BEYOND TYPOLOGY/ POPULATION DICHOTOMY. RETHINKING THE CONCEPT OF SPECIES IN NEO-LAMARCKISM AND ORTHOGENESIS

Michał Wagner

ABSTRACT: Historiography is becoming more critical of the typology/ population dichotomy introduced by Ernst Mayr. Therefore, one should look again at the problem of species in non-Darwinian theories: neo-Lamarckism and orthogenesis, and consider the possibility that this problem was overly simplified. What can be seen in both of them is the existence of a tension between the idea of evolution and the essence of species. In neo-Lamarckism, this tension was resolved by recognizing species as static entities which changed only when triggered by external stimulus. In orthogenesis, evolution was seen as constant phenomena and species – as naturally changeable entities. However, orthogeneticists assumed that not only species, but also whole phyletic lines had essences that constrained their further evolution. Thus, in both cases we can see interpretation of species in tune with essentialism, but essentialism is widely differently integrated with each of these concepts of evolution.

KEYWORDS: population, typology, essentialism, Darwinism, neo-Lamarckism, orthogenesis

Introduction

The "eclipse of Darwinism" was a term introduced into modern historiography by Julian Huxley (1945, 17-28) as the name of a historical period in the history of biology at the turn of the 20th century. It was manifested by a sudden decrease of interest in Charles Darwin's theory of evolution in favour of other non-Darwinian evolutionary theories, such as neo-Lamarckism, orthogenesis, saltationism and mutationism. The situation changed only in the 1930s, when the "synthetic theory of evolution" emerged and Darwin's theory was fully accepted. Ernst Mayr, one of the most influential figures in the history of biology, explained the cause of the "eclipse" by pointing out that external, irrational factors prevented naturalists from fully accepting Darwin's theory (1991, 38-39). One of the most important factors was essentialism, which influenced the way naturalists interpreted the idea of species species (Mayr 1982, 270). According to Mayr (1971, 10-11), essentialism led to the creation of the so-called "typological" concept of species. This concept was based on the assumption that natural phenomena are invariant and the species consist of similar individuals with the same essence. However, the application of essentialism to evolutionism led to the creation of theories very different from Darwinism, which did not fully accept natural selection (Mayr 1990, 90–91). Subsequently, these theories introduced other mechanisms of evolution, such as neo-Lamarckism which favoured Lamarck's laws of use and disuse, or orthogenesis postulating the existence of immanent growth forces. Its opposite was the "populational" concept of species, in which species were perceived as populations consisting of unique individual (Mayr 1959). The populational concept of species was only fully accepted in the context of the synthetic theory of evolution and, according to Mayr (1982, 561–566), this was the official end of typologism in evolutionary biology. Posterior interpretations of this period also referred to this distinction, and the best example of this notion serves the classic reinterpretation of "eclipse" by Peter Bowler. Notwithstanding that Bowler (1988, 107-110) ultimately disagreed with Mayr's conclusions, he agreed that the inability of the nineteenth-century scientific community to adopt "populational thinking" was the key to rejecting Darwinism.

Contemporary historiography is becoming increasingly critical of the distinction between typological and populational thinking, pointing to the artificiality of Mayr's division, who has repeatedly changed the interpretation of both terms, often making it dependent on the context in which he used them (Chung 2003). Modern historians of biology (i.e. Lewens 2009; Witteveen, 2017; Levit, Meister 2006; Amundson 1998) note that the distinction proposed by Mayr served him rather to construct a narrative according to which synthesis represented a correct view of species, as opposed to the misinterpretations proposed in the pre-Darwinian theories and the alternatives developed during the "eclipse." If this "essentialism story," as Mary P. Winsor (2006) calls it, did not have much coverage in historical facts, but rather had a revisionist character, we may ask a question: then how were species treated in non-Darwinian evolutionism? In order to answer it, we need to focus again on the problem of species in non-Darwinian theories of evolution. As emphasized by Maurizio Esposito (2021, 32), paying attention to the context of a given concept should be of paramount importance for historians of science. According to him, a historian of science should bear in mind that ideas fluctuate and are dependent on the historical and cultural context. As Paul Feyerabend (1981, 76-91) wrote, concepts change their meanings depending upon the context of the theories in which they are used. Consequently, they can be incommensurable to each other even though they refer to the same philosophical concept, e.g. essentialism. Given that neo-Lamarckism and orthogenesis represented different visions of evolution, we should expect that they had incommensurable concepts of species. Even if both of these theories were founded on an essentialist understanding of species, this essentialism was incorporated differently in their context.

In this article, I will focus on the issue related to the concept of species in non-Darwinian evolutionary theories: neo-Lamarckism and the theory of orthogenesis. The article will consist of three main parts: in the first one, I will show what concepts of species have been proposed in Darwinism and neo-Lamarckism; in the second one, I will show how species were understood in the theory of orthogenesis; in the third one, I will try to explain the source of the differences in the understanding of species in the theories falling under discussion. However, the aim of the article is not to fully reconstruct the concept of species in non-Darwinian theories, but rather to show the main features that the evolutionists, who created these theories, ascribed to species in the context of their visions of evolution. I will also use Ernst Mayr's terminology to describe the analysed concepts of the species. I justify this decision by the fact that I want to show that the elements of "typology" and "population" coexisted in non-Darwinian theories, which in turn will show how the dichotomy proposed by Mayr is misleading and blurs the more complex problem of understanding species in the theories falling under discussion.

Scope of Analysis

In order to present the concept of species adopted in neo-Lamarckism and orthogenesis, I have reviewed the views of the most significant scholars related to both of these trends, and by means of comparative analysis, I tried to identify common elements in their writing devoted to species. Within the framework of neo-Lamarckism, I have analysed the works of Samuel Butler, George Henslow, Edmund D. Cope, Alpheuss Hyatt, Alpheuss Packard, and John Ryder. Within the framework of orthogenesis, I have analysed the writings of Carl von Nägeli, Theodor Eimer, Henry F. Osborn, Leo Berg, and Henri Bergson.

