of exaptation addressed by the case study, with a further qualification concerning the mechanism driving the cooption: the focus of attention is put on readjustments following those changes in the ethological rules of survival (Weible 2012a: 77) which are not triggered by genetic mutations, but instead due to organisms’ behavioral plasticity.

As for Gould’s and Vrba’s historical forerunners (Weible 2012a: 77–79), the references already mentioned need to be extended in order to provide an overview as much representative as possible of a debate that, although not in the same terms, has spread over more than a century. Beyond its linguistic innovation, the notion of exaptation exhibits a background dating back to the sixth chapter (“Difficulties on theory”) of the first edition of Darwin’s *On the Origin of Species* (1859) and to the seventh chapter (“Miscellaneous objections to the theory of natural selection”) added in the sixth edition (1872). Besides, an understanding close to F. Jacob’s idea of evolution as tinkering (1977) — a process strictly linked to phenomena of biological co-option (Pievani 2003: 75) — is contained in Darwin’s book (1862) on the fertilization of orchids by insects:

Although an organ may not have been originally formed for some special purpose, if it now serves for this end we are justified in saying that it is specially contrived for it. On the same principle, if a man were to make a machine for some special purpose, but were to use old wheels, springs, and pulleys, only slightly altered, the whole machine, with all its parts, might be said to be specially contrived for that purpose. Thus throughout nature almost every part of each living being has probably served, in a slightly modified condition, for diverse purposes, and has acted in the living machinery of many ancient and distinct specific forms. (Darwin 1862: 368)

After Darwin's work, analogous ideas — one-to-many and many-to-one dynamical relations between structure and function; recycling and reassembling of existing traits; low specialized organs to be developed towards better adaptations; and so forth — did not stop circulating. The following quotation by Raabe (1971: 1), taken from an article on the theories of A. N. Sewertzoff, is emblematic in this respect:

In his work of 1931 Sewertzoff accepted conscientiously and broadened the following concepts: Dohrn's "principle of the change of organ function" (1875), Kleinenberg's "principle of organ substitution" (1886), Plate's "principle of the function extension" and "principle of function intensification" (1924), and finally Fedotov's "principle of physiological substitution" (1927).

Sewertzoff himself added new tenets — “phase fixation, extinction of mediating functions, reduction of the function number, substitution of functions, immobilization of functions, similarization of functions, and division of organs and functions” (Raabe 1971: 1) — and formulated a *principle of multi-functionality* that closely reminds, more than 60 years beforehand, Arnold's distinction (1994: 138) between “addition exaptations” (a second use is added to the first) and “transfer exaptations” (the shift to a new use with loss of the old). For example, presumably “when the ancestors of carnivorous hemipteran bugs transferred from sucking sap on feeding on the internal fluids of animals, there was at least a brief phase where they did both. So their hypodermic proboscis was initially an addition exaptation to exploiting animal fluids, but later became a transfer exaptation” (Arnold 1994: 138). This quotation (which has plainly suggested the case study on blood-sucking addressed in the last section of the introduction) shares close affinity with the following:

The principle of the primary multifunctionality of organs, as assumed by Sewertzoff [...] means that an organ after having been already formed but not yet specialized, possesses a possibility of performing a certain number of functions. One of them becomes its main function, the others are secondary. In the subsequent development of the organ, a loss of secondary functions may occur and the organ becomes distinctly specialized. A predominance of another less important function may take place which assumes the character of the main function and even of the single one only. (Raabe 1971: 1)

Such similarities should not astonish, given a strong and widespread awareness of the issue among evolutionary biologists since Darwin's publications. After their early inception into the discussion, changes and extensions of functions have always been heavily debated topics, mainly because of the problematic aspects related to the precise identification of their reasons of origin. Analogous considerations (often under the same label of *preadaptation*, though not neces-

sarily coherent with each other as for its explanation) are contained in the works of several scholars: Davenport (1903), Morgan (1903), Cuénot (1911; see also Fisher, Stock 1915; Limoges, 1976; Gayon, 1995), Shull (1936), Goldschmidt (1940), Huxley (1942), Simpson (1944), Dobzhansky (1955), Bock (1959), Mayr (1959; 1982), Osche (1962). However, what is surprising is the relative lack of recognition of the philosophical root of the issue, which deeply influenced the author of the *Origin* himself.

C. Wright (1830–1875) was an American philosopher and mathematician who participated, together with Ch. S. Peirce, W. James and other intellectuals, to the informal discussion group known as *The Metaphysical Club*, held firstly in Cambridge in 1872. Though an almost forgotten thinker, recently there has been a reprint of his major writings and letters (Ryan, Madden 2000), which offers an overview of his several interests and testifies the key role played by his ideas within the history of the interpretations of biological evolution (for current applications of Wright’s thought within a semiotic and biological perspective, see Ostdiek 2011; 2012; 2015). After having welcomed enthusiastically *On the Origin of Species*, he was one of the first “to defend Darwin’s theory of natural selection, and to publish applications of that theory to [...] biological problems” (Wiener 1949: 31); he “produced the most level-headed discussions of his time concerning the philosophical meaning of Darwin’s work” (Wiener 1949: 32).

Specifically, Wright published a series of essays in the *North American Review* meant to counter critiques raised against Darwin’s theory. The first article (“Limits of natural selection”, 1870) was a critical review of A. R. Wallace’s *The limits of natural selection as applied to man* (1869) and took as a polemical target the idea that Darwin’s natural selection could not be responsible for the origin of man’s most distinctive features, thereby leaving space to a supernatural principle justifying the gap with other living beings. The second (“The genesis of species”, 1871: a critical review of St. G. Mivart’s *On the Genesis of Species*, 1871) and third article (“Evolution by natural selection”, 1872, a counter-reply to the letter Mivart sent to Wright’s editor in response to his critique) contained a careful unmasking of several misunderstandings (including the wrong interpretation of the concept of ‘accident’ and the mistaken belief that Darwin was deeming natural selection as the sole agent to be accounted for evolutionary changes), as well as refutations of the doctrine of the ‘specific genesis’ and discontinuous transformations.

Darwin read the first essay and quoted Wright in two positive notes of his *Descent of Man* (1871; further direct references to the philosopher can be found in the sixth edition of the *Origin*, 1872, and in the second edition of the *Descent*, 1874). When in June 1871 Wright sent to Darwin a letter containing the drafts of his second article (“The genesis of species”), they started an assiduous epistolary relationship that went on till 1875, year of the untimely death of Wright. The English naturalist was impressed to such a point by Wright’s deep understanding of the theory of natural selection that he himself, at his own expenses, published in England the same article. In 1872 they met in person

during Wright's trip to Europe and later on Darwin asked him to apply the theory of descent with modifications to such complex human traits as will, self-consciousness and language, which resulted in the philosopher's most important work: "The evolution of self-consciousness" (1873).

Wright's critical considerations were also directed against Darwin himself. For instance, "[h]e has not in his works repeated with sufficient frequency his faith in the universality of the law of causation" (Wright 1877: 130–131) — and that was exactly the reason behind Mivart's misconception about how natural selection really operates; besides, in "The genesis of species" he quoted an excerpt from *The Descent of Man* to emphasize Darwin's self-criticism regarding this principle: "I now admit that in the earlier editions of my 'Origin of Species' I probably attributed too much to the action of Natural Selection, or the survival of the fittest [...]. I had not formerly sufficiently considered the existence of many structures which appear to be [...] neither beneficial nor injurious; and this I believe to be one of the greatest oversights as yet detected in my work" (Wright 1877: 138–139; cf. Darwin 1871: 152).

To my knowledge, the Italian philosopher Parravicini (2009/2010) has been the only scholar to recognize the conceptual connection between Wright's *principle of new uses of old powers*, meant to amend anthropomorphism within the theory of evolution, and the contemporary notion of exaptation: just as the latter questions the idea of identifying present utilities and reasons for selection, so Parravicini defines as a "genetic fallacy" (Parravicini 2009/2010: 282; my translation) the attitude to take the results of a process and retrocede them at the beginning, as if the effects were the antecedent cause. Wright acknowledged the existence of such interpretative twist since his first article-review (1870; cf. Parravicini 2009/2010: 309–310) regarding Wallace's theory. Subsequently, it was adopted both in the critical review (1871) of Mivart's book and the counter-reply (1872) to his answer, to end up with an extensive and detailed application to the origin of language and use of signs in his "The evolution of self-consciousness" (1873). In our context, the incipit of the last essay is worth quoting in its entirety:

The truth is, on the contrary, that according to the theory of evolution, new uses of old powers arise discontinuously both in the bodily and mental natures of the animal, and in its individual developments, as well as in the development of its race, although, at their rise, these uses are small and of the smallest importance to life. They seem merged in the powers to which they are incident, and seem also merged in the special purposes or functions in which, however, they really have no part, and which are no parts of them. Their services or functions in life, though realized only incidentally at first, and in the feeblest degree, are just as distinct as they afterwards come to appear in their fullest development. The new uses are related to older powers only as accidents, so far as the special services of the older powers are concerned, although, from the more general point of view of natural law, their relations to older uses have not the character of

accidents, since these relations are, for the most part, determined by universal properties and laws, which are not specially related to the needs and conditions of living beings. Thus the uses of limbs for swimming, crawling, walking, leaping, climbing, and flying are distinct uses, and are related to each other only through the general mechanical principles of locomotion, through which some one use, in its first exercise, may be incident to some other, though, in its full exercise and perfection of special service, it is independent of the other, or has only a common dependence with the other or more general conditions.

Many mental as well as bodily powers thus have mixed natures, or independent uses; as, for example, the powers of the voice to call and allure, to warn and repel, and its uses in music and language; or the numerous uses of the human hand in services of strength and dexterity. And, on the contrary, the same uses are, in some cases, realized by independent organs as, for example, respiration in water and in the air by gills and lungs, or flight by means of fins, feathers, and webs. The appearance of a really new power in nature (using this word in the wide meaning attached to it in science), the power of flight in the first birds, for example, is only involved potentially in previous phenomena. In the same way, no act of self-consciousness, however elementary, may have been realized before man's first self-conscious act in the animal world; yet the act may have been involved potentially in pre-existing powers or causes. (Wright 1877: 199–201)

Several elements here remind of exaptation. Firstly, the very definition of the principle as a discontinuous modification of function, whether by phylogeny or ontogeny, calls for a mode of evolution consistent with the overall Darwinian paradigm but complementary to gradualism, thereby coming near to the contemporary contention that something could perform a function solely by means of adaptation through selection of successive and casual small variations in its structure. Secondly, the meaning of these incidental functional changes is close to Gould's and Vrba's adoption of G. C. Williams' terminology, according to whom "[f]ortuitous effects always connote a consequence following "accidentally" (Gould, Vrba 1982: 5), and not arising directly from construction by natural selection", so that "[a]daptations have functions; exaptations have effects" (Gould, Vrba 1982: 6). Thirdly, Wright's insistence on the relation between old and new functions (merged only at the beginning, but fully differentiated when properly strengthened) and on latter's progressive refinement reminds of two other aspects of exaptation: one refers to Arnold's treatment and his above mentioned definition of *addition exaptations* (a new use is added to the previous and both work together in the same structure); the other refers to Gould and Vrba's idea that in nature you can often see "a sequential set of adaptations, each converted to an exaptation of different effect that sets the basis for a subsequent adaptation" (Gould, Vrba 1982: 8).

This dynamics, just hinted at in the incipit of the article, is well captured in a subsequent passage, which assesses the true nature of natural selection and deals with the emergence of human mind: if the powers of memory, internal imaging and abstractive attention, useful for external perception, had been turned to the new function of reflective thinking (as it seems to have actually occurred), “the agency of natural selection would have been the same in preserving, and also in improving, the new faculty, provided this faculty was capable of improvement by degrees, and was not perfect from the first”. Indeed, a case of adaptation follows an exaptation. Eventually, Wright’s discussion ends with an open acknowledgement of the structural-functional redundancy principle, emphasizing its importance — as openly as Gould (1984; 2002) does — for anthropogenesis. In this respect, in a footnote to *The Descent of Man* (1871: 335) Darwin himself gives Wright the credit of having stressed the importance of the phenomenon of multi-functionality and its relative independence from selective adaptation and admits his own use of the general principle in the second chapter of the same work to explain the acquisition by man of some of his mental characteristics. As a matter of fact, “[m]any analogous cases could be advanced of organs and instincts originally adapted for one purpose, having been utilized for some quite distinct purpose” (Darwin 1871: 335). As already noted, the last edition of the *Origin* will then make great use of the same idea in the added chapter.

Wright’s interpretation of Darwin’s theory (within an original utilitarian paradigm), well in advance of pragmatism and subsequent evolutionary epistemologies, brought out a logic of evolution extensible to the process of scientific development through hypotheses generation and experimental verification. That is, on one hand “organic or behavioral variations can be thought of as a kind of *experimental hypotheses leaning out to the future* [...] just as, according to Wright, science hypotheses did” (Parravicini 2009/2010: 284; my translation); on the other hand, “natural selection is a retroactive mechanism of validation [...] the experimental “test” to verify the results, with which nature screens its hypotheses (Parravicini 2009/2010: 285; my translation). Extremely relevant to the development of my analysis is the contention that, along with mutations, also changes in behavior surge (analogically) to the title of hypothetical reasoning; the next step will be to show in which sense behavioral plasticity, abductive inference and functional shift are linked together.

2. WRIGHT AND PEIRCE ON PRAGMATISM AND EVOLUTION

As a matter of fact, the concepts of exaptation and abduction historically co-occurred together (concepts, not always the terms), but, although belonging to strictly related theoretical horizons, they never met in a coherent systematization. On one hand, “it is very likely that Wright gave currency to his genial ideas on Darwinism within the pragmatist setting” (Parravicini 2009/2010: 8; my translation) and that, as a clear example of this, “Wright’s application of Darwin’s views to language and its role in human reasoning, as well as to the natural origins of “self-consciousness”, influenced both William James and Charles Peirce” (Wiener 1949: 54; cf. CP 2.753). On the other hand, the guessing instinct considered by Peirce to be at the core of abduction is brought back to evolution (though not in Wright’s sense): we have a special aptitude for guessing right and “not man merely, but all animals derive by inheritance (presumably by natural selection) two classes of ideas which adapt them to their environment” (CP 2.753). To say, the two lines of inquiry came very close, but never touched. Since Wright saw an analogy between science development and biological evolution, one should also expect to find in the former field something analog to the principle of new functions for old structures; conversely, had Peirce being influenced by Wright’s ‘evolutionary epistemology’ and his idea of a logical-structural correspondence between inferential reasoning and organisms’ historical transformations, he himself might have noticed or established a parallelism between the way we give birth to scientific variations and the way nature produces sometimes its own variations, namely by re-functionalization of existing powers.

Within the semiotic tradition, Wright is not a totally unknown figure. In his book on the history of semiotics in the United States, Sebeok reports the content of a private communication with the Toronto philosopher David Savan where it is remarked that, thanks among others to the work of Wright, “there was a strong concern with signs, evidence and evidences, representation and representatives, and the connection of all this with action. So that Peirce’s semiotic is not a *creatio ex nihilo* but can be seen as the culmination of 120 years of development” (Sebeok 1991: 7). For Parravicini (2009/2010: 155) there are roughly three main positions as for Wright’s relationship to American philosophy: for S. Ratner, Wright did found pragmatism; for others, such as G. Kennedy and P. P. Wiener, he simply prefigured it; eventually, for M. H. Fisch and E. H. Madden he influenced pragmatism, but there occur at the same time striking differences and developments.

In order to examine the probability of an historical meeting between the two notions, my focus falls on two of them. On one hand, the choice of Madden is dictated by his being acknowledged as the most important scholar of Wright, thus specifically useful to set up properly his connection with Peirce insofar the birth of pragmatism is concerned. Wiener has been chosen instead for his

attention on the 19th century controversy on evolution, before and after Darwin's revolution, and its pertinence for the development of Peirce's thought. The main goal is to look for explicit influences proving or not that there already happened an acknowledgement of the structural similarity between processes of biological functional change and hypothetical inferences.

For Madden (1953) Wright cannot be properly defined a founder of pragmatism, in many respects. Firstly, although he thought of scientific ideas as working hypothesis and provided a general logic of scientific procedure, he never went so far as to generalize the experimental method to thinking as such, that is "he didn't have a general 'theory' of mind, meaning, or truth" (Madden 1953: 65); on the contrary, "[p]hilosophers after Wright generalized the working hypothesis-criterion into the pragmatic conception of mind [...] all ideas are working hypotheses; all thinking is experimental, and scientific experimentation, insofar as it has ideal controls, is simply a limiting case of thinking" (Madden 1953: 65). Besides, for the pragmatists "the mental, on all biological levels, functionally considered, is adaptive behavior...and consequently continuity exists between the different phylogenetic levels" (Madden 1953: 65). Wright did put forward a "functional-adaptive view of consciousness" (Parravicini 2009/2010: 394; my translation), but he never extended it to the mental level of scientific thought.

Secondly, despite the tendency to take Peirce's pragmatic maxim and its later versions back to Wright's viewpoint, Madden maintains that "the element which Wright's meaning criterion has in common with the pragmatic principle is not peculiar to pragmatism and that the characteristic elements of the latter are not prefigured by Wright" (Madden 1953: 66). Although they had in common the principle of verification by sensuous experience, on one side Wright did not generalize it to simple empirical propositions: if for Peirce, for instance, the proposition "x is hard" is an hypothesis about further experiences, whose whole meaning consists of conceivable and actual practical consequences, for Wright instead it means that "x exhibits a certain property the meaning of which is provided denotatively by instances of direct sensory experiences" (Madden 1972: 49) and hence on this point he "cannot be said to anticipate Peirce's or any other pragmatic interpretation" (Madden 1972: 49). On the other side, the principle was not peculiar to him or pragmatism, since it was shared by other philosophical traditions and he just contributed to a revival. Above all, the greatest difference is perhaps "the pragmatist's emphasis on the manipulation that intervenes before verification" (Madden 1972: 68), something that cannot be found anywhere in Wright's writings.

Eventually, Madden (1956: 420) challenges the idea suggested by several commentators that "Wright's concepts of 'cosmical weather', 'accident', and the attendant notion of irregularity [...] anticipated and perhaps influenced the tychistic views of the younger men", that is Peirce and James. As for irregularity, if for Peirce it is due to absolute chance, an ontological reality operative in the cosmos (CP 6.302), on the contrary for Wright it is a function of causal complexity and thus just endowed with an epistemological status. The same

holds for accidents, “not a characteristic of events but of our knowledge of them; it does not mean that events are uncaused but that we do not know the cause” (Madden 1956: 422); in a word, “Wright believed what Peirce later denied” (Madden 1956: 422).

In conclusion, it is true that for Peirce the adoption of pragmatism and its elaboration in a method of philosophical inquiry came from the collective discussions held at *The Metaphysical Club* of Cambridge and, among the various members, “Chauncey Wright, something of a philosophical celebrity in those days, was never absent from our meetings” (CP 5.12). It is also true that the grounding writings of Peirce’s version of pragmatism — “The fixation of belief” (CP 5.358–5.387) and “How to make our ideas clear” (CP 5.286–5.302) — were nothing but an extended versions of a paper read at the club (CP 7.313; Parravicini 2009/2010: 96). Nonetheless, “Peirce and James did not seem to think that Wright had given them a push in the direction of what later came to be known as pragmatism” (Madden 1952: 29).

In the case of evolution, three areas of comparison can be singled out: the epistemological status of Darwin’s theory; their different approach to Lamarck’s account; the issue of evolutionism as a generalization from biology to other fields.

As for the first point, on one hand Peirce “could not concur with Wright in holding that Darwin’s theory of evolution was in line with the sensationalistic nominalism of Mill” (Wiener 1949: 72) and, more generally, they “did not see eye to eye on the significance of Darwin’s work” (Wiener 1949: 75). If Wright did show enthusiasm for the new theory of evolution, on the contrary Peirce even questioned its scientific validity (while accepting the empiric method): “his hypothesis [...] did not appear, at first, at all near to being proved; and to a sober mind its case looks less hopeful now than it did twenty years ago” (CP 6.297). Differently from Wright, Peirce was however able to detect the connection between Darwin’s idea of chance variations in biology and the application of probability theory and statistical methods to such different sciences as physics and sociology.

On the other hand, if for Wiener “Wright wished to confine evolution to natural selection” (Wiener 1949: 63) and (less radically) did not provide explicitly any clear and thorough analysis of the diverse mechanisms bringing about the functional shift at the basis of his principle, in Peirce’s view instead Darwin’s hypothesis was just one of three equally operative modes of organic, psychological and cosmological evolution. Along with the Darwinian mode, he thus granted evolutionary effectiveness to cataclysmal abrupt changes and the inheritance of acquired traits too; and this not on the basis of empirical evidence, but “on the neat ways in which they fitted into his metaphysical and theistic evolutionism” (Wiener 1949: 78).

Regarding Lamarck’s theory of the transmission of acquired characters, “Wright was cautious enough to state his acceptance with plenty of “ifs”” (Wiener 1949: 60) and in his last letter to Darwin in 1875 he openly professed the “abandonment of the Lamarckian idea of “use” as an evolutionary factor”

(Wiener 1949: 60). This refusal is in line with Wright's general stricture about the practice of referring in biology to such teleological ideas as beginning, directionality, progress and final state, among which Lamarck's purposive effort of individual organisms to overcome environmental difficulties was obviously at ease.

For Peirce was quite the opposite. Despite considering the publication of the *Origin of Species* and its demonstration of the existence of irreversible biological transformations to be responsible of "the greatest mental awakening since Newton and Leibniz" (Fisch *et al.* 1986: 254) and granting it a great methodological value, only "Lamarckian evolution coincides with the general description of the action of love" (CP 6.300), namely with *agapasm*, the chief evolutionary mode of which "tychasm [Darwinism] and anancasm are degenerate forms" (CP 6.303). With respect to the theme of final causes, "[t]o say that the future does not influence the present is untenable doctrine. It is as much as to say that there are no final causes, or ends. The organic world is full of refutations of that position. Such action [by final causation] constitutes evolution" (CP 2.86).

As for the third point, it must be noted that Peirce's acceptance of alternative modes of biological evolution was functional "to make the broadest possible use of the idea of evolution, to extend it to encompass the history and logic of thought" (Wiener 1949: 81). If both pointed out the statistical nature of biological laws (though on the basis of diametrically opposed conceptions about chance and, consequently, of radically different positions concerning their nominalist or realist status), Wright however "raised critical objections to the extension of Darwin's theory of natural selection beyond biological and psychological phenomena to cosmological and theological domains" (Wiener 1949: 9). For Wiener, Peirce didn't adhere coherently to a key point of his own pragmatic maxim: if the meaning of a concept consists in the summation of its conceivable effects and the latter split into verifiable hypothesis and unverifiable metaphysical generalizations, then "in the important case of evolution, Wright restricted its meaning to the former class of effects, whereas Peirce was led into an endless labyrinth of metaphysical problems by speculating on a cosmic evolutionism, despite the warnings of his older friend Wright" (Wiener 1949: 65). That is, the latter didn't take into account at all the former's advice that "it was far from established that the detailed evidence from the various sciences warranted any metaphysical extension of the evolutionary concept from the organic to the vaster inorganic world" (Wiener 1949: 63).

Two factors prevented Wright from establishing a coincidence between biological evolution and scientific development: absence of full-fledged continuity between mental activity and scientific thought and partial denial of the capacity of living beings' behavioral activities to shape their evolutionary paths. This said, an element of affinity with Peirce can anyway be acknowledged. Since they knew and kept in high consideration W. Whewell's *History of the inductive sciences* (1837) and *Philosophy of the inductive science* (1840), both put in the foreground the role of hypotheses and their confirmation through

experimentation (Parravicini 2009/2010: 149). Besides, they acknowledged the imaginative and counterfactual features of scientific thinking (Parravicini 2009/2010: 199) and Wright's account of the explanative process—in line with his adherence to the postulate of universal causality, which denied the reality of casual or undetermined novelties — came very close to Peirce's concept of abduction: for both, to explicate is to bring the unknown back to the know as the case of a rule (Parravicini 2009/2010: 294). This logic was applied by Wright to make continuous such seemingly discontinuous phenomena as the emergence of biological novelties, i.e. his principle of new uses for old powers included. In a word, he was somehow already applying abduction to exaptation without recognizing their intimate connection.

Most of all, Wright's view on scientific hypotheses was not only consistent with Peirce's analysis of abductive reasoning — creative, but nonetheless inferential and thus linked to the past — but all the same he insisted on their perceptive side. For the latter, “all knowledge without exception comes from observation” (MS CSP L75 C, 1902, 91–92; quoted from Stjernfelt 2007: xiii) and that is particularly true of abduction; for the former, while maintaining that the natural philosopher must educate himself in the way empirical sciences “make knowledge profitable in the ascertainment of new truths”, their utility depends “on their capacity to enlarge our experience by bringing to *notice* residual phenomena, and making us *observe* what we have entirely *overlooked*, or search out what has eluded our *observation*. [...] They are rather the *eyes* with which nature is *seen*” (Wright 1877: 55; emphases mine). Later on, it will be clear that, as for processes of re-functionalization, this is more than a metaphor.

3. PEIRCE'S EVOLUTIONISM: THE ROLE OF CONTINUITY AND ICONIC ABDUCTION

Whatever the historical truth — whether Wright founded, prefigured or influenced the nascent pragmatism (and Peirce), or whether it came out spontaneously from the sharing of ideas developed in collective discussions — it is for sure that in Peirce's writings no direct reference to Wright's principle of redundancy between structures and functions can be found. Two favorable opportunities had however occurred. Firstly, if for Wiener Peirce's belief of a correspondence between history of science and natural evolution grew up "probably under the influence of the evolutionary conception of consciousness which Wright had elaborated in his "psycho-zoology" or "Evolution of Self-Consciousness"" (Wiener 1949: 80), then he did get in touch with the principle of new uses for old powers, without considering it enough important to be integrated in his later evolutionary cosmology, even as a corrective to strict Darwinism. Secondly, "it's very likely that, as suggested by Max Fisch, all members of the "Metaphysical Club" read Wright's work on the *Limits of natural selection*" (Parravicini 2009/2010: 356) and the same principle appears here as well. To sum, Peirce did come in touch at least twice with the core idea of what would have been developed under the concepts of preadaptation or exaptation and went beyond, not granting it enough theoretical weight.

Exaptation and abduction never met. Neither in Wright, with his analogy between biological evolution and scientific development, not meant to be a genealogical isomorphism (novel natural traits and scientific hypothesis *do* occur by means of similar and evolutionary linked processes); nor in Peirce, with his genealogical isomorphism (for instance, the three forms of inference — abduction, induction, deduction — are scientific, psychological and biological modalities of development, with no solution of continuity), but neglecting at the same time Wright's suggestion of a specific mechanism of production of variations consistent with Darwinism.

A major problem arises: how can exaptation and abduction be integrated if the latter has been organically included in a cosmology where the chief evolutionary role is played by Lamarckism, while the former places itself as a competing proposal within a paradigm that, by being defined "post-Darwinian" (Favareau 2010: 436; Hoffmeyer 2008; Kull 1999), is not against Darwin's work, but definitely does not accept Lamarck's solution? Two questions need therefore then to be answered: was Peirce's position really anti-Darwinian? What did it actually mean for him to support a Lamarckian viewpoint?

As for the nature of Peirce's attacks towards Darwinism, it has been noticed by P. Skagestad that he was the first thinker who seriously tackled the issue of "how come evolution through natural selection has produced a new and different mode of evolution which does *not* operate through natural selection?" (Skagestad 1979: 88). Although he regarded Darwin's theory as a matter of logic and pointed out "an aspect which Darwin himself tried to conceal in

embarrassment, namely the employment of chance as a mode of explanation” (Skagestad 1979: 90), he did not consider it sufficient.

On one hand, quite a number of Peirce’s remarks were made “in the context of discussions of the origin and growth of intellectual activities in general, and of science in particular” (Skagestad 1979: 91). Somewhat close to Wright’s description of the evolutionary origin of our conceptual distinctions between mind and world, subject and object, and so forth, he conferred on such “rudimentary world-view” ideas as force and matter an adaptive value because of their development in the human mind through the action of natural selection (Skagestad 1979: 91–93; see also CP 5.591).

On the other hand, he denied “that natural selection can play any significant role in the internal development of science” (Skagestad 1979: 94), for three reasons: firstly, science also progresses by means of intentional modifications of old theories to make them fit newly observed facts and great conceptual revolutions (that is, biologically speaking, via Lamarckism and cataclysmic events); secondly, the relative exactitude on the long run of scientific hypotheses is in contrast with the adaptations of nature, which for Peirce “are never found to be quite perfect” (CP 6.50); thirdly, “pure science has nothing at all to do with action...nothing is *vital* for science” and the scientist, as for his conclusions, “risks nothing upon them. He stands ready to abandon one or all as soon as experience opposes them” (CP 1.635) — scientific hypotheses are not beliefs, because “we *believe* the proposition we are ready to act upon” (CP 1.635), and therefore science is not a tool for action.

Since Peirce was “warning against the threat to scientific progress of placing science under externally imposed social and political goals” and “arguing against the intrusion of provisional and tentative scientific conclusions [...] into practical affairs, such as those of religion” (Skagestad 1979: 101), it is possible “to interpret his criticisms of Darwin’s theory as really part of a polemic against the “Darwinian” instrumentalists of his time” (Skagestad 1979: 102). Besides, because of the theory of synechism, Peirce approached evolution according to his logic of scientific development and method. This is consistent with several statements by Wiener: “[t]he historical order of Peirce’s writings [...] shows plainly that traditional metaphysical and logical problems and ways of thinking [...] *antedated his evolutionism*” (Wiener 1949: 79; emphasis mine); “in order to make the broadest possible use of the idea of evolution, *to extend it to encompass the history and logic of thought...Peirce enlarged the idea of evolution*” (Wiener 1949: 81; emphasis mine) to include Lamarck’s theory and cataclysmic changes; “Peirce regarded Darwin’s “chance variations” as illustrating his metaphysical category of Firstness [...] Darwin’s “struggle for existence” as illustrating Secondness [...] the quasi-teleological idea of natural selection by survival of the fittest and the Lamarckian reproduction of adaptive characters, illustrate Thirdness” (Wiener 1949: 85).

Given this clarification, it is thus possible to fully agree with Wiener’s assertion that Peirce’s Lamarckism was not based on biological evidence. At the same time, Skagestad’s conclusions on his anti-Darwinism are consistent with

the present topic. If Peirce's problem was to bring together the necessity to apply biological evolution to cultural and scientific development on one hand and the uselessness of science (in the short run) on the other hand, "[w]hat still needs explaining, therefore, is how evolution through natural selection can have given rise to a different mode of evolution, *not* acting through natural selection" (Skagestad 1979: 109). For Peirce, "[i]n the lower stages of his mental activity, man...evolves through organic adaptation...; in the higher stages, he evolves through a process where each individual step may be counter-adaptive" (Skagestad 1979: 109). While elaborating on the article "The Fixation of Belief" and dealing with the similar dilemma of how the method of science could have evolved and picked up by natural selection despite its nature, Skagestad's answer is the following:

what Peirce is saying is that *rationality is 'pleiotropic'* — i.e. it comes in a package-deal, like the gene which protects against malaria, but causes sickle-cell anemia. *The evolution of rationality is itself an adaptive step* in the process of developing fixed belief; but, once rationality has evolved, it may act through counter-adaptive intermediate steps, thereby generating its own, novel mode of evolution. Hence one may consistently view *science as an animal activity*, which has originated from, and is maintained by, natural selection, but *whose internal growth is yet governed by its own, non-natural mechanisms of variation and selection*.