The Concept of the Species in Darwinism and neo-Lamarckism

Discussing the problem of species, one shall start with Darwin himself. His concept of a species is the subject of much debate due to the fact that the author himself in the publication *On the Origin of Species* did not specify what a species is. In a rather controversial statement, Darwin (1859, 52) wrote: "I look at the term species, as one arbitrarily given for the sake of convenience to a set of individuals closely resembling each other." This statement later led Ernst Mayr to conclude that Darwin adopted a nominalist vision of species. According to Mayr (1982, 267-269), Darwin adopted populationist thinking about species in his theory, but then he began to move away from it while studying botanical works that directed him towards nominalism. The claim that Darwin was a nominalist is an obvious exaggeration. Darwin defended himself against critics' allegations that he did not believe in species by writing to Asa Gray: "How absurd that logical quibble;—if species do not exist how can they vary? As if anyone doubted their temporary existence" (Darwin Correspondence Project, "Letter no. 2896"). Darwin's critique did not concern the taxonomy itself, but rather the classical systematics in which term "species," as he noted, "…includes the unknown element of a distinct act of creation" (1859, 44). Thus, according to Darwin, taxonomy should be reformed to more accurately reflect the relationships existing between animals, and to be able to classify them according to their origin. Hence, ultimately, he saw the future of taxonomy in embryological research, studies of atavisms and geological record – that is, in research similar to the one presented by Ernst Haeckel in his *Generelle Morphologie* (Darwin 1872, 381). Modern historians of science (Gayon 1998; Winsor 2013; De Quieroz 1997) acknowledge that Darwin had ultimately failed to reform the taxonomy. Nineteenth-century naturalists continued to use Linnaeus taxonomy, recognizing in the theory of evolution the justification for the realness of taxonomic divisions. And so, a close associate of Darwin, Joseph D. Hooker (1859, II-V), stated that the work of the creationist-taxonomist and the evolutionist-taxonomist would be the same, with the difference, however, that the latter would take into account that species would change their place in the taxonomic hierarchy over time. In later years, this situation was commented on by William Bateson (1913, 10-16), who wrote that Darwin failed to reform the taxonomy, and naturalists still assumed that species constitute permanent and unchanging entities.

Mayr also pointed out that this problem could have been caused by Darwin himself: "Unfortunately, Darwin used strictly typological language, and by using terms like 'form' and 'varieties,' instead of 'individuals' or 'populations,' he introduced confusing ambiguity" (1982, 268). Darwin, as stated by Mayr, used typological language to express a vision of a species that was initially populationalist and later nominalist. It supposedly contributed to evoking this harmful "ambiguity." However, Mayr's assessment is anachronistic. We should not forget that a naturalist always works in a certain historical and cultural context, which determines their language and the metaphors they use to explain their thesis. Mayr's claim that Darwin was guilty of not introducing populational language into his work is unfounded, as he had to use available and already known terms to make his theory intersubjectively intelligible. Moreover, it seems that there is a simpler explanation of what kind of species' concept Darwin had and why it could lead back to "typologism," without referring to different levels of "ambiguity" in his terminology as Mayr did.

The easiest way to explain Darwin's concept of species is to refer to the entire context of his theory of evolution. According to the theory, species had to have such a "structure" that natural selection was able to act on them, i.e. they had to be variable. Darwin (1859, 45) wrote that: "No one supposes that all the individuals of the same species are cast in the very same mould." There must have been a multitude of features among individuals, since the natural selection itself did not create the features *ex novo* and only evaluated the existing ones from the perspective of their adaptation (Darwin 1859, 466-467). This vision of the species will be called later "fluctuation" model (Morgan 1908, 267) and will be most precisely expressed by Alfred R. Wallace. According to Wallace (1900, 302): "The species is therefore composed of a fluctuating mass of variable units which yet maintain the same general average of characters." The species were not homogeneous populations, but consisted of multiple different individuals – therefore, under the influence of selection pressure, they were able to survive in a changeable environment. Wallace perceived variability as a universal law of nature. However, was it the same with Darwin? Although Darwin indeed accepted that species are naturally malleable (Darwin 1859, 31), he did not consider this as a permanent feature of species. In discussion devoted to the variability of the domesticated races, he stated that variability is not something that occurs constantly (Darwin 1859, 43). Variability was governed by certain fixed, but unknown to Darwin (1859, 159), laws, e.g. he recognized environmental change as one of the possible causes of variability. The change in the environment could therefore have an effect on the reproductive organs of the individuals, which resulted in the emergence of new varieties that could be later affected by natural selection (Darwin 1859, 131-134). This information also gives an intriguing insight into how selection worked – "unless profitable variations do occur, natural selection can do nothing" (1859, 82). Thus, selection process was always ready to work, yet did not need to work always, for the reason that there needed to be some diversity that it could operate on. And this diversity is caused by the laws of variation unknown to anyone, which, for example, may be dependent on the change in the environment. The picture of evolution that Darwin draws for the reader is structured in the following manner: the species remains unchanged, then emerges a factor, e.g. environmental, which causes variability in the species, natural selection acts on these varieties, and, consequently, transforms the species (i.e. species evolve). Although Darwin assumed that species do not consist of individuals who are identical copies (1859, 45), however, unlike the co-author of his evolutionary concept, he believed that there must be some factor that would produce enough diversity, that would allow natural selection to work. A similar understanding of species development can be observed in neo-Lamarckism.