[...] Peirce in fact anticipated questions which are still in the fore of the discussion, and proposed answers which are at least not outdated by the subsequent progress of biology. His arguments remain a powerful challenge to the recent trends of sociobiology and evolutionary epistemology. (Skagestad 1979: 112; my emphases)

However strong and binding such an interpretation might be, a further issue calls for clarification: was Peirce a true follower of Lamarck? Did he really support the theory of inheritance of acquired characters? These are some claims of his:

The changes have not been fortuitous but wholly the result of strivings of the individuals (CP 1.104)

The Lamarckian theory also supposes that the development of species has taken place by a long series of insensible changes, but it supposes that those changes have taken place during the lives of the individuals, in consequence of effort and exercise, and that reproduction plays no part in the process except in preserving these modifications. Thus, the Lamarckian theory only explains the development of characters for which individuals strive, while the Darwinian theory only explains the production of characters really beneficial to the race, though these may be fatal to individuals. But more broadly and philosophically conceived,

Darwinian evolution is evolution by the operation of chance, and the destruction of bad results, while Lamarckian evolution is evolution by the effect of habit and effort. (CP 6.16)

A third method, which supersedes their strife, lies enwrapped in the theory of Lamarck. According to his view, all that distinguishes the highest organic forms from the most rudimentary has been brought about by little hypertrophies or atrophies which have affected individuals early in their lives, and have been transmitted to their offspring. Such a transmission of acquired characters is of the general nature of habit-taking, and this is the representative and derivative within the physiological domain of the law of mind [...] The Lamarckians further suppose that, although some of the modifications of form so transmitted were originally due to mechanical causes, yet the chief factors of their first production were the straining of endeavor and the overgrowth superinduced by exercise, together with the opposite actions (CP 6.299)

Lamarckian evolution is thus evolution by the force of habit [...] Now it is energetic projaculation (lucky there is such a word, or this untried hand might have been put to inventing one) by which in the typical instances of Lamarckian evolution the new elements of form are first created. Habit, however, forces them to take practical shapes, compatible with the structures they affect, and, in the form of heredity and otherwise, gradually replaces the spontaneous energy that sustains them. Thus, habit plays a double part; it serves to establish the new features, and also to bring them into harmony with the general morphology and function of the animals and plants to which they belong (CP 6.300)

Despite such Lamarckian profession of faith, it has been argued (Pietarinen 2012: 76) that Peirce's "evolution by creative love" may be close to the so-called Baldwin effect (which is consistent with Pievani's third type of exaptation); therefore, there might be a basis on which to attempt to frame evolutionary functional shifts within a Peircean paradigm. Besides, this reading goes as far as to conjecture that Baldwin's ideas — "ontogenetic adaptations are really new, not performed; and they are really reproduced in succeeding generations, although not physically inherited" (Pietarinen 2012: 77) — could have been influenced by Peirce's 1893 *Monist* article "Evolutionary Love". Pietarinen's proposal stands on the assumption that, had Peirce explicitly spoken of contextual changes, liable to be equated in a way to behavioral lifetime constructions of new ecological niches, he would have predated and influenced that simulated form of Lamarckism which Baldwinian evolution is. However, this can not be inferred from the previous excerpt: firstly, "energetic projaculation" does not indicate a way of transmission, but rather a cause of transformation; secondly, changes are always ascribed to "forms", which seem to suggest organs rather than contexts. The only possible clue still remaining is that habit, "in the form

of heredity and *otherwise*, gradually replaces the spontaneous energy that sustains them” (CP 6.300; emphasis mine)—too little to build on a speculative interpretation.

In order to understand how Peirce’s Lamarckism truly works — and to reveal it in a theoretical form compatible with the current modeling project—attention must be paid to two articles: “Evolutionary Love” (from which some of the definitions above mentioned are taken), and “The Law of Mind”. In the first one, via assimilation to the action of love, it is characterized (not only analogically, but literally) as mind-like, thus intentional or goal directed and regarding the development of ideas (rules of action or habits); ultimately, it identifies with learning: Lamarckian evolution, by being induced by individual efforts, derives from psychological laws and “growth by exercise takes place also in the mind. Indeed, that is what it is to learn [...]. Patient attention will be able to trace all these elements in the transaction called learning” (CP 6.301).

Given the overlap between beliefs or ideas and habits, there is a problem of interpretation: does Peirce’s Lamarckism concern primarily the acquisition of new pragmatic rules or their expansion through new applications? This is important to be clarified, especially when it will come to abduction, which has been articulated by scholars in several subspecies and whose implication as a modeling device is not that simple at first. Peirce is ambiguous thereupon. On one hand, the love-driven development of thought consists in the “*adoption* of certain mental tendencies, not altogether heedlessly, as in tychasm, nor quite blindly by the mere force of circumstances or of logic, as in anancasm, but by an immediate attraction for the idea itself” (CP 6.307; emphasis mine). This seems to imply the adoption of something new altogether. On the other hand, other expressions are pointing in a different direction: “The agapastic development of thought should, if it exists, be distinguished by its purposive character, this purpose being the *development* of an idea” (CP 6.315; emphasis mine). Besides, the previous excerpts regarding Peirce’s definitions do not tell precisely whether the habit establishing new features has been constructed ex-novo or not. At least in “Evolutionary Love”, the concept of development does not seem to focus much on the internal or cognitive process of extending one’s own ideas, but rather on the way they are communicated and apprehended within a community or by single individuals; that is, development means in this case “extension” or “diffusion” and conflates partially with the meaning of “adoption”.

A complementary understanding gets in if one turns to the second article, in this following the indications of the author himself: “endeavor, since it is directed toward an end, is essentially psychical, even though it be sometimes unconscious; and the growth due to exercise, as I argued in my last paper, follows a law of a character quite contrary to that of mechanics” (CP 6.299). Given that ideas spread through continuity among people, they develop in the same way inside each single mind too and this is the only way to create a sound analogy between the “agapastic development of thought” and natural evolution, unless admitting that organisms do transmit each other habits during their

lifetime (impossible for those lower forms devoid of any ability to change behavior by imitation). In such cases, how does an idea gain its power to become effective? In Peirce's words, "[h]abit is that specialization of the law of mind whereby a general idea gains the power of exciting reactions. But in order that the general idea should attain all its functionality, it is necessary, also, that it should become suggestible by sensations. That is accomplished by a psychical process having the form of hypothetic inference" (CP 6.145). Thus, within the realm of biology, Lamarckian evolution does not represent neither *deduction*, where the mind is already under the dominion of a prior general rule of action, nor *induction*, through which a habit becomes established or corroborated, but *abduction*.

It must be noticed that elsewhere Peirce denies the connection between Lamarckism and abduction, which is typical of scientific discoveries: the former "is not the way in which science mainly progresses. It advances *by leaps*; and the impulse for each leap is either some new observational resource, or some novel way of reasoning about the observations [...] it draws attention to relations between facts which would previously have been passed by unperceived" (CP 1.109); as for new theories, "we see new ideas connected with new observational methods [...] It is not by *insensible steps*" (CP 1.109). However, firstly the contrast regards more the effects (radical novelties against gradual changes) than other aspects, such as for example the internal logic ruling both processes; secondly, precisely this logic is isomorphic: on one side, for a habit to be taken or become functional, it must be connected to sensations previously unable to trigger its rule of action; on the other side, hypotheses are built on the basis of new or hitherto unexplained facts which become accountable by existing theories. Eventually, such setting accommodates Peirce's description of the action of love too: "Love, recognizing germs of loveliness in the hateful, gradually warms it into life, and makes it lovely" (CP 6.289).

For the continuity between these two processes to be fully realized, one has to recognize the physiological meaning of the concept of inference or reasoning, according to Peirce's famous example of the frog. Given that the cognition of rules needs not to be conscious and cases, results and rules correspond respectively to sensations, volitions or decisions to act and habit or rules of action, then the following:

a syllogism in Barbara virtually takes place when we irritate the foot of a decapitated frog. The connection between the afferent and efferent nerve, whatever it may be, constitutes a nervous habit, a rule of action, which is the physiological analogue of the major premiss. The disturbance of the ganglionic equilibrium, owing to the irritation, is the physiological form of that which, psychologically considered, is a sensation; and, logically considered, is the occurrence of a case. The explosion through the efferent nerve is the physiological form of that which psychologically is a volition, and logically the inference of a result (CP 2.711).

Peirce produces a neat physiological translation of deduction (which proceeds from rule and case to result): “a general idea suggests in each case a corresponding reaction. But a certain sensation is seen to involve that idea. Consequently, that sensation is followed by that reaction. That is the way the hind legs of a frog, separated from the rest of the body, reason, when you pinch them” (CP 6.144). At the same time, it is not difficult to conceive the formation process of such a connection, accomplished through induction (which proceeds from case and result to rule): after several repetitions of a specific detrimental event, which is perceived by the frog’s body, and the following of a specific action or movement of relief or clearing, able to cope successfully with the situation, the succession becomes established as invariant from that moment onwards. But how is abduction (which proceeds from rule and result to case) to be understood from a physiological perspective?

Some clues come from Peirce’s statement that hypothetical inference “is the formula of the acquirement of secondary sensation — a process by which a confused concatenation of predicates is brought into order under a synthetizing predicate” (CP 2.712). Moreover, an idea attains proper functionality by becoming suggestible by sensations and this equates to *induction from qualities*:

For example, I know that the kind of man known and classed as a "mugwump" has certain characteristics. He has a high self-respect and places great value upon social distinction. He laments the great part that rowdyism and unrefined good fellowship play in the dealings of American politicians with their constituency. He thinks that the reform which would follow from the abandonment of the system by which the distribution of offices is made to strengthen party organizations and a return to the original and essential conception of office-filling would be found an unmixed good. He holds that monetary considerations should usually be the decisive ones in questions of public policy. He respects the principle of individualism and of laissez-faire as the greatest agency of civilization. These views, among others, I know to be obtrusive marks of a "mugwump." Now, suppose I casually meet a man in a railway train, and falling into conversation find that he holds opinions of this sort; I am naturally led to suppose that he is a "mugwump." That is hypothetic inference. That is to say, *a number of readily verifiable marks of a mugwump being selected, I find this man has these, and infer that he has all the other characters which go to make a thinker of that stripe.* (CP 6.145; emphases mine)

Here it becomes clear one of the meanings of the concept of knowledge, namely knowing as re-cognizing something unfamiliar as familiar. This is almost tautological and, in fact, the innovative power of abduction does not come from its logical form, but rather from an act of “creative perception” (Stjernfelt 2007: 331–332). What is perceived exactly? For Peirce, “[t]he mode of suggestion by which, in abduction, the facts suggest the hypothesis is by *resemblance*...the

resemblance of the facts to the *consequences* of the hypothesis” (CP 7.218; emphasis mine). This stands out in another example quite similar:

Suppose, then, that, being seated in a street car, I remark a man opposite to me whose appearance and behavior unite characters which I am surprised to find together in the same person. I ask myself, How can this be? Suppose I find this problematic reply: Perhaps he is an ex-priest. He is the very image of such a person; he presents an *icon* of an ex-priest. Here is an *iconic argument*, or *abduction* of it (quoted from Stjernfelt 2007: 340; emphases mine).

Elsewhere, Peirce reiterates the same: “Hypothesis is [...] where we find that in certain respects two objects have a strong resemblance, and infer that they resemble one another strongly in other respects” (CP 2.624). Since Peirce thinks of icons as signs “whose significant character which causes them to be so interpreted is their possessing a *quality*, in consequence of which they may be taken as *representative of anything* that may happen to exist *that has that quality*” (Peirce 1903; MS [R] 462: 86; emphases mine), then both mental experiments display situations where present qualities of persons or objects are resembling those (and recalling others) which have already been collected under a common typifying label, thereby suggesting a possible categorization to be applied in the new context too. Back to the frog example, if its sensory apparatus came into contact for instance with a substance presenting some degree of similarity to those stimuli (or inducing corresponding sensations) which became associated with specific reactions in the first place, and if an identical action were elicited, then as a matter of fact the organism as a whole would produce an abduction. In this way, the frog’s ability to remove from skin sources of irritation (result or action) and the general connection of this behavior (rule or habit) to specific past stimulations should become able to be applied to new or additional sensations (cases).

This apply both to multiple and single facts: “abduction is often presented as if the surprising phenomenon is only a single fact [...] but a better picture is provided by emphasizing a constellation of facts or characteristics” (Paavola 2011: 307), which are brought back to unity through its synthetizing activity. On one hand, “[a] mass of facts is before us” and “they seem to be so multiplex intricate that we can neither satisfy ourselves that what we have set down represents the facts [...]. But suddenly [...] it occurs to us that if we were to assume something to be true that we do not know to be true, these facts would arrange themselves luminously. That is abduction” (Peirce 1998; EPII 531). Previously unrelated events are gathered together under a common conceptual umbrella, thereby turning them all into cases of the same rule. On the other hand, with an eye on the single phenomenon to be explained, Peirce logically formalizes abduction as follows: “The surprising fact, C, is observed; But if A were true, C would be a matter of course, Hence, there is reason to suspect that A is true” (CP 5.189). Behaviorally understood: something happens and is perceived

(fact); if a particular habit were chosen, the fact would become recognized as an instance (case) of that rule of behavior and dealt with properly; so, the habit (rule) is selected. But most of all, either instances rely on iconicity, as for instance the example referred in philosophy of science of Ignaz Semmelweis' discovery of the cause of childbed fever shows: the solution came "when he noticed that the symptoms caused by blood poisoning are similar to symptoms of the childbed fever, and he made a hypothesis on the basis of this [...]. By recognizing this similarity, Semmelweis used an iconic relationship, and concluded that there are good reasons to think that the cause *might* be *similar* in these two cases" (Paavola 2011: 306–307).

For iconicity to be operative and interpretation to occur, similarities need to be perceived. Now, for Peirce perceptual judgments themselves involve abduction: "abductive inference shades into perceptual judgment without any sharp line of demarcation between them; or, in other words, our first premisses, the perceptual judgments, are to be regarded as an extreme case of abductive inferences, from which they differ in being absolutely beyond criticism" (CP 5.181). What links perceptions to *hypothetical inference* is their interpretative nature, that is the fact they entail *possible general* modes of different categorization of identical stimuli: in other words, the same thing, considered as a single token, can be said to belong to more than one type and, in unusual or problematic contexts, the decision compares to a guess. By defining something as the token of a type, perception performs the same classification process through which in scientific or common reasoning a fact is turned into the case of a rule. The logical formula turns therefore openly in a physiological sequence (CP 8.64):

A well-recognized kind of object, M, has for its ordinary predicates P[1], P[2], P[3], etc., indistinctly recognized.

The suggesting object, S, has these same predicates, P[1], P[2], P[3], etc.

Hence, S is of the kind M.

By all means, perception and abduction differ in some respect and the parallel involves problems. As for the former, percepts themselves need to be distinguished from their propositional expression, that is perceptual judgments (although either are constructed from the same sensorial qualities), and both are "absolutely forced upon my acceptance, and that by a process which I am utterly unable to control and consequently am unable to criticize" (CP 5.157). As for the latter, along with being critical to knowledge growth through conscious self-criticism, it splits into several subtypes (Hoffmann 2010; Bonfantini 2003) that have no equivalent at the physiological level. This said, it equally holds true that "[i]n perception, the conclusion has the peculiarity of not being abstractly thought, but actually seen, so that it is not exactly a judgment, *though it is tantamount to one*" (CP 8.65; emphasis mine). Besides, inference does not coincide with consciousness and self-control, so "[i]f we were to subject this subconscious process to logical analysis, we should find that it terminated in what that analysis would represent as an abductive inference" (CP 5.181). Eventually:

It seems to be clear, however, that we hardly create anything “new” in perceiving something, although we could say that we are “forming an explanatory hypothesis” with regard to what is in front of our eyes. Thus, if perception is accepted as a form of abduction, we need to make a distinction between *creating* an “explanatory hypothesis” and *selecting* one from a given database. For example, when reading a word, the word we read is a hypothesis that “explains” a perceived sequence of letters. In this case, we are selecting an explanatory hypothesis from the set of words we already know without creating a new one; we associate a certain sequence of letters with a hypothesis that exists already in our mind (Hoffmann 2010).

To sum up the issue about Peirce’s evolutionism, Lamarckian habit taking *implicitly* takes the form of abductive inference and involves the selection of a pre-existing rule of action and its application to novel sensory or perceptive stimuli, through their iconic similarity to previous experiences. This is not restricted to vision, for “an icon is a pure image, not necessarily visual” (Peirce 1902: 41–43), and whenever it takes place, given proper favorable circumstances, morphological changes can be triggered and made effective in the long run. Thus conceived, biological evolution is mirrored by scientific progress, the abrupt character of the latter aside.