The question of what causes variability was one of the main problems posed by neo-Lamarckists, as well as their main objection to Darwin's theory. As it was emphasized, selection, as a mechanism of elimination, could not produce new features on its own, and due to that, some factor which would stimulate organisms to produce them was needed. Neo-Lamarckists continued their deliberations about variability from the point where Darwin had left them. This continuation led them to Lamarck's laws of use and disuse. According to this law, when the environment changed, the organism tried to adapt to it. But what happened when the environment did not change and there was no factor to stimulate the organism to transform? One should suppose that the neo-Lamarckists also stated that evolution would not have taken place in such a case. This stemmed from the fact that they assumed a fairly simple vision of inheritance, which was based on copying the features of the ancestors without any modification. According to this process, species were not variable, and for a varieties to exist, something had to “disturb” process of the inheritance. Even in Cope's theory, in which the changes took place under the so-called growth force controlled by the consciousness of the organisms themselves, their transformations were still dependent on whether a factor initiating the process of change emerged. According to Cope's theory of psycho-Lamarckism, organisms responded to the environmental changes with the use or disuse of their organs, which led to directing their immanent growth force in such a way that they developed the appropriate features. These changes could be regarded as volitional for the reason that organisms have always been guided by their own good (Cope 1871, 246-256; Cope 1887, 35-36). However, as was added by Cope, the consciousness that guided their actions was hereditary. It means that the parents passed onto their children a will, that appropriately directs the location of the growth forces, in a way that the descendants ultimately reproduced their form (Cope 1904, 479-480; Cope 1887, 29). In order for the offspring to be able to change the form inherited from their parents, they had to encounter some new environmental impulse, which would stimulate them to act, react and to allocate the growth forces in a new way (Cope 1887, 428). Samuel Butler, also proclaiming the volitional nature of evolutionary changes, envisioned evolution in an akin way.

According to Butler, inheritance was about transmitting memory. Memory was the carrier of the skills that the organism possessed, which allowed it to survive in a given environment, and determined its structure. In order for a change to take place, the organism had to be in a new environment that would evoke the need to adapt, and thus create new features (1878, 126-138). So once again, as similarly observed in Cope's concept, we see the assumption that in a static environment species remained unchanged and evolution did not take place. The requirement for this evolutionary "determinant" was also reflected in neo-Lamarckists' criticism of Darwin's theory. At this point it should be emphasized that the postulate of the necessity of the existence of such a "determinant" was justified only assuming the inherent invariability of the species. Due to the fact that inheritance was based on exactly copying the features from one generation to another, such species could be interpreted in a "typological" way. This assumption made Butler (1878, 226-227, 264-265) ask the question: if organisms do not change from generation to generation, why would they develop new features? Hence, it was necessary to indicate the external environmental factor which "activates" Lamarck's laws and thus causes variability. Hyatt (1884b, 149), Packard (1894, 340), Henslow (1895, 9-28) and Ryder (1895, 600-602) also pointed to the necessity of the existence of an external determinant contributing to the emergence of new characteristics.

Ernst Mayr (Mayr, Linsley, Usinger 1953, 9-11) initially pointed out that neo-Lamarckian theories assumed a populational vision of the species. In his later works, he usually ignored the populational aspect of the neo-Lamarckist theories, while in his famous *The Growth of Biological Thought*, it was limited only to mentioning that they accepted "populational speciation" (1982, 506). Therefore, one may wonder whether in neo-Lamarckism there are actually noticeable populational threads in the way of understanding species. And it seems there are. This conclusion is drawn from the fact that some neo-Lamarckists accepted natural selection as one of the mechanisms of evolution (e.g. Henslow 1895, 10-11; Henslow 1908, 14-15; Hyatt 1880, 196; Packard 1904, 421). Of course, the role of selection in neo-Lamarckian theories was not as crucial as in Darwinism and was limited (as Mayr also noted; 1982, 489-490) to the mechanism for eliminating maladjusted individuals. However, the mere fact that they relied on this mechanism meant that their vision of the species must have been populational to some extent. The existence of a mechanism to eliminate maladjusted individuals meant that neo-Lamarckists assumed the possibility that not all organisms were able to adapt to the environmental changes. Edward Dinker Cope (1871, 258-259) even wrote about the "intelligent selection," which was to derive from the fact that only those individuals who discovered a successful way of adapting in the new environment survived. When the environment changed, the species ceased to be regarded as something stable and unchanging, and began to be seen as a population filled with individuals who reacted differently to the environmental stimulants, and thus stood different chances of survival. If neo-Lamarckian theories were purely typological, one would expect that all members of a species would always react in the same way to a given environmental stimulant, and that the species as a whole would transform into a form adapted to the new environment. And so, evolution would look the same as in Lamarck's theory. However, the use of selection in neo-Lamarckism meant that success in adaptation was not guaranteed.

In neo-Lamarckian works, we can observe a clear division of the "life cycle" of species into two modes: 1) when the environment remains unchanged, then the species remains a static entity; 2) when the environment changes, then the species is a changeable entity, evolving through the laws of use and disuse. Moreover, some neo-Lamarckists clearly divided these two periods, distinguishing them as moments of the internal harmony and disharmony of organisms. Following the footsteps of Herbert Spencer, they wrote about the existence of molecules that compose a coherent system forming the organism (Ryder 1893, 195-198), about the harmony between the inherited memory of an ancestor and the environment in which a given organism functioned (Butler 1878, 221-224), or about recognizing process of adaptation as a way of harmonizing different elements of nature (Henslow 1873, 210-212). The pattern, however, always remained the same: when a species functioned in a stable environment, it was characterized by internal harmony, and when new factors began to work on it, the harmony was disturbed. Regaining harmony was associated with the transformation of the whole organism. Disharmony was therefore a sign of the beginning of evolutionary changes.

Therefore, Neo-Lamarckism and Darwin's original theory shared a similar pattern of evolutionary change, which was divided into stable periods when the species remained unchanged, and a time of change when it began to differentiate under the influence of an external factor. Evolution, in both cases, had to be triggered by a factor that stimulated species' variation. Translating this into Mayr's language, one can say that there must have been an impulse that pushed the species from the "typological" to the "populational" state.

The Concept of Species in the Orthogenesis

Orthogenesis, a trend of the nineteenth-century evolutionism, was perceived in the source literature as a concept that is difficult to characterize unambiguously. As noted by Igor Popov (2018, 202-203), most of the features traditionally attributed to the theory of orthogenesis, such as the promotion of vitalism, were not universal and appeared only in exceptional cases. Peter Bowler (1992, 141), noticing the multitude of orthogenetic views, characterized this trend as simply the most anti-Darwinian among the theories of evolution that arose during the "eclipse." However, there are some common features of orthogenetic theories (at least in the cases analysed by me), which are most distinguishable in comparison with the neo-Lamarckian theories.

In orthogenesis, similarly to neo-Lamarckism, the influence of the environment on the organism was a key evolutionary factor. The theories of orthogenesis that I've analysed also accepted the laws of use and disuse, but treated them as a secondary evolutionary mechanism. Early orthogeneticists, such as Nägeli (1914, 23) and Eimer, argued that environmental influences directly impacted species causing their evolution – so there was no need for an activity of organism to enable its transformation. Eimer (1890, 153) wrote directly about how environmental factors transform organisms without the need for use and disuse of organs: "… I Believe (…) that external influences – climate, light, warmth, moisture, and differences of food – modify organisms directly, even without the aid of selection, and that inasmuch as the modifications so caused are inherited, they will give rise and must give rise to new species." The species did not have to actively adapt to the environment – the changes took place "automatically." At this point, it is worth to emphasize that the neo-Lamarckists accepted this type of evolutionary mechanism – Cope referred to it as "physiogenesis" (1904, 227) – but limited its influence only to the plant. In the case of orthogenesis, the mechanism of physiogenesis was not only the leading evolutionary law, but also had an impact on how orthogeneticists imagined the structure of organisms. Eimer, Nägeli and Berg stated that there are specific components of the structure of organisms, thanks to which organisms had a naturally mouldable character. In Nägeli's case, this element was idioplasm, which was part of the organism's protoplasm. It acted as a carrier of the organism's characteristics and was subject to inheritance. In the course of inheritance, the transferred idioplasm modified itself, improving the characteristics it was carrying, and also generating the new ones under the influence of external factors (Nägeli 1914, 6-17). In Berg's case, the basic factor of change was the recombination of the molecules which composed the organism and which also constituted hereditary material. This recombination was a natural consequence of the inheritance process, which also resulted in the immediate structure transformation of the organisms (Berg 1969, 68-69). Similar to Nägeli's views, Berg (1969, 115-118) also argued that the changes might additionally take place under the influence of environmental factors, but still they were of a secondary nature when compared to the internal factors. In Eimer's case, the role of hereditary material was played by protoplasm which also constituted the factor responsible for the possibility of organisms' transformation: "protoplasm has the property of being altered and transformed by the action of external stimuli" (1890, 317).

In orthogenesis, the dependence of evolution on the internal factor was associated with the postulate of an immanent evolutionary force's existence. Evolution therefore took place thanks to the immanent forces, which were most often associated with either biochemical processes (Nägeli 1914, 28-29; Eimer 1898, 15; Osbron 1933, 699), or with those of a metaphysical nature (as in the case of Bergson's *elain vital*). Due to the existence of an internal evolutionary force, species developed spontaneously, improving their features and adapting to the environment. In orthogenesis, species' variability was therefore understood as their natural feature. Leo Berg (1969, 10-11) even discredited neo-Lamarckist questions about the causes of the variability, claiming that changes in the structure of organisms are their inherent property. Here we can observe a substantial difference between the Darwinian/neo-Lamarckian vision and the proposition of the orthogenesis. In the first case, evolution had to be "started," in the second one – the process was "automatic." Moreover, since the process of evolution was not dependent on the organism's reaction, but took place "automatically," being determined by the environmental factors and immanent forces, the species in orthogenesis became naturally dynamic entities, and not, as in neo-Lamarckism, were the transformations of had to be somehow "triggered," naturally static.

This difference is well depicted by Osborn's studies on the evolution of the extinct mammals from the Titanotheres family (Brontotheriidae). According to the concept he proposed (Osborn 1911, 825-826), evolution took place in four possible ways: firstly, by increasing the volume of the organism; secondly, by losing its features; thirdly, by changing the proportions in parts of the organism (he called the phenomenon allometry, and the features resulting from it – allometrons); and fourthly, by the development of new features as a result of adaptation (he called this process rectigradation). Pondering over the evolution of the Titanotheres family, he inscribed it in the seemingly neo-Lamarckian pattern – organisms developed in a "normal" manner under constant environmental conditions, and when the conditions changed, they acquired new adaptive features. For neo-Lamarckists, this change acted as an environmental stimulus needed to "trigger" evolution. However, the entire evolutionary process was not limited to the "rectigradation" process, because according to Osborn, even in an stable environment species changed under the influence of allometric mechanisms. The organisms developed regardless of the changes in the environment. Moreover, the new features, that the species acquired under the influence of an external factor, were further modified in the process of allometry (Osborn 1911, 826-827). Osborn thus believed that the natural state of species was the state of constant modification of the proportions of their organs. This vision was similar to the descriptions of the evolutionary changes of Berg, Nägeli, and Bergson. Species were to develop all the time, regardless of the influence of environmental factors, be it either through the influence of the internal force of the organisms (Bergson 1911, 81-94; Nägeli 1914, 33), or through modifications in the hereditary material (Berg 1969, 68).