4. ABDUCTION AND EXAPTATION

It is often overlooked the fact that Peirce himself provided a solution able to turn his Lamarckism in true, so to speak, “Baldwinism”, not to say in out-and-out “Gouldism”. Along with casual variations and the transmission of inherited characters, there is in fact a third mode of evolution, “cataclysmal evolution”, and in biological history the different modalities are anything but mutually exclusive — “it seems altogether probable that all three of these modes of evolution have acted” (CP 1.105) — and cooperate in the construction of new living forms. Specifically:

species [...] are rapidly altered after cataclysms or rapid geological changes. Under novel circumstances, we often see animals and plants sporting excessively in reproduction, and sometimes even undergoing transformations during individual life, phenomena no doubt due partly to the enfeeblement of vitality from the breaking up of habitual modes of life, partly to changed food, partly to direct specific influence of the element in which the organism is immersed. If evolution has been brought about in this way, not only have its single steps not been insensible, as both Darwinians and Lamarckians suppose, but they are furthermore neither haphazard on the one hand, nor yet determined by an inward striving on the other, but on the contrary are effects of the changed environment, and have a positive general tendency to adapt the organism to that environment, since variation will particularly affect organs at once enfeebled and stimulated. (CP 6.17)

the theory of cataclysmal evolution, according to which the changes have not been small and have not been fortuitous; but they have taken place chiefly in reproduction. According to this view, sudden changes of the environment have taken place from time to time. These changes have put certain organs at a disadvantage, and *there has been an effort to use them in new ways*. Such organs are particularly apt to sport in reproduction and *to change in the way which adapts them better to their recent mode of exercise*. (CP 1.104; emphases mine)

The surprising aspect of these excerpts lies in the fact that, together with what said thus far and by taking into account that “tychasm [evolution by chance or Darwinism] and anancasm [evolution by mechanical necessity or cataclysmal evolution] are degenerate forms of agapasm [which therefore combine them all]” (CP 6.303), there are all the ingredients to claim that, however unwittingly and not in the same terms, *Peirce did suggest an evolutionary scenario combining abduction and exaptation*. Some behavioral choices during the lifetime of an organism, which firstly are based on purely sensory-perceptive mechanisms of recognition of similarities among previously unrelated objects (now to be pragmatically categorized under the same habit or rule of action, hypothetically

applied as for its subsequent success) and secondly determine significant transformations in its ecological relations (to the extent that it can be said that now the environment is in some respect substantially different from the previous one), induce functional changes in the usage of existing organs (exaptation) and, over generations, their refinement through genes-driven (natural selection and adaptation) progressive small modifications.

Such reading fits at the same time Peirce's "extended fallibilism", the idea that knowledge is always tentative and subject to revision, in all its forms. Throughout, it proceeds by means of hypotheses, which are either constructed anew or suggested before inexplicable facts (abduction), but always experimentally developed in their consequences (deduction) and then tested (induction). Natural history follows the same pattern. In Stjernfelt's words, "the Ab-De-In cycle has its naturalist counterpart in the trial-and-error of Uexküllian functional circles and maybe even — so Peirce — in process of evolution: variation (abduction), species consequences of variation (deduction), and natural selection (induction)" (Stjernfelt 2007: 342).

However important this structural correspondence, the critical component of the analogy (or better, of the continuity) between biological evolution and scientific progress — what actually represents the theoretical key to the detection of a case study and sets out the conditions for an experimental proposal — is another. Once again, Peirce provides the decisive clue: "There is no greater nor more frequent mistake in practical logic than to suppose that things which resemble one another strongly in some respects are any the more likely for that to be alike in others (CP 2.634)". Namely, abduction can be deceptive and lead to wrong conclusions. From a logical point of view, it is a fallacy that goes by the name of *affirming the consequent*. To understand how it is possible for a living organism to make a perceptive mistake, attention must be focused on a central feature of iconicity, that is *substitutability*: "An *Icon* is a Representamen whose Representative Quality is a Firstness of it as a First. That is, a quality that it has *qua* thing renders it fit to be a representamen. Thus, anything is fit to be a *Substitute* for anything that it is like" (CP 2.276). What looks like a weakness at first — icons have been subjected to severe criticism against their motivated status, for anything can be said to resemble anything else and actual interpretation needs necessarily conventionalization — turns out to be a strength too, since ambiguity makes them creative: exactly because they embody indeterminateness and possibility and can represent whatever object possessing their quality, our knowledge can be extended and learning itself, by growing through novel applications to different but analogous cases of preexisting concepts or ideas, can occur. As Stjernfelt (2007: 28) puts it, "an icon potentially refers to an indefinite class of objects, namely all those objects which have, in some respect, a relation of similarity to it"; we never observe just singular things, since "already in ordinary perception, generality and continuity play a central role — e.g. in our spontaneous recognition that this or that aspect of perception is an instantiation of some general type or process" (Stjernfelt 2007: 9).

It must be noticed that the idea of *similarity as commutability* was already present in the work of Jakob von Uexküll (1982):

We know from Sarris's experiments that a dog trained to the command 'chair' learns to sit on a chair, and will be on the look-out for other seating-accommodations if the chair is removed; indeed, he searches for canine sitting-accommodations, which need in no way be suitable for human use. The various sitting-accommodations all have the same 'sitting-quality' (Sitz-Ton)', they are meaning-carriers for sitting because they can be exchanged with each other at will, and the dog will make use of them indiscriminately upon hearing the command 'chair'. (Uexküll 1982: 28–29; emphases mine)

The deaf and blind tick is solely constituted to make every mammal in its Umwelt appear as the same meaning-carrier [...]. For the tick, the meaning-carrier has only one smell, which comes from the sweat common to all mammals. That meaning-carrier is also tangible and warm, and allows itself to be bored into and to have blood extracted from it. In this way it is possible to reduce all mammals — no matter how greatly they differ in shape, color, sound, and smell in our Umwelt — to a common denominator. On approach, the properties of any mammal — be it a human, a dog, a deer, or a mouse — contrapuntally activate the life-rule of the tick (Uexküll 1982: 57; emphases mine).

In this case, an error would consist in treating like a mammal an organism that does emanate an odor identical or close to butyric acid, but without actually being that kind of living being. Here it is the corresponding translation in a wrong hypothetical inference or abduction: due to past phylogenetic experience, a fact or result (sensory detection of a specific biochemical volatile element) is automatically categorized as something functional to the organism's inner metabolism and thus turned via sensory abduction into the case (mammal) of a rule (if mammal, then butyric acid); immediately, the following deductive phase is triggered, where the case (mammal) becomes now an instance of a second rule (if mammal, then plopping), whose result is to be tested through induction by the actual finding of a warm-blood animal, which fails. Perhaps, the wrong sensory inference can be better appreciated in the case of electric traps for mosquitoes: by emitting carbon dioxide, they attract insects and kill them with electrification. By categorizing this compound as the property of something from which nutritive blood with high protein content can be sucked out, mosquitoes condemn themselves to death, since in a world far beyond their general cognitive abilities the equation between carbon dioxide and exploitable food is not necessary. In their case, an inferential mistake starts an automatic response whose verification proves to be fatal.

Needless to say that such articulation of the sensory phase is purely epistemological and does not belong to the immediacy characterizing insects'

simple neural systems. But it is true that, if reflexes or automatic response behaviors are the physiological equivalent of deduction — “a syllogism in Barbara virtually takes place when we irritate the foot of a decapitated frog” — and they are by force preceded by a step of sensorial recognition, reasons of information economy on one side and the generality and continuity of chemical-physical laws and their perception on the other side make them inferential. That is to say, an abduction lies at the very core of every deduction. The difficulty to acknowledge this point rests mainly on the simple and univocal nature of the recognition processes just mentioned: with higher nervous systems able to construct complex and multi-sensorial representations of objects (able thus to experience *percepts* and not just isolated sensations), Peirce’s induction of qualities becomes evident (by recognizing a single sensorial component, the remaining elements are inferred and the object as a whole is postulated); contrariwise, in the multiphase chains characterizing the feeding behaviors of ticks and mosquitoes, at every step each single sensation or quality defines a complete object, or better it coincides with the class of all objects possessing it (according to Peirce’s claims on the generality and continuity of icons) and errors are inevitably behind the corner (since not all objects exhibiting a single quality have others too).

That iconic relations based on some type of similarity can lead to mistaken substitutions is well exemplified by Stjernfelt’s views on categorical perception. In his discussion on bacterial chemotaxis, he states the following:

Here, the signals are based on categorical perception — a perception which immediately categorizes the entity perceived and thus *remains blind to internal differences within the category* [...]. This has, however, huge semiotic implications, for this entails that *E. coli* — exactly like us — *maybe fooled by artificial sweeteners bearing the same ‘active site’ on their outer perimeter, even if being completely different chemicals* [...]. *E. coli* has the ability to categorize a series of sugars — but, by the same token, *the economy involved in judging objects from their surface only has an unavoidable flip side: it involves the possibility of mistake*, of being fooled by allowing impostors in your categorization (Stjernfelt 2007: 207–209; emphases mine)

Since the bacterium cannot discriminate between edible glucose and irrelevant saccharine,” the two substances are categorized together due to a morphological similarity between the ‘active sites’ on the macromolecules’ outside as perceived by the bacteria” (Stjernfelt 2007: 212). In addition, for the more complex the organism, the subtler its perceptual granularity and hence greater its ability of inter-categorical discrimination, one might conjecture that living beings with simple sensory systems should possess, under specific circumstances, higher rates of speciation, due to their easier tendency to make mistakes. This idea could also be condensed in a complementary maxim to the definition of iconicity in terms of generality and continuity: *all sweet things, by being sweet, are*

the same thing. Misleading indeed, but such proneness to error might be the key factor playing an important role in some evolutionary scenarios, as the case study will attempt to show.

Terrence Deacon (1997), in his account of iconic relations, provides a clear idea about their intimate connection to fallacious discriminative processes:

Consider camouflage, as in the case of natural protective coloration. A moth on a tree whose wings resemble the graininess and color of the bark, though not perfectly, can still escape being eaten by a bird if the bird is inattentive and interprets the moth's wings as just more tree [...]. Some features of the moth's wings were iconic of the bark, irrespective of their degree of similarity, merely because under some interpretation (an inattentive bird) *they were not distinguished from it* [...]. What makes the moth wings iconic is an interpretive process produced by the bird, not something about the moth's wings. Their coloration was taken to be an icon because of something that the bird didn't do. What the bird was doing was actively scanning bark, its brain seeing just more of the same (bark, bark, bark...). What it didn't do was alter this process (e.g., bark, bark, not-bark, bark...). *It applied the same interpretive perceptual process to the moth as it did to the bark. It didn't distinguish between them, and so confused them with one another.* This established the iconic relationship between moth and bark. Iconic reference is the default [...]. Iconism is where the referential buck stops when nothing more is added. And at some level, due either to limitations in abilities to produce distinguishing responses or simply a lack of effort to produce them, the production of new interpretants stops. Whether because of boredom or limitations of a minimal nervous system, there are times when almost anything can be iconic of anything else (stuff, stuff, stuff...) (Deacon 1997: 75–76)

In summary, the interpretive process that generates iconic reference is none other than what in other terms we call *recognition* (mostly perceptual recognition, but not necessarily). Breaking down the term re-cognition says it all: to "think [about something] again." (Deacon 1997: 76)

Thus, by re-cognizing something as something that in fact it is not on the basis of sensory and perceptual clues implying some degree of similarity, the bird — just as ticks and bacteria — performs a wrong abduction.

The connection between erroneous interpretative perceptions and differential biological consequences represents the pivot around which the second article (Weible 2012a) has developed its argument. It must be remembered that, whatever the particular expression employed — new uses of old powers; change, extension, intensification or substitution of function; multi-functionality; preadaptation; exaptation — a common element in many authors is the acknowledgment of the key role of living beings' activities (and not just of

genetic chance) in determining their evolutionary paths (for instance through the selection and construction of new ecological niches, thereby triggering either generalizations or innovations in the exploitation of specific traits). With a view to modeling, the connection between behavioral plasticity and functional shift did not pose any major problems; but now that the last section has shown how organisms' agency can be framed to match with humans' hypothetical reasoning, the main difficulty turns out to be the discovery of *sensory-driven changes of behavior causing exaptation*.

Ritualization does exhibit features that meet the requirements of such changes. Firstly, ritualized actions or movements owe the acquirement of novel intraspecific meanings to the fact of being displayed, namely they are what they are because “*reacted to* by other individuals belonging to the same species” (Tinbergen 1952: 23; emphasis mine). In the context of interspecific communication, ritualization comes close to some phenomena of mimicry, where the perceptive nature of the evolutionary process at stake stands out with equal importance. For Maran and Kleisner (2010: 195–196; emphases mine), “semiotic cooption” and “semiotic selection” represent respectively “an event when something is newly interpreted as meaningful *within the Umwelt* [the environment as *perceived* and acted upon] of an organism and further adopted for a particular role” and “a connection between the *animal's inner perceptual sphere* and physical forms in nature”.

Secondly, the elements being perceived with additional meanings follow the same historical destiny that is reserved to organs with new functions: just as the latter are subjected to incremental adaptation via natural selection, so for the former “[t]his new function must have started a new evolutionary development during which the displacement activities became increasingly *better adapted* to it” (Tinbergen 1952: 23; emphasis mine); in the words of K. Lorenz, “[t]he second characteristic of ritualized motor patterns is a change of form which the unritualized prototype underwent in the service of its new communicative function and which quite obviously was brought about by the *selection pressure exerted by the survival value of communication*” (Lorenz 1966: 276; emphasis mine).

Thirdly, the “Ab-De-In cycle” may be said to apply too. Mimicry is deceptive resemblance and, as a communicative system, it is “a process in which a message (feature or signal) of one organism, the *mimic*, resembles some message of another organism, the *model* [...]. This resemblance should have some functionality for the mimic by being deceptive for a third participant, the *receiver*, whose recognition and response is relevant for the mimic” (Maran 2015: 211–212). Thus, there happens a similarity-based iconic interpretation where something is re-recognized as something that it is not — a wrong abductive perceptual judgment. This proves to be positive for one participant of the mimicry system and negative for the other (the slipping off of potential food), as a syllogistic-deductive response of no predation. Eventually, in the long run natural selection refines the mimetic features of the mimic in order to make

them better adapted to the deceptive function (and this can be seen as a type of negative induction).

My second article, with the emphasis on perception, had the credit to create implicitly the connection between two scientific paradigms: on one side, there is the epistemological account according to which common knowledge and scientific progress develop through hypothetical inferences and empirical testing of their logical consequences; on the other side, greater attention has been paid in the last decades to modes of evolution complementary to the neo-Darwinian approach and the role of functional changes triggered by epigenetic and ontogenetic events has acquired progressively a central position. Once the prominence of sensory and perceptive mechanisms is highlighted, the “Ab-De-In cycle” and the exaptation-fitness-adaptation sequence become overtly superimposable and it is here that Peirce’s ‘pragmatism’ meets Gould’s post-Darwinism.

This has a far deeper significance than usual parallelisms drawn between evolution and science, where genetic variance by random mutations is equated to hypotheses selection or construction. Abductive inference has nothing to do with chance, since “it is a primary hypothesis underlying all abduction that the human mind is akin to the truth in the sense that in a finite number of guesses it will light upon the correct hypothesis” (CP 7.220); as for the entertainment of a specific theory that proves to be true, “[y]ou cannot say that it happened by chance, because the possible theories, if not strictly innumerable, at any rate exceed a trillion” (CP 5.591). If Darwinian fortuitous variations are blind to their phenotypic effects, sensory-driven choices, despite being at first tentative, rest upon a variability which is confined within a regularity — that is the ultimate meaning of Peirce’s continuity when applied to iconicity. This is clear when it comes to science and can be extended downward to animal behavior: “man has a certain Insight [...] into the Thirdnesses, the general elements, of Nature. An Insight, I call it, because it is to be referred to the same general class of operations to which Perceptive Judgments belong” (CP 5.173). That is to say, if an instinct or habit is applied successfully in response to a specific sensory quality, the same holds true *hypothetically* for the set of all objects possessing it.