All the orthogenesis theories that I have analysed had two things in common: first, they assumed the natural mouldability of an organism – which meant that species did not actively try to change (as in neo-Lamarckism), and that change happened naturally under the influence of the environment; second, they assumed the existence of an inherent "driving force" of evolution which was constantly at work. In short, orthogeneticists considered variability as a permanent feature of species rather than an outburst of activity triggered by an environment, which was the case in neo-Lamarckian theories. The assumed dynamicity of species was therefore a significant difference to the static model assumed in the previous evolutionary theories. From Bergson's perspective, it was even the basis for research into the animate nature. According to Bergson (1911, 17-30), living beings, remaining in constant motion, eluded human mind, which was accustomed to the static nature of physical entities. The most obvious example of such a mistake were attempts to inscribe evolution in the cause-and-effect relationships. In the case of living creatures, it was not possible, because, firstly, they were influenced by many causes, and secondly, there was no such thing as an effect, for the reason that they were subject to continuous, never-ending development. Bergson clearly deviates from the scheme of "environmental determinant – an organism's response," proposed in neo-Lamarckism, in favour of a more dynamic vision of the species as an entity constantly subject to evolutionary forces.

Interestingly enough, the dynamic concept of species was still in line with essentialism. Orthogeneticists have assumed that there are some inherent structural limitations that steer the evolution of species. The evolutionary path of species was limited by their anatomical structure – orthogeneticists saw the process of evolution as linear due to the reason that species could only change form in a limited number of ways. The evolution of organisms has been compared by Eimer (1890, 23) to that of a crystal. Organisms, similar to crystals, develop certain shapes that limit the directions of further modifications. Nägeli (1914, 3), Osborn (1921, 157-159) and Berg (1969, 382-384) also adopted a similar vision of self-determination. This idea led Mayr to the conclusion that orthogeneticists were adopting an essentialist concept of species. He wrote that, since species evolved according to an evolutionary trend determined by their structure, their transformation resembled an actualization of the potentiality in classical metaphysics (Mayr 1982, 352). Indeed, among orthogeneticists, there were direct references to hylomorphism, e.g. Berg (1969, 153) and Osborn (1934, 228-230) did not hide that they were inspired by the philosophy of Aristotle. However, the question is whether this essentialism completely excluded populationism? Or maybe the essentialist interpretation of the species was also accompanied by elements of populational thinking, as was the case in neo-Lamarckism?

Reading the works of orthogeneticists, it can be seen that they were aware of the variability of species resulting from either the different ways in which organisms respond to the same environmental factors (Berg 1969, 369-397; Eimer 1890, 382), or the modification of hereditary material (Nägeli 1914, 16-17), or the unpredictable effects of allometry (Osborn 1934, 702). Eimer (1890, 380-384) explicitly noticed that the constraints of the structure of organisms mean that they can react in different ways to the same environmental factor. A similar dependence was also noticed by Berg (1969, 103) and Nägeli (1914, 34-35), who stated that the constitution of organisms, apart from limiting the possibility of their transformation, additionally makes them react differently to the influence of the environment – hence, the new species could develop through geographic speciation. The supporters of orthogenesis accepted the existence of diversity within a species, which led them to the conclusion that new species can develop through speciation. In this sense, it can be concluded that in orthogenesis, populationalist threads of interpretation of the species are noticeable.

What is seen in both neo-Lamarckism and orthogenesis is the tension between the idea of evolution and essentialism. In neo-Lamarckism, it was resolved by recognizing species as naturally stable entities that changed only as a result of an organism's active response to external stimuli. Contrary to this perspective, in orthogenesis, the evolution was portrayed as a constant phenomenon that required no special "trigger", and species were perceived as naturally variable entities. In addition, orthogeneticists assumed that not only species, but also entire phyletic lines, have essences that limit their further evolution. In both concepts, we can observe an interpretation of species presented in the spirit of essentialism, but it was integrated with them dissimilarly.

Where Do the Differences in the Understanding of Species Come From?

As mentioned earlier, the understanding of the concept of species should change depending on context in which it was applied. Larry Laudan (1984) explained that the ontological differences postulated in various theories are caused by influence of such factors as methodology accepted by certain scientist or their research goals. Thus, the methodology correlates with the assumptions of the scientists regarding the world they are studying (i.e. ontology), and in turn this vision of the world influences the goals and methods that scientists adopt in their research. This conclusion, even if it may seem too obvious, may be helpful in analysing the differences in species concepts that existed between Darwinism, neo-Lamarckism, and orthogenesis. If they had different concepts of the species, we should also expect different goals, i.e. different problems that their followers wanted to solve through the research.

In Darwin's case, his research goal was clearly defined. As he wrote: "These facts (i.e. data collected during the journey on Beagle – comment by MW) seemed to me to throw some light on the origin of species – that mystery of mysteries, as it has been called by one of our greatest philosophers" (Darwin 1859, 1). However, the question remains: what did Darwin exactly mean by the origin of species? Did he mean the origin of all species that appeared in the history of the Earth? Or maybe he wanted to explain the reasons for the emergence of modern species? The first option would require Darwin to address the issue of the origins of life. This problem was considered by Darwin to be too complicated (Darwin 2009, 335), hence in *Origin of Species* he referred to it in a metaphorical way, writing about life as something that was "breathed" (1859, 484) into the first organisms. Unlike other evolutionists of that period (Bowler 1996, 79-81), Darwin was not interested in the reconstruction of species phylogeny. The question of the evolutionary past of the species was of course important to him, but only as a means of clarifying issues related to the present state of nature. Ultimately, his interest focused on the geographic distribution of species, improving their taxonomic classification, and explaining the existence of higher taxa (Darwin 1859, 484-487). For Darwin, the basic problem with the reconstruction of the phyletic lines was the incompleteness of the fossil record, which would not allow him to undertake such a task (Darwin 1859, 301-302). But even if the records were complete, the chances of reconstruction would still be minimal – as can be seen in the example of the origin of farm animals. In *On the Origin of Species* he writes: "But, in fact, a breed, like a dialect of a language, can hardly be said to have had a definitive origin. A man preserves and breeds from an individual with some slight deviation of structure, or takes more care than usual in matching his best animals and thus improves them, and the improved individuals slowly spread in the immediate neighbourhood. But as yet they will hardly have a distinct name, and from being only slightly valued, their history will be disregarded. When further improved by the same slow and gradual process, they will spread more widely, and will get recognized as something distinct and valuable, and will then probably first receive a provincial name" (1859, 40).