This said, a further step must be taken. If in the mimicry system the subject undergoing modifications because of the selective pressure of a perceiver is passive, the fullest overlap between exaptation and abduction requires the detection of situations where the very organism — the species it represents — performing the misleading perception is accountable for its own morphological transformations over the following generations. The notion of *context*, on which my second work dwelt diffusely to try to single out the logical elements involved in the functional shift (be it either communicative or not) of a trait, can be translated in that of *ecological niche*. Since it comprises, along with environmental features promoting fitness, the behavioral adaptations of a living being (with the inherent possibility of their plastic tuning to similar conditions), the linking of exaptation and abduction meets the paradigm of a constructivist ecology where organisms create their own conditions of survival through a truly experimental attitude.

5. THE ICONIC AND EXAPTIVE LOGIC OF TECHNOLOGICAL DEVELOPMENT

The third article (Weible 2013) has taken on the shape of a pilot study, rather than being a finished work standing by itself. In this, together with the attempt to open up new research directions, it has confirmed some of the results previously achieved. First of all, the switch of context accountable for the functional shift has been redefined in terms of “selective regime” (Baum, Larson 1991: 5; emphases mine), which “assesses, *given the ecological circumstance*, how selection is expected to sort character variation” and thus “describes the action of natural selection *contingent upon the organism's ecology*”. The subordination of micro-evolutionary events to ecological dynamics can be due, among different alternatives, to behavioral innovations, so that “a novel organismal feature can change the way selection acts upon other organismal character variation and hence modify the selective regime” (Baum, Larson 1991: 5). Specifically, the following case study conjectures a scenario where a new feeding habit, by modifying the ecological rules, has led to a morphological exaptation and its further adaptation.

Secondly, the two analogies drawn between organs and tools — problem-solving solutions and recursive hierarchy — left in the background one aspect that now, after having shown the convergence between specific types of exaptation and abduction, comes out in all its centrality. In his work on the nature of technology, Arthur detects many similarities between its development, biological evolution and scientific progress. On one hand, beneath the commonplace approach that views them as complementary activities, thereby reducing technology to applied science, there lies a deeper connection, which goes back to their being intellectual enterprises grounded on the same cognitive matrix. Several passages by Arthur (2009) confirms this:

What about scientific experiments? Are these related to technology too? Certainly some are mere prospectings in the hope of lucky discoveries. But the serious ones are systematic probes into the workings of nature and are undertaken always with a definite purpose in mind. *They are therefore means to human purposes; they are method technologies, encased or embodied in physical apparatus* (Arthur 2009: 62; emphasis mine).

Science [...] builds its understanding from its scientific explanations, from its reasonings and theories about how the world works. Surely, we can say, these at least are far away from technology.

Well, not quite. Explanations certainly do not feel like technologies. But *they are constructions with a purpose*.

[...] From all this it follows that science not only uses technology, it builds itself from technology. Not the standard set of technologies such

as bridges and steel production methods and shipping, of course. Science builds itself from the instruments, methods, experiments, and conceptual constructions it uses. This should not be surprising. Science, after all, is a method: a method for understanding, for probing, for explaining. A method composed of many sub methods. Stripped to its core structure, *science is a form of technology* (Arthur 2009: 63–64; emphases mine).

That origination in science or in mathematics is not fundamentally different from that in technology should not be surprising. The correspondences exist not because science and mathematics are the same as technology. They exist because all three are purposed systems — means to purposes, broadly interpreted — and therefore must follow the same logic. *All three are constructed from forms or principles*: in the case of technology, conceptual methods; in the case of science, *explanatory structures*; in the case of mathematics, truth structures consistent with basic axioms. Technology, scientific explanation, and mathematics therefore come into being via similar types of heuristic process — fundamentally a *linking between a problem and the forms that will satisfy it* (Arthur 2009: 129; emphases mine).

If the same logical structure applies to the connection between scientific explanations and natural data on one side and between technological artifacts and problematic situations on the other side, a spontaneous question arises: does technology involve abduction? My third article has documented how closely living beings and artifacts resemble each other insofar the phenomenon of re-functionalization is concerned; to use Arthur’s words, the “lock-in of an older successful principle causes a phenomenon I will call *adaptive stretch*. When a new circumstance comes along or a demand for a different sphere of application arrives, it is easier to reach for the old technology — the old base principle — and adapt it by “stretching” it to cover the new circumstances” (Arthur 2009: 140). In the Italian translation of Arthur’s book, there occurs a footnote qualifying that “it looks like the biological phenomenon of exaptation” (Arthur 2011: 124). When such quotations are compared to Peirce’s writings, it does seem that technology depends on something akin to hypothetical inference and exhibits the Ab-De-In cycle. In science, as well as in daily reasoning, explanations as solutions are *suggested* by the situation itself and, in turn, *suggestion comes along through association by similarity* (and by spatial-temporal contiguity). As for this aspect, namely how explanatory theories are generated to account for surprising facts, Peirce has insisted on it throughout his long thinking over the issue:

Upon finding himself confronted with a phenomenon unlike what he would have expected under the circumstances, he looks over its features and notices some remarkable character or relation among them, which he at once recognizes as being characteristic of some conception with which

his mind is already stored, so that a theory is *suggested* which would explain (that is, render necessary) that which is surprising in the phenomena. (CP 2.776)

Abduction, in the sense I give the word, is any reasoning of a large class of which the provisional adoption of an explanatory hypothesis is the type. But it includes processes of thought which lead only to the *suggestion* of questions to be considered, and includes much besides. (CP 4.541)

The abductive *suggestion* comes to us like a flash. It is an act of insight, although of extremely fallible insight. It is true that the different elements of the hypothesis were in our minds before; but it is the idea of putting together what we had never before dreamed of putting together which flashes the new *suggestion* before our contemplation. (CP 5.181)

Abduction merely *suggests* that something may be. Its only justification is that from its suggestion deduction can draw a prediction which can be tested by induction, and that, if we are ever to learn anything or to understand phenomena at all, it must be by abduction that this is to be brought about. No reason whatsoever can be given for it, as far as I can discover; and it needs no reason, since it merely offers *suggestions*. (CP 5.171)

If you carefully consider the question of pragmatism you will see that it is nothing else than the question of the logic of abduction. That is, pragmatism proposes a certain maxim which, if sound, must render needless any further rule as to the admissibility of hypotheses to rank as hypotheses, that is to say, as explanations of phenomena held as hopeful *suggestions*. (CP 5.196)

Every concept, doubtless, first arises when upon a strong, but more or less vague, sense of need is superinduced some involuntary experience of a *suggestive* nature; that being *suggestive* which has a certain occult relation to the build of the mind. We may assume that it is the same with the instinctive ideas of animals; and man's ideas are quite as miraculous as those of the bird, the beaver, and the ant [...]. Every concept, every general proposition of the great edifice of science, first came to us as a conjecture. These ideas are the first logical interpretants of the phenomena that *suggest* them, and which, as suggesting them, are signs, of which they are the (really conjectural) interpretants. (CP 5.480)

Such a repeated use of the same term indicates a conceptual choice that is not casual and supposes a precise account of how theories or hypothesis come to mind. Although Peirce did not offer an explicit definition of the psychological mechanism of suggestion, the very same process has been however described with a little more detail by another pragmatist and this can provide some help

and insight in understanding its meaning. For John Dewey, when facing a difficulty, “the next step is *suggestion* of some way out — the formation of some tentative plan or project, the entertaining of some theory which will account for the peculiarities in question, the consideration of some solution for the problem” (Dewey 1910: 12; emphasis mine); the data at hand supply hints by means of past experience and prior knowledge, which must be considered the actual sources of suggestion: “If the person has had some acquaintance with *similar* situations, if he has dealt with material *of the same sort* before, suggestions more or less apt and helpful are likely to arise” (Dewey 1910: 12; emphases mine); again, solutions cannot be provided “unless there has been experience in some degree *analogous*” (Dewey 1910: 12; emphasis mine). If similarity and analogy are involved, it is plausible that something akin to iconicity is affecting the cognitive process of suggestion.

Further examination shows this is the correct interpretation. Here it is the example adopted by Dewey to clarify the mechanism:

A man is walking on a warm day. The sky was clear the last time he observed it; but presently he notes, while occupied primarily with other things, that the air is cooler. It occurs to him that it is probably going to rain; looking up, he sees a dark cloud between him and the sun, and he then quickens his steps. What, if any thing, in such a situation can be called thought? Neither the act of walking nor the noting of the cold is a thought. Walking is one direction of activity; looking and noting are other modes of activity. The likelihood that it will rain is, however, something suggested. The pedestrian feels the cold; he thinks of clouds and a coming shower. (Dewey 1910: 6-7)

This can be formalized according to Peirce’s three modes of inference. Firstly, an abduction occurs — if it is getting colder (fact), it is *like* (iconic relation) any previous time (past experience at disposal) where *cooling was associated with raining* (rule), so the fact can be tentatively interpreted as a result of such rule and the case that is going to rain soon is established (mere possibility, since there happens instances where cold temperature is in fact dissociated from rains). Secondly, the hypothesis needs to be tested and therefore consequences or further connections to be verified empirically must be developed: rain comes from clouds. Eventually, clouding is spotted and the explanation supported inductively. Instead of recurring to common images, Dewey’s description is a good case of thermoceptive abduction or iconicity; obviously, the same holds true for vision: “there is the same sort of situation as when one looking at a cloud is reminded of a human figure and face. Thinking [...] involves a noted or perceived fact, followed by something else which is not observed but which is brought to mind, suggested by the thing seen. One reminds us, as we say, of the other” (Dewey 1910: 7). The example of rain is however remarkable in its affinity with the logical place of hypothetical inference within Peirce’s classification of modalities: “The danger of rain...presents itself to us as a genuine *possibility*

— as a *possible* fact of the same nature as the observed coolness. Put differently [...] we consider the possibility and nature of the connection between the object seen and the object suggested” (Dewey 1910: 7; emphases mine).

If the imaginative process of suggestion in scientific and daily problem-solving follows the logic of abduction, it is by no surprise that technology — itself a human achievement based on imagination — obeys the same rules. To begin with, the idea of technological development as something linear, mechanic and repetitive must be abandoned: “[e]ngineering is often held to be less creative than other fields where design is important — architecture, for example, or music [...]. The design process in engineering is not different in principle from that in architecture, or fashion, or music for that matter. It is a form of composition, of expression, and as such it is open to all the creativity we associate with these” (Arthur 2009: 98). Besides, just as people reactivate past experience to deal with everyday problems and reuse solutions that have proved to be effective, so technology is based on the same selective working: at the heart of invention “lies the act of seeing a suitable solution in action — seeing a suitable principle that will do the job” (Arthur 2009: 121) and to do so “I am reaching into my store of everyday functionalities, selecting some to combine” (Arthur 2009: 121); thus, “[t]he originator reaches into a store of these and imagines what will happen when certain ones are combined” (Arthur 2009: 122). To synthesize, “[i]nvention at its core is mental *association*” (Arthur 2009: 122; emphasis mine).

But what kind of association? For Arthur “[w]hen originators need a certain function they can *associate* back to a principle that produced a one in a field they know about. At the core of this mechanism — call it principle transfer — is *seeing an analogy*. This is another form of mental association” (Arthur 2009: 122; emphases mine). When facing a problem that requires a technical solution, people resort to tools that, in similar conditions, have already been applied successfully. The cognitive working at stake is outright abductive — Peirce meets Arthur, almost with the same words: “[o]rigination in scientific theorizing, as in technology, is at bottom a *linking* — a linking of the observational givens of a problem with a principle (a conceptual insight) that roughly *suggests* these, and eventually with a complete set of principles that reproduces these” (Arthur 2009: 128; emphases mine). Darwin developed the theory of natural selection because of the *similarities* between his discoveries in nature and the consequences of Malthus’ account on populations’ dynamics. Kepler “found that the observed longitudes of Mars [...] were thus, in so far, a *likeness* of those of motion in an elliptic orbit” and this “did incline him to that idea so much as to decide him to undertake to ascertain whether virtual predictions about the latitudes and parallaxes based on this hypothesis would be verified or not” (CP 2.96). Similarly, correspondence between given and past problems prompt us to adopt the same options and technical progress follows in part the logical formalization of hypotheses adoption: “The surprising fact, C, is observed; But if A were true, C would be a matter of course, Hence, there is reason to suspect that A is true” (CP 5.189) — a problem C arises and needs a

solution; but if the solution A were adopted, C would be solved (on the basis of the similarities perceived between the defining features of C and those solved by the application of A); hence, there is reason to suspect that A is the solving possibility among the storehouse of available options. In turn, this reproduces the Ab-De-In cycle, since once adopted (either mentally, in case of methods or projects, or physically) the available artifacts need to be implemented in the actual context, where the supposed likeness might in fact turn out to be deceitful and lead to non optimal or wrong results.

The merit of the third article lies therefore in its having paved the way to the acknowledgement that organs and tools, when belonging to specific subtypes of technological development and biological evolution, undergo re-functionalization in pretty much the same way, by means of behavioral acts (whether they be highly abstract or pure reflexes) grounded on perceived similarities which elicit specific interpretations. All which has been achieved thus far can now be put on trial with the description of a case study and the relative call for experimental testing.

6. THE ORIGIN OF BLOODSUCKING: A CASE OF EVOLUTIONARY ABDUCTION?

As I quoted at the very beginning of this introduction, for Arnold (1994: 138) “when the ancestors of carnivorous hemipteran bugs transferred from sucking sap on feeding on the internal fluids of animals, there was at least a brief phase where they did both. So their hypodermic proboscis was initially an addition exaptation to exploiting animal fluids, but later became a transfer exaptation”. Indeed, there is quite an agreement among evolutionary biologists that a similar behavior, hematophagy or blood-sucking, might have evolved in insects through the application of existing adaptations to a different feeding habit.

Lehane (2005) provides a useful introduction thereupon, arguing that feeding on blood arose independently at least six times among the arthropods of the Jurassic and Cretaceous periods, following two possible routes. In the first, “haematophagous forms may have developed subsequent to a prolonged association between vertebrates and insects that had no specializations immediately suiting them to the bloodsucking way of life” (Lehane 2005: 7). In the second, which interests me most, “blood feeding developed in some insect lineages from ancestral insects that were morphologically pre-adapted for piercing surfaces” (Lehane 2005: 13). Waage (1979) discusses this possibility in detail and provides many examples. For instance, “[e]ctoparasitism appears to have evolved in the *Hemiptera* through (1) a primary *preadaptation* of mouthparts for piercing and sucking, (2) secondary evolution of an association with vertebrate dwellings and (3) facultative haematophagy followed by behavioural and physiological adaptations permitting more efficient blood-feeding” (Waage 1979: 192; emphasis mine). Or, “*Nematocera* and *Brachycera Tabaniformia* [...] appear to have evolved from a stock *preadapted* as adults for bloodsucking by their piercing mouthparts and predatory behaviour, with regular host associations being a subsequent evolutionary step” (Waage 1979: 199; emphasis mine). Also, “[t]he mouthparts of most moths are clearly *preadapted* for feeding on tears and other free liquids [...]. True blood-sucking behaviour, however, has evolved in the noctuid, *Calpe eustrigata* [...]. This species belongs to a group of moths which as adults suck the juices of fruits after piercing the rinds with highly modified, sharp-tipped proboscis [...]. These feeding modifications clearly *preadapted* members of this group for a shift to piercing vertebrate tissues” (Waage 1979: 202; emphases mine).