According to Darwin, the reconstruction of the evolutionary history of species was dependent on the time perspective, and due to the gradual nature of evolution, we are unable to observe it in action. The changes can only be seen by comparing the current and past condition of the species (Darwin 1859, 263). While Darwin was not particularly interested in reconstructing the evolutionary history of living organisms, he believed that genealogy played an important role in biological research. It made it possible to formulate falsifiable hypotheses about the development of species based on the data available in the geological record. Darwin's research was often based on recreating the hypothetical past of a species, which is well depicted in his research into the domestic pigeon breeds. In this case, his deliberations lead to the thesis that all species of pigeons are descended from one common ancestor. According to him, this conclusion had an advantage over the creationist position because of its simplicity, and thus greater probability (Darwin 1859, 25-26). Darwin was interested in the evolutionary past of species only insofar as it allowed to explain the present order of nature. As Richard Delisle (2019, 26) put it, we can find in the *On the origin of species*: "… Darwin's profound commitment to a 'horizontal' approach to evolution: to travel in geographical space (today) is to travel in geological time (past)." In his view, the phenomenon of evolution is part of the species' past, constituting in a way the *conditio sine qua non* of their present existence. The problem was that the key question in his theory – what was the reason for the intraspecific variation on the basis of which the selection created modern species? – was left unanswered.

Goals similar to those of Darwin were also assumed by the neo-Lamarckists who were analysed for the purpose of this article. The work of neo-Lamarckists was as much based on creating hypotheses and confronting them with empirical data, as on the deductive-hypothetical method used by Darwin in his research. As observed by Bowler (1988, 146), the research of the nineteenth-century evolutionists consisted mainly of creating hypothetical evolutionary scenarios that were to explain how a given species emerged and how its adaptive features developed. And indeed, when reading the works of neo-Lamarckists, it can be noticed that they focused their attention mainly on recognizing what force could have influenced the organism to produce a given feature as a consequence. Hence, when describing the formation of the turtle shell, Ryder (1878a, 159-160) points to the attacks by predators that forced turtles to produce this characterisitc; and when Henslow (1895, 231-233) deals with the differences in the stem lengths of plants – he will make them dependent on the availability of the sun. Even if it was acknowledged that the feature under study was not created as a result of the environmental influences, but rather thanks to the immanent forces of the organism, neo-Lamarckists were still able to identify a specific cause responsible for it – as, for example, Cope (1904, 275-282) did, linking the changes in the vertebrate skeletal system with the increased movement of specific muscles. In neo-Lamarckism, a species was analysed in terms of how its specific organs developed, and for this aim, an attempt was made to come up with a hypothetical evolutionary scenario that would explain their development. The teleologism of the evolutionary process introduced in neo-Lamarckian theories confirmed the validity of this type of research – it showed that the organism was able to react to a change in the environment by developing an appropriate feature. Thanks to this assumption, deliberations on evolution could be presented as cause-effect sequences in which an environmental stimulant provoked a reaction of the organism and which could be reconstructed during the research. This action-reaction model, through the prism of which the neo-Lamarckists imagined the operation of nature, was well expressed by Henslow, who was defending his methodology in the following way: "When one discovers scores of plants of no affinity putting on precisely the same structures under identically the same conditions of life, we are justified in recognizing a cause and effect" (1908, 20).

This way of outlining the research goals coincides with the vision of the species of Darwinism and neo-Lamarckism. If evolution must be "triggered," the naturalist's goal is to stipulate what the exact "trigger" was. However, Darwin, not knowing the causes of the variability, was unable to identify the immediate cause of the origin of species. His concept did not show a clear reason for the emergence of a particular species, due to the fact that the theory of natural selection, probabilistic in its nature, did not allow for an accurate reconstruction of the evolutionary path of the species. And here come the neo-Lamarckists who were able to pinpoint the exact reason why certain features evolved – they focused on specifying the stimulus that "triggered" the evolution. Thus in the 19th century, neo-Lamarckism could be seen as an improvement of Darwinism.

In the case of orthogenesis, we have another shift in research interests related with the vision of the species. Orthogeneticists clearly departed from the method of research which was based on identifying the possible causes that led to the development of a given characteristic. In the writings of the representatives of this trend, we can find multiple explanations why such research is to be considered unsustainable. Firstly, because of the belief that the environment affected the organism as a whole, so there was no single specific cause responsible for developing adaptation (Osbron 1934, 207; Berg 1969, 264-265); secondly, it was difficult to distinguish which features developed as a result of adaptation and which developed naturally by the action of immanent evolutionary forces and did not have adaptive value (Eimer 1898, 24). For example, Osborn, when analysing the development of mammalian teeth, noticed that not all changes could be explained only by the process of use and disuse. Finally, pointing to allometry and aristogenesis as the main evolutionary processes, he gave up considering what the specific cause of these changes were: “What evokes an aristogene from the gene plasm is as mysterious to Us as what evokes a horn rudiment in the skull of the titanothere. We remain (…) purely on observational and inductive grounds and simply make statements of fact or of principle without offering any explanation” (Osborn 1934, 227).