The issue is summed up as follow:

For the great majority of insects, vertebrate associations are accidental and of neutral or negative value to the insect’s fitness. The transition from this sort of relationship to a positive commensal or ectoparasitic relationship has required, in every case, a number of morphological, behavioural and physiological adaptations. These adaptations may be classified into two general groups:

- (1) Adaptations promoting regular physical association with the host. These include habitat preference, host-finding behaviour and morphological adaptations to living on the host.
- (2) Adaptations promoting the capacity to feed on the host. These include mouthpart structure, the physiological capacity to digest host substances and the behaviour associated with the initiation and termination of feeding. (Waage 1979: 203)

A key characteristic of these two hypothetical pathways is *the presence of preadaptations towards ectoparasitism prior to selection for adaptations directly promoting this lifestyle*. Characters preadaptive for one pathway are evolved secondarily in the other. A crucial role for preadaptation is general to the evolution of parasitic relationships. (Waage 1979: 206; emphasis mine)

What remains implicit is however the role of those modifications taking place during organisms' lifetime, due to learning and able to stabilize in a sufficient permanent way the ecto-parasitic relationship. That the second evolutionary route leading to hematophagy is very likely a good instance of Baldwin's organic selection is testified somehow by Downes (1971), who — after noticing that “mouthparts of biting flies are adapted for cutting through a membrane and taking up by suction the fluid or semi-fluid material thus exposed, but [...] they do not appear to be specialized for blood-sucking as such” (Downes 1971: 245) and remembering that *Mecoptera* have also been seen to feed on both live and dead insect — asks the following: “Are we then observing here the original condition in the *Diptera* — a biting and sucking feeding apparatus fully established in structure and function, but not yet *canalized by behaviour* to living, and still less to vertebrate, sources of food?” (Downes 1971: 245; emphasis mine). This supposition looks like obeying the ecological and behavioral pattern of the exaptation-fitness-adaptation sequence referred to before: a change in behavior (vertebrate association) modifies the selective regime and coopts existing organs for a slightly different function, which in turn, since promoting fitness in the form of longevity and fecundity, becomes susceptible to the screening of natural selection and undergoes progressive and gradual adaptive refinements.

The scenario meets the requirements of the Ab-De-In cycle too: the new feeding habit, a (slight) *variation* with respect to the previous instinctive action and *hypothetical* at its inception as for the capacity to enhance organisms' aptitude towards the environment, has *proved* to be successful — “[t]he nutritional advantage of feeding on host tissues, ultimately blood, is presumably associated with the acquisition of nitrogen to promote longevity and egg production” (Waage 1979: 207); specific *consequences* have made it “visible” to the *testing* action of natural selection, which has worked incrementally on the traits performing the new task. What remains to be shown, however, is that the original and incidental host association triggering the cascade effects was abductive

itself, namely depending on a sensory mechanism based on some kind of similarity and its iconic recognition.

My analysis is restricted to the functional shift of mouthparts, but it must be emphasized the multifactorial nature of the historical process that gave birth to the different types of bloodsucking. After examination, any single lineage can exhibit the intersection of several complementary exaptive changes, involving not only single organs, but physiological compounds and action schemas as well: as a matter of fact, cooption can affect morphological, physiological or/and behavioral traits. For instance, “the presumed ancestors of these haematophagous groups, the *Anthocoridae* and predatory *Reduviidae*, both use salivary venom to immobilize prey [...]. Perhaps these secretions represent, in both groups, the progenitors of anesthetic secretions which permitted painless feeding on hosts in later-evolved haematophagous forms” (Waage 1979: 192). Or, since “blood is richest in nitrogen, but much of this is locked in haemoglobin (Hb) and other proteins which may be inaccessible to evolving vertebrate associates”, then “[i]nsects switching from entomophagy to haematophagy (Pathway II) might be expected to possess some of the necessary proteases, in other forms this digestive capacity may evolve more gradually” (Waage 1979: 207). Eventually, in *Ceratopogon*, *Clinohoelea*, *Palpomyia* and other related genera the females hunt in swarms keep together by visual landmarks of the same nature as those that define the site of the mating assembly, namely “it appears in fact that the specialization of these midges consists in the adoption by the female of a behaviour pattern typically associated with mating in her hunting behavior also” (Downes 1970: 245).

When questioning how the changeover might have come about, along with being multifactorial it has probably originated at the same time from very different precursory feeding habits. On one hand, entomophagous insects, while hunting for their preys in nests or burrows or regularly congregating in wet areas used as breeding sites, “could have made repeated and possibly prolonged contact with vertebrates. These predatory insects would have physiological and morphological adaptations [...] facilitating the switch to haematophagy” (Lehane 2005: 13). On the other hand, the shift might have regarded plant-feeding or sap-sucking ancestors: “[t]his is certainly a possibility as many plant-feeding insects possess piercing and sucking mouthparts that would pre-adapt them for haematophagy” (Lehane 2005: 14). Once attracted to free-living vertebrates to feed on bodily secretions or fruits and seeds stored by them, close and continued association with the host would have then prompted the path towards modern-day blood feeders.

In general, support to the theory of preadaptation (i.e., exaptation) comes from two important considerations. From a morphological and physiological viewpoint, “features which are characteristic of parasites are by no means peculiar to them” (Rothschild 1957: 52) and thus “it is easy to see that any animal might already possess one or several of these specializations before it took to the parasitic mode of life” (Rothschild 1957: 53). Furthermore, “if individuals vary at all pre-adaptation must exist [...]. To say that plants and animals may be

pre-adapted is really only another way of saying they are not all alike, for every variation is potentially both adaptive and pre-adaptive” (Rothschild 1957: 53).

Since blood is a nutritious organic substance, other animal classes have developed feeding habits resembling the insects’ pierce-and-suck scheme—insect themselves, not surprisingly, have come to be subjected to parasitism by nematodes, whose possibility to start a parasitic life “was clearly improved by a set of preadaptations or preconditions that evolved as a complex of adaptations to a saprobiontic life in short-lived substrates formed by decaying material” (Sudhaus 2008: 146), before turning to exploit insect intestine. In bats, for instance, hematophagy has evolved once, leading to three living species of vampires: *Desmodus rotundus*, *Diaemus youngi* and *Diphylla eadada*. Three theories have been advanced to account for its origin (Fenton 1992: 164): for the first, “vampire bats evolved from frugivorous species with teeth capable of cutting the hard ring of fruit”; for the second, “a progenitor of vampire bats fed on the ectoparasites of large mammals and by this route adopted a sanguivorous life style”; for the third, “sanguivory is a specialization derived from feeding at wounds on large mammals”. The last theory is particularly interesting, since it suits well the hypothesis of an evolutionary scenario involving at the same time ontogenetic behavioral modifications and coopted organs. As for the first aspect, “[p]rotovampire bats *would have learned* that at wound sites they could feed on insects as well as on the tissues and blood of the large mammals” (Fenton 1992: 166; emphasis mine); as for the second, access to such kind and range of food opportunities would have been affected by the upper incisor teeth of bats: specifically, “blade-like upper incisor teeth would have permitted bats frontal access to wounds, and sharper teeth would have made the bats’ activities at wounds less conspicuous to the host” (Fenton 1992: 167). This is how Fenton sums it up:

To feed effectively at existing wounds, protovampire bats would have had to possess strong upper incisor teeth and the *behavioral flexibility to recognize* and exploit this feeding opportunity. The involvement of the tongue outside the mouth also would have been important and this pattern of behaviour is one that vampire bats share with modern flower-visiting phyllostomids. The combination of phyllostomid *exaptations* (*sensu* Gould & Vrba, 1982) and the unique South American mammal fauna may together explain the origin of blood-feeding bats in the Neotropics. (Fenton 1992: 169; emphases mine)

Schutt (2008) has modified the second evolutionary scenario by claiming that blood feeding might have originated from grooming behavior aimed at getting rid of ectoparasites. However, small size and difficulty to locate them, along with the contrast between their worldwide distribution and bats’ restricted habitats, work against this thesis (Schutt 2008: 49). As for the wound-feeding hypothesis, it collides with the uselessness of echolocation in differentiating wounded from unwounded preys and it is very difficult to envisage what kind

of selective pressure might have driven protovampires to switch from an insect-eating lifestyle to one dependent on locating large wounds and especially on blood, because of the difficulty to obtain it (Schutt 2008: 50–51). Eventually, the frugivore hypothesis poses problems too, because the exact dynamics of the changeover has never been satisfactorily developed so has to explain clearly how or why it occurred (Schutt 2008: 51). Whatever the exact scenario, since they were encountering an increasingly diverse arboreal fauna too large to be stalked and killed with existing strategies, it is plausible that over time “isolated populations of some carnivorous phyllostomid *may have undergone a behavioral shift* that allowed them to exploit these larger animals as a food source” (Schutt 2008: 54; emphasis mine).

In the case of birds, what can be seen nowadays in Darwin’s Galápagos finches could actually be thought of like a natural evolutionary ‘laboratory’, displaying ‘live’ how things could have gone, *mutatis mutandis*, in other classes. As for *Geospiza difficilis septentrionalis*, it appears to be “the first example from the bird world of a species in which one of the *primary* objectives in foraging is the procurement of blood” (Bowman, Billeb 1965: 29). Occasionally, also other species perform the same method of feeding: the Red-billed oxpecker or Tick-bird (*Buphagus erythrorhynchus*), for example, “feeds on ticks (primary food) infesting domestic stock and wild game and at times drinks the blood (secondary food) when it oozes from an animal and clots at a spot where several ticks have been attached” (Bowman, Billeb 1965: 40). Some common features have been advanced to define in general such predatory behavior, whether intentional or accidental: the attacks occur at times when usual food is less available; only some individuals acquire it, presumably *by learning*; behavioral predispositions are needed, such as lack of fear, curiosity, boldness, omnivorousness. As for the possible origin of the habit, the following explanation (somehow halfway between the second and third scenarios envisioned for vampire bats evolution) is put forward:

In their foraging on the ground, the finches come into close proximity to nesting and loafing Masked Boobies. During the dry season, when free-living insects are less available, the boobies present a concentration of black hippoboscids flies that are very visible on the white plumage. The agile and fearless finches readily pursue the hippoboscids on the boobies, and, as a result of their success, turn regularly to this new near-constant source of food. The finches *acquire a taste for blood*, possibly by eating blood-engorged flies, or by overzealous stabbing at flies amidst the plumage, causing an accidental puncture of the booby skin. When the white plumage of the booby becomes accidentally smeared with blood, non-hippoboscids flies are attracted to it, which serves to heighten the interest of the finches in the boobies. (Bowman, Billeb 1965: 41–42; emphases mine)

In addition to being probably sensory-driven by the gustatory recognition of blood, the omnivorous habit is supported at the same time by a “sufficiently generalized” (Bowman, Billeb 1965: 41) elongate, smallish, conical bill, able to be recruited for different actions: on Wolf Island members of *Geospiza difficilis* use their bills to pierce and eat the contents of seabirds' eggs; or “[h]opping about the rocks and ashy soil, this species turns over leaf litter using the bill” (Bowman, Billeb 1965: 37); besides, also cactus feeding has been observed. Since blood “probably constitutes only a minor part of the total food intake of the species” (Bowman, Billeb 1965: 37), it is reasonable to assume that hematophagy in birds does involve an exaptation-like cooption of the bill for slightly different functions, on the basis of ecological opportunities newly exploited and sustained by behavioral attitudes.

Does such a live observation of a possible new evolutionary trend suggest anything that might be applied retrospectively to the past changeovers occurred for insects? A clue comes from the fact that *Geospiza difficilis* feeds on avian blood “in the absence of a ready source of fresh drinking water” (Bowman, Billeb 1965: 38); equally, “attacks [...] occur at times when natural foods are less available” (Bowman, Billeb 1965: 41). The same is said by Curry and Anderson (1987: 519): “Blood drinking may occur predominantly during dry seasons when other foods are scarce. The blood drinking we observed took place during dry periods in both 1984 and 1985. Blood drinking was less frequent under wetter conditions in 1986”. It must be remembered that, for vampire bats, Fenton’s hypothesis “involves a transition from an insectivorous diet to one mixing insect larvae and *body fluids* and thence to one involving only blood” (Fenton 1992: 168).

In some respect, there happens thus the phenomenon of *substitution* above referred to, in this case ecologically affected by food distribution. But, if water and blood (because of its water-content) have analogous and partly interchangeable physiological values, does it imply that Galápagos finches are *perceiving* them similar to each other too? Their exploratory behavior has been selected on the basis of several ecological factors and, although it “may be motivated by neophilia, which is defined as the spontaneous attraction of an animal to a food item, place, or object because it is *novel*” (Tebich *et al.* 2009: 592; emphasis mine) — thereby implying not resemblance, but rather contrast — however it has been shown that in captivity “woodpecker finches soon approached objects of *similar* size and structure, but it often took several hours until they started manipulating them (Tebich *et al.* 2009: 601; emphasis mine). Under given constraints, finches’ need for water might well compel them to extend the drinking attempts to anything recognized as *liquid* and, because of operant conditioning, to learn new potential sources. If it is not easy to decide whether for members of *Geospiza difficilis* the blood feeding habit is grounded or not on ‘wrong’ — to say, generalized — perceptions, what about insects? Do they make mistakes? Rothschild is explicit in this respect:

Many of the arthropod parasites of birds, such as bugs, mosquitoes, and ticks, were originally suckers of plant juices. As the geological record proves, these groups evolved before birds and mammals and, no doubt, in the past were essentially vegetarians. It is a relatively easy matter for them to pierce the skin of an animal *either accidentally, in error, or deliberately* if no other food is available, and to extract its body fluids. These accidental and casual drinks of blood which no doubt originally took the form of an occasional meal might easily become a habit, and then a necessity. (Rothschild 1957: 48; emphasis mine)

Literature abounds with examples and, in light of the hypothesis I am putting forward, it is important to stress those factors influencing the unusual behavior. Faúndez and Carvajal (2011: 408; emphasis mine) have reported, despite Nabids being general predators of small arthropods, a human case of biting by *Nabis punctipennis*, so explained: “[b]ecause the nabid was not detected until it attacked, and because of the amount of blood found in its abdomen, we believe the bug was attempting to obtain *water and/or solutes*”. Baena (2011: 400; emphasis mine) provides a list of references about unusual feeding habits of *Heteroptera* and reports that, although a predator of small insects, “genus *Geocoris* is known as accidental biter to man [...] in *arid regions* of North Africa”. Waage (1979: 191) reports of several phytophagous and insectivorous *Hemiptera* that have been seen ‘biting’ humans and quotes the case of *Lyctocoris campestris*, which has been seen on a number of occasions to pierce human skin — and “will, in fact, take a blood meal” — and is especially interesting since intermediate between predatory ‘flower bugs’ and hematophagous ‘bed bugs’. Besides, “[s]ome predatory *Diptera* are occasionally attracted to vertebrates; the rhagionid [...] has been observed to feed on human sweat [...] a behaviour possibly related to the habit of feeding on *water droplets* and *aphid* and *plant exudates* exhibited by other rhagionids” (Waage (1979: 195; emphases mine). Also Lehane (2005: 13–14) underlines that the lifestyle of different extant insects supports the evolutionary scenario from entomophagy to hematophagy and, as a personal experience, describes the case of a flower bug *Anthocoris nemorum*: normally, he lives around flowers pouncing on small insects visiting them, “[w]hile its probings of my skin cause a sharp pain, I have yet to find one that has obviously ingested any blood; however, it still establishes the fact that entomophagous insects will often show an interest in vertebrates as potential sources of a meal”. Bailey (1936) refers about thrips (normally considered phytophagous and to some extent predaceous) attacking man transitorily and, supposedly, attempting to suck in order to obtain moisture and not blood; by quoting J. W. Evans, he writes that “thrips act in this manner during periods of high temperature accompanied by low humidity (better expressed as saturation deficit), the reaction being entirely due to the fact that *the insects will alight on any moist surface at these times*” (Bailey 1936: 96; emphasis mine). There also happens something akin to the effect of electric traps for mosquitoes: once drawn to the wet surface of large tanks of water, they have been drowned and

“the insects do not merely rest on the wet surface but attempt [...] to draw up the water” (Bailey 1936: 96).

Myers (1929) offers akin suggestions. After having pointed out that all the cases of occasional biting and blood-sucking have taken place under exceptional circumstances, he comes close to my research hypothesis:

The *Homoptera* especially, being much more generalized feeders than the *Heteroptera*, are accustomed to drawing their liquid nourishment *from almost any portion of the vegetable substratum on which they normally rest*. How easily leafhoppers may be induced to pierce and suck under entirely unnatural conditions is shown in the ingenious technique of Carter. The liquid used — whether plain water or various solutions of plant sap — was contained in a rough bag made by tying up a piece of “fish skin” (apparently swim-bladder). This was suspended from the roof of the cage and was freely sucked by the insects. The psychic element in piercing and sucking when a leafhopper finds itself on a pierceable surface with liquid beneath must be so small as to be almost negligible. Under great mental stress, we pace up and down unconsciously and uselessly. Similarly a leafhopper, under the overwhelming influence of one great stimulus, that of artificial light, flies about its source, alights on nearby objects, and if these be animal bodies, pierces and sucks them (Myers 1929: 477–478; emphasis mine).

In a way, this consequence can be understood as though the discriminative threshold on some sensory dimension had been amplified, thereby inducing the animal to categorize as functionally or perceptually similar objects that, normally, are kept distinct. Were two entities ideally different under any respect from a perceptive viewpoint, this would not invalidate their iconicity however, since it is an interpretative process that must not be confused with factual similarity. And this of course is in line with Peirce’s pragmatic maxim: if two objects have same bearings, they have the same meaning and can be thought of as being analogous entities.

Provided to be liquid, anything goes. The need of salt determines comparable conducts and the case of moths is exemplificative. Within the order *Lepidoptera*, hematophagy is restricted to the moth genus *Calyptra*, whose members have adapted mouthparts that enable them to pierce through the skin of animals. Only ten out of the seventeen species described perform the habit under natural or experimental conditions and only males take blood meals as a facultative choice. By reporting field observations and experiments with *Calyptra minuticornis*, *C. orthograptus* and *C. labilis*, Bänziger (1979) suggests that these three species of moth are likely to be at least occasional blood-suckers. No direct skin-piercing was observed on animals, but: firstly, it did happen with the author’s finger; secondly, the general piercing mechanism and proboscis morphology range from similar to almost identical to those of the classical skin-piercing blood-sucking *C. eustrigata*. There are good reasons to believe

then that this feeding habit is likely to occur in natural conditions. To explain in part the behavior of these *Lepidoptera*, Bänziger (1979: 35; emphasis mine) remarks that “water loss through evaporation in dry-hot air may be compensated for by production of metabolic water through combustion of fat as in clothes-moths [...] or possibly diminished by larger intake of salt. *Blood offers both*”. Thus, a particular ecological setting can in fact sustain an occasional attitude aimed at obtaining the same nutrients from different sources, which become functionally equivalent.

Besides, genus *Calyptra* belongs to a larger subfamily *Calpinae* whose adult members include, within the range of their feeding behaviors, fruit-piercing. Zaspel *et al.* (2012: 790), despite not investigating the conditions that might have affected the initial shift, by using a Bayesian method of ancestral state reconstruction (molecular phylogenetic analysis) concludes that male adult hematophagy in *Calpini* aroused from a “directional *addition* of feeding types from nectar feeding to fruit piercing, to skin piercing and blood feeding” and, above all, “[s]election for salt collection and transfer to females is the most likely explanation for this facultative behavior”. In addition, the skin-piercing blood-sucking *Calyptra eustrigata* is closely related to the fruit-piercing moth *C. thalictri*, with “the two species resembling each other so strongly that only the comparison of the genitalia allows their exact determination” and “observations confirmed that the piercing behaviour of the fruit-piercing and the skin-piercing moths is very similar” (Bänziger 1970: 54), to the extent that the former can be studied indirectly through analysis of the latter.

In conclusion, in the case of moths it is possible to observe, within a single genus, many of the features defining the leading hypothesis: functional equivalence between different foods, grounded on their sharing a common element (sodium); a behavior-driven choice (occasional blood-feeding) depending on ecological factors; the same organ (mouthparts for piercing and sucking) adopted — and perhaps *exapted* — for slightly different functions in related species. Given certain environmental conditions, the quest for water or salt and their generalized detection are able to trigger the stereotypical feeding sequence involving alighting, probing, piercing and sucking, which in turn brings insects into contact with entities not belonging normally to the set of their ecological relations; in a way, all the humid and salty things become the same thing and contextual stimuli that usually would elicit an avoidance reaction are ignored. The same principle holds true for the evolution of analogous feeding habits too: for instance, as for the origin of lachryphagy, “initial feeding on dung, urine and carrion is found in many *Lepidoptera* [...] and these substances may share with animal secretions certain nutrients or attractants which facilitated the shift to feeding on vertebrates, such as salt [...] amino acids or fatty acids” (Waage 1979: 202; for other organic compounds which can elicit unusual feeding acts, cf. Plotkin, Goddard 2012; Bänziger *et al.* 2009; Bergevin 1925; Shannon 1928)

The idea of occasional hematophagy as a consequence of failed discrimination or hyper-generalized behavior (on the basis of organic constituents determining a minimal similarity) meets the conclusions of two important arti-

cles. Usinger (1934) reports several records of phytophagous *Hemiptera* sucking blood and, after agreeing with Bergevin that attraction to exposed liquids undoubtedly plays an important part, then adds what follows:

The change from the sucking of plant juices to bloodsucking at first appears to be very great. However, upon comparison of the chemical constituents, it is found that, in general, *the same elements are found in plants as in blood and often in very similar combinations although in very different proportions* [...]. Blood contains almost all of the sugars, proteins, salts, etc., found in plants but it is a great deal richer in nitrogenous materials as a whole and the type of protein is very different from that found in cytoplasm. *Likewise the concentration* [...] *is not so different as to prevent the use of one or the other to an insect not accustomed to both*. Consequently we see that *what is ordinarily considered to be a tremendous change, namely the jump from plant sucking to blood sucking, may be quite within the range of possibility*. (Usinger 1934: 99; emphases mine)

Accidental biting is attributed then to three influences — unusual environmental conditions, *attractive qualities of exposed liquids* and *hunger* — and the evolution of the habit, among other factors, is linked to the comparable properties of sap and blood. The same might have been true for the changeover from hemolymph to blood (i.e., from entomophagy to hematophagy) too, since the reverse, at least under experimental condition, does occur: in the laboratory, some mosquitoes have been observed to feed on insect larvae and produce viable eggs, which suggests that “hemolymph may be taken as a last resort if vertebrate hosts are not available” (Harris *et al.* 1969: 185).

If Usinger’s work and lab results are useful to put the stress on the relative substitutability of such organic liquids, so that a basic mechanism of post-ingestive feedback might account for the repetition and persistence of initially fortuitous acts, Hill *et al.* (2010) solves a major problem: accidental biting is rare and individual and does not seem to exhibit the sufficient behavioral stability and diffusion to elicit a Baldwinian evolutionary scenario. However, some experimental results supply a way out:

The description of a subset of *C. thalictri* males with reduced numbers of olfactory sensilla that take a proffered blood meal under confined experimental conditions while other males do not, provides the opportunity for us to observe the *characteristics that may be responsible for a broadening of host range within a single species to include blood feeding*. Behavioural evidence in this study [...] describes non-blood feeding moths as orienting and moving away from a vertebrate-host, indicating that the non-blood feeding moth response to vertebrate odour cues is repulsion. We propose that a reduction in this behavioural repulsion to vertebrates may be the foundation of the interaction we have observed

between male moth and human thumb, and ultimately the use of blood as a new resource. The decreased number of *s. coeloconica* in blood feeding males suggests a loss of the vertebrate odour-sensitive OSNs housed within these sensilla and the concomitant *decrease in sensitivity* to vertebrate olfactory cues. A decrease in the sensitivity to such vertebrate cues by individual males may indeed result in a loss of this repulsion from vertebrates, leading to increased zoophilic interactions and the potential for these moths to blood feed. Investigation into observable differences between the males that did not take a blood meal and those that did, particularly in *sensory structures associated with food acquisition*, may give us insight into at least one avenue for the adaption to blood feed. (Hill *et al.* 2010: 331; emphases mine)

Both generalized behavior and failed discrimination, whether due to morphological modifications of sensory organs (cf. also Cande *et al.* 2012, on how changes at the level of chemosensory systems contribute to the diversification of behaviors, with evolutionary implications) or contextual physiological/ecological conditions, point in the same direction, namely the occurrence of iconic phenomena as defined by Deacon. He relates iconic reference to learning and stimulus generalization (Deacon 1997: 78–81) and, as a matter of fact, specialist literature on insect learning confirms the interpretative line hitherto adopted insofar the issue of perception is concerned.

Stimulus generalization is a phenomenon that has been studied in detail in the psychological literature and takes place when “responses conditioned to one stimulus can also be elicited by other stimuli on the same dimension” (Kalish 1969: 209). It involves a gradient — “the amplitude or frequency of response decreases with increased differences (psychological or physical) between the CS [conditioned stimulus] and the test stimuli” (Kalish 1969: 209) — that can be obtained “for virtually any sense modality and with any stimulus dimension having ordinal properties” (Kalish 1969: 210). Experiments indicate that it is “basic to the functioning of virtually all human and infrahuman organisms. Pavlov regarded generalization as an exceedingly important element in the survival of the organism” (Kalish 1969: 210).

Smith’s article “Merging mechanism and adaptation: An ethological approach to learning and generalization” (1993) contains many of the conceptual elements on which I have been assembling my hypothesis. Firstly, the concept of *error* steps in, since “[s]uperficially, generalization looks like a mistake because a subject responds to a stimulus that has never been associated with a reward” (Smith 1993: 130). However, exactly such motivational variables as hunger or thirst affect the gradient and turn possible mistakes into exploitable opportunities: “might a honey bee on the brink of starvation for whom a small reward might be very important for ensuring survival over a short period generalize more broadly than a bee that is satiated?” (Smith 1993: 131). In fact, flattened gradients (which means response generalization) have been constantly found for stress situations in human and animals (Kalish 1969: 263), so as

increases in drive level under hunger, thirst and shock have resulted in increased responsiveness (Kalish 1969: 264). This is consistent with literature on insect behavior under starvation; for instance, Chapman and de Boer (1995: 126) report the following:

In some situations, as when an insect has been deprived of food for a long period, it may begin to feed in the absence of suitable chemosensory input. For example, there are many examples of locusts and grasshoppers eating plants that are rejected by well-fed insects (e.g., Bernays *et al.*, 1976). In some cases this may be the result of a shortage of water, and perhaps water in the unusual host acts as a phagostimulant. There are also examples in the literature of locusts eating inert materials, such as nylon screen or polystyrene. Perhaps in these situations, the palps provide no chemosensory information because potentially stimulating chemicals are absent from the material. This situation is analogous to palpectomy experiments.

Secondly, what matters most is the conceptual and terminological affinity between stimulus generalization and *iconicity*: the “inverse hypothesis”, for example, assumes that “the organism’s *inability to respond differentially* to changes in the stimulus dimension (discriminability) is the basis for stimulus generalization” (Chapman, de Boer 1995: 233; emphasis mine); or “discrimination is facilitated when the amount of similarity between stimuli is decreased. The finding that appears most consistently in the literature is that discrimination becomes more difficult if the *similarity* of the stimuli *is* increased” (Chapman and de Boer 1995: 249). Unusual stimuli that are more similar to the CS will trigger therefore stronger responses than those that are less similar on a given sensory modality and perceptual dimension. In this respect, an “animal might be able to track individual components of complex stimuli such as color, shape, and odor, and thus learn only those stimuli that most reliably predict a resource” (Smith 1993: 131). An organism’s ability to detect single components belonging to different compounds, as in cases of salt, water or amino acids, might be responsible therefore for its proneness (in connection with physiological drives amplifying specific sensory discriminative thresholds) to adapt feeding habits to different foods, thereby starting up ecological changes and possibly exaptive evolutionary events.

Thirdly, generalization is inferential, has a predictive value and is grounded on probability; thus, it meets some of the requirements of hypothetical reasoning. After having learned that a pattern of sensory stimulation predicts quite reliably certain outcomes, a subjects needs to identify future instances of the same pattern, while neglecting those that do not have predictive value. Since it is unlikely under natural conditions the exact reproduction of objects and events, animals must have mechanism for generalizing learned information, that is for extending what has been acquired by associative and instrumental learning to other cases than those previously experienced. Grounded on those

components of complex stimuli that grant favorable predictions, stimulus generalization recalls Peirce's induction by qualities and therefore abduction. By classifying entities as token of types, it exploits formerly established connections between stimuli and rewards and between perceptions and actions, a temporal consequentiality that, according to Peirce, can be equated to logical reasoning. On this basis, the partial stability of the environment allows prediction, while intermediate variability makes it unpredictable too. Eventually, the probable nature of stimulus generalization is well outlined by this Smith's excerpt:

For example, floral odors that foraging honeybees use to identify resources such as nectar and pollen are complex mixtures of many individual odorants. Even among flowers that contain the resource, the exact composition of the odor signal may vary due to such factors as age, physiological condition, and genetic constitution. Under these conditions, a bee that constrains itself to search for the same complex of stimuli that it experienced from a flower at which it received a reward might, in the extreme, only revisit the flower it just depleted of resources. The bee would pass over many flowers of the same species that contain a reward but which vary slightly from the pattern given off by the flower at which the bee found nectar and/or pollen. In the other extreme, a bee that generalizes too broadly might visit every flower regardless of its species identity or reward potential; that is, it might not easily recognize stimuli that predict that a flower contains no pollen or nectar. (Smith 1993: 130)

7. CONCLUDING REMARKS ON THE CASE STUDY

The introduction to my papers, in a more specific sense than its general function, is meant to be an hypothetical proposal concerning how blood-sucking might have developed from a perspective focusing on Peirce's theory of signs and inference. The conjectural nature of the work is in line with the partial ignorance regarding the origin of hematophagy: "in most cases, the paleontological findings do not elucidate the initial phases of hematophagy development in different taxa. Historically, the period of switching to blood-feeding appears to have been rather short as compared to the total duration of the taxon evolution, so that it left no traces in the paleontological history" (Balashov 1999: 945); hence, the result is that "even though the origin and evolution of hematophagy in insects and ticks have been the topic of many publications, the hypotheses proposed are to a large extent speculative" (Balashov 1999: 950).

Some points are nevertheless quite well shared among scholars. Firstly, "[t]he most essential prerequisites to the origin of hematophagy were spatial contacts, trophic associations, and morphophysiological preadaptations" (Balashov 1999: 950). Secondly, as for the sensory system, "[i]nsects switched to haematophagy without developing new sensory organs" (Balashov 1999: 945), thereby suggesting their adequacy to being extended or generalized in meeting the requirements of the new feeding habit.

The plausibility or logical acceptability of the modeling attempt is grounded on the following argument: if hypothetical inference is based on a perceptive mechanism of iconic type and iconism involves generality, then generalization is the other side of the coin of abduction, which applies equally to animal sensory and behavioral generalizations. In turn, since to generalize means and implies to coopt, abduction frames exaptation too.

Such reasoning has been carried on starting from an historical overview of the basic idea underlying the coinage and adoption of the concept of exaptation, starting from Darwin himself; specific attention has been paid on Ch. Wright, because of his influence on the author of the *Origin* and the significance of his principle of new uses of old powers, whose elaboration was conceived to contrast detractors and critics of the new theory of natural selection.

By comparing Wright to Peirce, emphasis has been put on the historical fact that exaptation and abduction did come to light in the same theoretical horizon and within the speculations of authors whose thoughts met on several points. Reasons explaining why, however, they never came in touch have been provided: chiefly, disagreements about the nature of Darwinism, Lamarckism, mind's logic and the ability of organisms to shape their own evolution via life-time behavioral choices.

Next, Peirce's evolutionism has been subjected to examination, especially insofar his acceptance of Lamarck's theory of inheritance of acquired characters is concerned. From this it resulted an evolutionary pluralism broader than Wright's account and to same extent closer to the current understanding. Peirce's stress on behavior as a factor of evolution has switched the focus of

analysis on learning and inference, resulting in the tentative interpretation that his Lamarckism mirrored the working of hypothetical reasoning. To do this, the physiological corresponding of each inferential modality has been displayed, showing that abduction relies on iconic interpretations of perceived similarities among objects and, accordingly, that organisms' habit taking can be formalized in the same manner.

The concepts of mistake and substitution have been employed then as theoretical keys able, first, to provide a complementary understanding of (wrong) behavioral abductions; second, to report cases of sensory-driven changes of behaviors causing exaptation and thus, more generally, triggering new evolutionary directions; third, to prepare the final analysis of the case study.