For orthogeneticists, pointing to specific reasons for the formation of given features became something beyond scientific possibilities. Such a change of research goals was closely related to the ontology promoted in orthogenesis. The assumption that evolution is a natural phenomenon which does not have to be triggered decreased the importance of the question regarding evolution's causes. This was also explicitly expressed by Berg (1969, 10-11). Orthogenesis began to focus on recognizing certain constant evolutionary laws that would be helpful in predicting what the evolutionary future of the species would look like. As a result, prognostic laws were created, such as Eimer's universal law of transmutation and Berg's phylogenetic acceleration. The first one indicated that the changes in pigmentation will always run from single-coloured longitudinal stripes or spots to a uniform colouring (Eimer 1898, 26). The second stated that the features appearing in young animals and disappearing in adults are a harbinger of the future evolutionary changes (Berg 1969, 73-80). This attitude toward finding permanent evolutionary laws will be further emphasized by Osborn and Berg, who in turn will link their search for the laws of evolution with the legacy of Aristotle's philosophy. As both argued (Osborn 1905, 37-57; Berg 1969, 153, 405), evolutionary biology should be constructed on the basis of certain fixed laws of science, thereby departing from the chaotic picture of nature proposed by Darwin. One of the later supporters of orthogenesis, Otto Whitman (1919, 10-13), stated that orthogenesis was a response to biological theories proclaiming the unpredictability of evolutionary mechanisms, and by the same token, introducing the vision of fixed, predictable laws of nature abandoned with Lamarck's teleologism.

Orthogeneticists, observing species as naturally evolving beings, stopped looking for the causes of their variability, and tried to recognize the laws which determined their evolution. One can notice in orthogenesis the beginnings of treating evolution as a permanent element of the natural world, which did not have to be triggered by any external factor. Orthogenesis could therefore be considered a refinement of both neo-Lamarckism and Darwinism, as it deviated from the static view of the species, promoting its more dynamic vision, which was more in line with the idea of evolution as a natural phenomenon occurring in nature. For Darwin, evolution was merely a process by which he could retroactively explain the existence of modern biodiversity; then for orthogeneticists, evolution became a continuous process in which species, understood as naturally mouldable entities, were constantly transformed by the laws of nature.

Summary

In this article, I have tried to show that the dichotomy of essentialism/typologism and populationism oversimplifies the concepts of species that have been proposed in neo-Lamarckism and orthogenesis. In these evolutionary theories, both typological and populationist themes can be spotted. The thesis that non-Darwinian theories were bases on only one premise – as Mayr contended in the context of essentialism – was wrong. Moreover, in the article, I tried to show that non-Darwinian theories developed original concepts of species – if in Darwinism and neo-Lamarckism, a species was static and evolution had to be triggered by external factors, then in orthogenesis, the understanding of species was more dynamic and was understood as naturally mouldable and evolving. This change was related to the change of research interests. Darwin's original work was focused on explaining the genesis of the existing species. The evolutionary past of species was treated by the creator of natural selection theory as a hypothetical reason for the existence of the present order of nature. However, Darwin, not knowing the reasons for the occurrence of variability, was unable to provide the specific reasons for the emergence of the given characteristics. As observed by Mayr (1982, 412-413), Darwin did not give the reasons for the speciation – even dismissing Mortiz Wagner's geographic speciation as inconsistent with his own theory (Mayr 1982, 565). In neo-Lamarckism, attempts were made to recognize the causes of the formation of species by referring to the laws of Lamarck. Considering that neo-Lamarckists assumed the same "life cycle" of a species as Darwin – they saw in species static entities whose evolution had to be "triggered" by something – it can be concluded that they presented a more accurate evolutionary theory (as for the conditions of the 19th century natural science), as they indicated the cause of variability, i.e. the factor "causing" the evolution of species. Orthogenesis, by promoting the concept of species as a naturally evolving entity and eliminating the "trigger" for change, made a natural step forward in evolutionary biology. Naturalists were able to move away from considering what "triggers" evolution, and began to wonder which laws govern its course.

Due to the limited scope of research, the considerations presented in the article do not constitute an exhaustive analysis of the concept of a species in neo-Lamarckism and the theories of orthogenesis. However, they can make a meaningful contribution to the in-depth research of this kind. Especially that in the present historiography we can observe a shift from the pejorative interpretation of the so-called "the eclipse of Darwinism," popularized by Ernst Mayr (e.g. Largent, 2009;

Delisle, 2017; Ochoa, 2017). The species problem in non-Darwinian theories was far more complex than the existing populationalist/typologist narrative would suggest.

References:

Amundson, Ron. 1998. "Typology Reconsidered: Two Doctrines on the History of Evolutionary Biology." *Biology and Philosophy* (13): 153–177. https://doi.org/10.1023/A:1006599002775.

Bateson, William. 1913. *Problems of genetics*. London, New Haven: Oxford University Press, Yale University Press.

Berg, Leo S. 1969. *Nomogenesis or Evolution determined by Law*. Translated by J .N. Rostovtsov. Cambridge: MIT Press.

Bergson, Henri. 1911. *Creative evolution*. London: Macmillan and co.

Bowler, Peter J. 1988. *The non-Darwinian revolution. Reinterpreting a historical myth*. Baltimore, London: The Johns Hopkins University Press.

Bowler, Peter J. 1992. *The eclipse of Darwinism. Anti-Darwinian evolution theories in the decades around 1900*. Baltimore, London: The John Hopkins University Press.

Bowler, Peter J. 1996. *Life's splendid drama. Evolutionary biology and the reconstruction of life's ancestry 1860-1940*. Chicago, London: The University of Chicago Press.