The section on technological development has further elaborated on the analogy between technology and biology, i.e. between tools and organs, this time testing the just achieved original idea of a deep sensory-based connection of abduction with exaptation on the results of my third article (Weible 2013); in this respect, this introduction and the third article mutually corroborate each other.

The evolutionary hypothesis has been put on trial by choosing a case of exaptation — the origin of bloodsucking — and looking for clues able to confirm the presence of many or all the basic elements of the construct, such as mistakes, generalizations, objects similarities, behavior and learning, etc. To give a look as scientific as possible to a purely theoretical speculation, I have tested my abduction on the supposition of an isomorphism between abductive and exaptive sequences.

As for behavior, there is consensus about the fact that it might have canalized the changeover towards blood as a new source of food with the re-functionalization or extension of existing biting and sucking mouthparts. Downes (1970) expresses himself in such terms; Waage (1979) speaks about behavioral prerequisites to hematophagy; Fenton (1992) refers to the flexibility of behavior in protovampire bats; Schutt (2008) suggests that a behavioral shift may have allowed carnivorous phyllostomids to exploit blood of larger mammals; Bowman and Billeb (1965) maintain that behavioral predispositions account for occasional blood feeding in finches. Osche (2002: 15) is lapidary on the issue: “Transferring of existing (preadaptive) structures to new functions and roles requires changes in behaviour and implies, therefore, inclusion of an additional discipline into the synthetic view”. Fundamental is also the whole monograph (Schmitt 2002) dedicated to the “evolutionary ecology” of Gerd von Wahlert, with the participation of scholars whose viewpoint on evolution is expressly behavior-centered; for instance, in the words of Sudhaus (2002: 146):

Fundamental in animals are “ethological key innovations” [...] which allow them to exploit existing resources in new ways. Evolutionary change in behavior or physiology in order to exploit a new resource can put organisms and their preadaptive structures into a new ecological

situation. The changed behavior thus at first brings an extension of function, but then might also lead to an ecological change of function [...]. In retrospect, such changes of behavior therefore end up being the "pacesetters of evolution" [...]. They precede morphological changes and effect various alterations in structure as they influence the further direction of selection and evolution of characters. Organisms and all their properties, preadaptive and otherwise, are governed by new selective forces caused by a new relationship to their environment. Over many generations this leads to evolutionary change which improves the adaptations to the new mode of life; that means that they become more economical in terms of the energy output necessary to maintain them. "Ethological key innovations" are thus followed by adaptations in morphology to a new mode of life ("morphological key innovations" [...])

As for errors in the pursuit of food, I have quoted many examples (Rothschild 1957; Faúndez, Carvajal 2011; Baena 2011; Waage 1979; Lehane 2005; Bailey 1936; Myers 1929), so that accidental biting of man and mammals by not hematophagous species is quite widespread a phenomenon. Besides, such possibility is exactly what allows animal traps to work.

In addition, animal mistakes synthesize the complementarity of generalization and similarity. In electric mosquitoes traps, for instance, the usual association in mammal hosts between carbon dioxide and blood, along with the alighting behavior which is triggered, are extended and generalized (wrongly) to whatever emitting this particular molecule; in turn, mammals and cages do need to be similar in some respect to be interpreted iconically and substituted for each other. The relevance of similarity is thus twofold — perceptive and physical — and mirrors the very nature of Peirce's metaphysical speculation on the correspondence between phenomenology and ontology (realism of the categories of Firstness, Secondness and Thirdness). The actual sharing of properties among different objects is what makes the organism-environment coupling ambiguous and equivocal. Within a remarkable conceptual approach synthesizing perception, theory of signs as operational cues and psychological classical associationism, Tolman and Brunswik (1935: 53) claim that, in the relationship with objects, "univocal relations do not really obtain. Quite different discriminanda [perceivable objects properties, such as shape, color, size, etc.] may be coupled on different occasions with one and the same manipulanda [objects properties that allow behavioral manipulations]. Apples are sometimes red but they are also sometimes yellow". Most important, "*one and the same discriminanda will on different occasions be used as signs of different manipulanda*. Brown is sometimes coupled with and used as a sign of chocolate but at other times it is coupled with and used as a sign of, say, a negro skin" (Brunswik 1935: 54; emphasis mine".

Especially in lower living forms, generality and continuity of icons rest on the radical commonality of chemical-physical properties among world entities and events; but what enables organisms to establish reliable predictions depend-

ing on such regularities is what makes them fallible too. There are “ambiguous” cues, which are caused with great frequency by both the given object and other objects, and “misleading” cues, which may be caused with little frequency by the given object and with great frequency by other objects. The implications are clear:

Again, we would throw out the suggestion that the ambiguous and the misleading cues may for some individuals and under some conditions constitute a rather special common group to be designated as “hazardous.” For both types of cue present a high degree of probability of leading the individual astray, i.e. of having been caused by other objects, C, D, E, etc. instead of the to-be-sought for good means-object B. (Hazardous cues would thus be analogous to “dangerous” means-objects). (Brunswik 1935: 57)

In animal perceiving and behaving, such concepts as generalization, mistake, and stimulus similarity are deeply interconnected; not by chance, when investigating unusual habits or accidental biting scientists are trying to find out which organic compounds, normally reacted to in ordinary searching, might have prompted the feeding attempts. In other words, salt, water, nucleotides and others, because of their widespread diffusion, provide ambiguous and misleading cues that support at the same time right inferences and wrong abductions.

In line with Tolman’s and Brunswik’s framework and their recognition of the theoretical affinity between sign theory and classical psychology, literature on stimulus generalization confirms the connection and suggests how my proposal concerning the possible perceptive origin of some of the evolutionary paths leading to the development of hematophagy could be translated experimentally. Studies on animal learning within the tradition of classical and operational conditioning have a well established empirical methodology which can be adopted to test in laboratory whether those free-living forms showing ecological and taxonomic affinities with existing vertebrate associates — for instance, members of *Psocoptera*, phytophagous and insectivorous *Hemiptera*, fruit-piercing *Lepidoptera*, etc. — can be induced to blood feeding through the manipulation of different attractants. Especially, the focus of research should fall on those free-living forms exhibiting no vertebrate associations but possessing preadaptive feeding structures or behavior, whose cooption should be verified (Arnold 1994; Pievani, Serrelli 2011) against adaptive hypotheses depending on natural selection. Besides, the occasional feeding habit thus induced should be proven to be enough stable over the generations grown in the laboratory to result in an “irreversible transformation” (Kull 2014) towards obligate parasitism. Eventually, all phases of insects feeding behavior (alighting, probing, piercing, sucking, tasting and gorging; cf. Chapman, Boer 1995) should be scrutinized and tested to detect the exact point or points where the switch might have come about. The present work merely puts forward a plausible scenario and further research is needed.

8. GENERAL CONCLUSIONS

My thesis claims the feasibility of Peirce's theory of signs and inference to be applied to biology as a modeling device. More precisely, semiotics models evolution and the phenomenon of exaptation and proves itself useful in highlighting the perceptual dynamics involved in those behavioral modifications during organisms' lifetimes liable to trigger new evolutionary trajectories. In this, it goes hand in hand with past and contemporary interpretations of this concept and makes a thread through the classical Darwinian, neo-Darwinian and post-Darwinian approaches.

Reinterpretation and generalization of the concept of exaptation on the basis of signs theory and abduction have been achieved by historical and epistemological analysis. Historical research has led to the acknowledgment of the wide circulation of the precursory notion of preadaptation and similar principles in the earliest evolutionary biologists after Darwin's revolution—even in the key texts of the modern evolutionary synthesis. Darwin himself owed some of the qualifications and corrections to his initial ideas to Ch. Wright's principle of new uses of old powers. On the other hand, Wright and Peirce did know each other's theories but neither came up with a comprehensive view able to join together coherently hypothetical inference and biological evolution: differences concerning the nature of mind and scientific thought on one side and the role and value of Lamarck's theory on the other side kept them apart and didn't favor the theoretical meeting.

If restricted to indirect consequences of behavioral plasticity and learning (i.e., Baldwinian organic selection), Peirce's Lamarckism does offer however all elements to accomplish the synthesis between abduction and exaptation: on one hand, it identifies with learning and can be interpreted like the extension of previously existing ideas or rules of action to new data or events and objects; on the other hand, once understood in Baldwinian terms, it is identical with a specific subtype of cooption phenomena driven by behavior. In either cases (by definition for abduction, supposedly for exaptation), perceptive similarity and its iconic interpretation or recognition are the key factors allowing the passage from one process to the other and grounding the modeling.

The application of this reasoning to technological development and manufacturing is nothing but a corollary to the common iconic and abductive mechanism underlying human and animal learning plasticity. Indeed, on the basis of my generalization via Peirce's signs theory, biological exaptation takes on the status of a case of 'learning set transfer' (Deacon 1997: 80). In this respect, there is no more appropriate way to conclude than taking a cue from Gould's idea (Gould 2002: 1214–1218) that Nietzsche's distinction between current utility and historical origin represents the best introduction possible to the theoretical importance of exaptation — the German philosopher is particularly suitable to epitomize this research too, with a definition of *knowledge as recognition* that openly sums up the core of the several issues hitherto treated: "I take this explanation from the street; I heard one of the people say that 'he

knew me right away' — and I asked myself: what do the people actually take knowledge to be? what do they want when they want 'knowledge'? Nothing more than this: *something unfamiliar is to be traced back to something familiar*. And we philosophers—have we really meant anything *more* by knowledge? (Nietzsche 2008: 214; § 355).

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OVERVIEWS OF ARTICLES

The main body of this thesis is composed of three articles, published between 2012 and 2013. The first has framed the issue of exaptation with reference to semiotics and put forward the idea of a possible connection with Peirce's theory. The second has investigated some perceptual aspects linked to evolution and cooption, thereby suggesting a way to properly set up the modeling. The third represents an attempt of generalization of re-functionalization phenomena, aiming at removing some of the usual distinctions between human and animal behavior. All three contain fundamental elements, precursors of the decisive hypothesis developed and tested in the present introduction, which constitutes to all effects the fourth and conclusive part of the research.

I. The Concept of Exaptation between Biology and Semiotics. The paper introduces Gould's and Lewontin's criticism against Neo-Darwinism and the general principles of a post-Darwinian evolutionary biology and epistemology. Gould's and Vrba's seminal article on exaptation is presented, with a brief historical survey of its conceptual antecedents and emphasis on further developments, applications and experimental validation; besides, its articulation in a four-cases typology is illustrated. A casuistry of phenomena linked to exaptation is reported, including the adoption of the notion in research fields other than evolutionary biology, such as linguistics, semiotics and biosemiotics. Eventually, Hoffmeyer's in passing suggestion of a connection (likely metaphorical) between exaptation and abduction is taken concretely as the leading hypothesis guiding the whole research project and connected to Baldwin's organic selection, so as to bring both back to the more inclusive topic of behavior.

II. Ritualization and Exaptation: Towards a Theory of Hierarchical Contextuality? The paper translates the notion of ritualization into that of exaptation and focuses on the role of perception in affecting morphological and behavioral changes. Functional shifts of biological traits are reframed in terms of contextual changeovers and emphasis is put on the dialectics between initial cooption and subsequent adaptation, so as to integrate together classical Darwinism and post-Darwinian ideas.

III. Approaching a Semiotics of Exaptation – Preliminary Reflections at the Intersection between Biological Evolution and Technological Development. The paper clarifies what is meant by semiotic modeling of exaptation and elaborates on the common sense analogy between animal organs and human artifacts to address the issue. Arnold's typology of exaptation is applied from biological evolution to technological development and parallels between the two domains are highlighted. Specifically, a genetic and pragmatic analogy is exposed: instruments and organs are similar in the way they are produced by (respectively) culture and nature on one hand and in the way they allow their

owners to actively mediate the relationship with the environment. A unifying formula on biological and technological functional changes is advanced, so as to define schematically first-use, addition and transfer exaptations and distinguish between non-adaptive and adaptive modifications. Conclusively, similarities are shown between language and evolution as systemic and perception-based phenomena.

SUMMARY

The present dissertation attempts a modeling of the evolutionary (and semiotic) phenomenon of exaptation according to C. S. Peirce's theory of signs and inference. In the first article I analyze the historical background from which the concept of exaptation comes out; along with presenting a synthetic overview of its application in research fields other than evolutionary biology, special attention is paid to its connection to semiotics and biosemiotics. In particular, the possible relation with both Peirce's concept of abduction and J. M. Baldwin's concept of organic selection is here first outlined.

The second paper focuses on the possibility of organisms' perceptive abilities to trigger such evolutionary changeovers as the adoption of new functions for old traits. It relies on both classic ethological studies about ritualization and the notion of context as understood from a semiotic perspective. However implicitly, the role of Peirce's theory of perception as inference becomes integrated within the ontogenetic and phylogenetic dynamics between cooption and adaptation.

My third work parallels the biological shaping of animal organs to the technological development of human artifacts. It draws a genetic (in the sense of origin) and pragmatic analogy between the two domains, so as to further corroborate Peirce's idea of a substantial continuity between natural and intellectual products. Arnold's typology of exaptation is applied to technology and a unifying formula on biological and technological functional changes is advanced.

The *Introduction* to the three articles sums up the whole issue and establishes a common thread among the several topics addressed separately. Some deepening is provided for specific parts: attention is paid to the historical importance of Ch. Wright for both philosophy and biology and his relationship with Peirce is investigated; as for the latter, his specific position towards Darwinism and evolutionism is described and interpreted to make it compatible with modern understandings; most of all, a specific analysis of abduction highlights its perceptive, iconic and physiological aspects. Eventually, a final section tests the hypothesis presented through a comparison with literature on the evolution of blood-sucking in insects.

SUMMARY IN ESTONIAN

Eksaptatsioon: ühe bioloogilise mõiste semiootilise kirjelduse poole

Käesolev doktoritöö modelleerib eksaptatsiooni kui evolutsioonilist ja ühtaegu semiootilist nähtust, lähtudes C. S. Peirce'i märgi- ja tuletusteooriast. Esimeses artiklis analüüsitakse eksaptatsiooni mõiste ajaloolist tausta ning antakse sünteesiv ülevaade selle rakendustest väljaspool evolutsioonilist bioloogiat. Erilist tähelepanu pööratakse selle mõiste seoste semiootika ja biosemiootikaga. Tuuakse välja võimalik seos nii Peirce'i abduktsiooni mõiste kui Baldwini orgaanilise valiku mõistega.

Teine artikkel keskendub organismi tajulisele võimele esile kutsuda evolutsioonilisi üleminekuid, omistades olemasolevatele tunnustele uusi funktsioone. Seejuures toetatakse nii klassikalistele etoloogia uurimustele rituaalidest kui ka konteksti mõiste semiootilistele käsitlustele. Peirce'i teooria tajust kui tuletusest seondub implitsiitselt ontogeneetilise ja fülogeneetilise dünaamikaga kooptsiooni ja adaptatsiooni vahel.

Kolmas artikkel tõmbab paralleele loomaorganite bioloogilise kujunemise ja inimese artefaktide tehnoloogilise arendamise vahel. Tuuakse välja geneetiline (algupära mõttes) ja pragmaatiline analoogia kahe valdkonna vahel, et tõestada Peirce'i ideed looduslike ja vaimsete nähtuste vahelisest olemuslikust pidevusest. Arnold'i eksaptatsioonitüpoloogiat rakendatakse tehnoloogiale ning arendatakse ühtset bioloogiliste ja tehnoloogiliste funktsionaalsete muutuste teooriat.

Kolme artikli sissejuhatus võtab kogu teema kokku ja toob välja ühised jooned erinevate teemade vahel. Töö osadele antakse süvendatud ja üldistatud käsitlus: pööratakse tähelepanu Ch. Wright'i ajaloolisele tähtsusele nii bioloogia kui filosoofia jaoks, samuti tema seosele Peirce'iga. Kirjeldatakse ja tõlgendatakse tema erilist suhet darvinismi ja evolutsionismiga, et luua seos tänaste arusaamadega. Eelkõige toob spetsiifiline abduktsiooni analüüs välja selle tajulisi, ikoonilisi ning füsioloogilisi aspekte. Viimases osas testitakse hüpoteesi, tuginedes verd imevate putukate evolutsiooni alastele uurimustele.

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