Butler, Samuel. 1878. *Life and habit*. London: Trubner.

Chung, Carl. 2003. "On the origin of the typological/population distinction in Ernst Mayr's changing views of species, 1942–1959." *Studies in History and Philosophy of Science Part C: Studies in History and Philosophy of Biological and Biomedical Sciences* (34): 277–296. https://doi.org/10.1016/S1369-8486(03)00026-8.

Cope, Edward D. 1887. *The origin of the fittest. Essays on evolution*. New York: D. Appleton and Company.

Cope, Edward D. 1904. *The primary factors of organic evolution*. London: Open Court.

Cope, Edward D. 1871. "The Method of Creation of Organic Forms." *Proceedings of the American Philosophical Society* 12(86): 229-263.

Darwin Correspondence Project, "Letter no. 2896," accessed on 16 November 2021, https://www.darwinproject.ac.uk/letter/?docId=letters/DCP-LETT-2896.xml

Darwin, Charles R. 1859. *On the Origin of Species by Means of Natural Selection, or the Preservation of Favored Races in the Struggle for Life*. London: John Murray.

Darwin, Charles R. 1872. *The origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. London: John Murray.

Darwin, Charles R. 2009. "The doctrine of heterogeny and modification of species." In *Charles Darwin's Shorter Publications 1829-1883*, edited by John Van Wyhe, 334-336. Cambridge: Cambridge University Press.

De Quieroz, Kevin. 1997. "The Linnaean hierarchy and the evolutionization of taxonomy, with emphasis on the problem of nomenclature." *The Rancho Santa Ana Botanica Garden* 15(2): 125-144. DOI: 10.5642/aliso.19961502.07

Delisle, Richard G. 2017. "From Charles Darwin to the Evolutionary Synthesis: Weak and Diffused Connections Only." In *The Darwinian Tradition in Context*, edited by Richard G. Delisle, 133-167. Cham: Springer. https://doi.org/10.1007/978-3-319-69123-7_7.

Delisle, Richard G. 2019. *Charles Darwin's Incomplete Revolution. The Origin of Species and the Static Worldview*. Cham: Springer.

Eimer, Theodore. 1890. *Organic evolution as the result of the inheritance of acquired characters according to the laws of organic growth*. Translated by T. J. Cunningham. London, New York: Macmillan.

Eimer, Theodore. 1898. *On orthogenesis and the impotence of natural selection in Species-formation*. Translated by T. J. McCormack. Chicago: Open Court.

Esposito, Maurizio. 2021. "Cathedrals, Corals and Mycelia: Three Analogies for the History of Evolutionary Biology." In *Natural Selection. Revisiting its Explanatory Role in Evolutionary Biology*, edited by Richard G. Delisle, 11-35. Cham: Springer,. https://doi.org/10.1007/978-3-030-65536-5_2.

Feyerabend, Paul K. 1981. "Explanation, reduction and empiricism." In *Realism, rationalism, and scientific method. Philosophical papers. Vol.1*, 44-96. Cambridge: Cambridge University Press.

Gayon, Jean. 1998. *Darwinism's Struggle for Survival. Heredity and the Hypothesis of Natural Selection*. Translated by Matthew Cobb. Cambirdge: Cambridge University Press.

Henslow, George. 1873. *The theory of evolution of living things and the application of the principles of evolution to religion*. London: Macmillan.

Henslow, George. 1895. *The origin of plant structure by self-adaptation to the environment*. London: Kegan Paul.

Henslow, George. 1908. *The heredity of acquired characters in plants*. London: John Murray.

Hooker, Joseph D. 1859. *On The Flora Of Australia. Its Origin, Affinities, And Distribution Being An Introductory Essay To The Flora Of Tasmania*. London: Lovell Reeve.

Huxley, Julian. 1945. *Evolution. The modern synthesis*. London: George Allen and Unwin.

Hyatt, Alpheus. 1880 "Transformation of Planorbis. A practical illustration of the evolution of species." *Science* 11(1):196.

Hyatt, Alpheus. 1884. "The evolution of the cephalopoda – II." *Science* 53(3): 145-149.

Largent, Mark A. 2009. "The So-Called Eclipse of Darwinism." In *Descended from Darwin Insights into the History of Evolutionary Studies, 1900-1970*, edited by Joe Cain and Michael Ruse, 3-21. Philadelphia: American Philosophical Society.

Laudan, Larry. 1984. *Science and values. The aims of science and theory role in scientific debate*. Berkeley, Los Angeles, London: University of California Press.

Levit, Georgy S., Meister Kay. 2006. "The history of essentialism vs. Ernst Mayr's 'Essentialism Story:' A case study of German idealistic morphology." *Theory in Biosciences* (124): 281-307. DOI: 10.1016/j.thbio.2005.11.003.

Lewens, Tim. 2009. "What Is Wrong with Typological Thinking?" *Philosophy of Science* 76 (3): 355-371. https://doi.org/10.1086/649810.

Mayr, Ernst. 1971. *Populations, species, and evolution; an abridgment of Animal species and evolution*. Cambridge, Massachusetts: Belknap Press of Harvard University Press.

Mayr, Ernst. 1982. *The growth of biological thought. Diversity, Evolution, and Inheritance*. Cambridge, London: The Belknap Press of Harvard University Press.

Mayr, Ernst. 1991. *One long argument. Charles Darwin and the Genesis of Modern Evolutionary Thought*. Cambridge, Massachusetts: Harvard University Press.

Mayr, Ernst, Linsley, Earle G., Usinger, Robert L. 1953. *Methods and Principles of Systematic Zoology*. New York, Toronto, London: McGraw-Hill Book Company, Inc.

Mayr, Ernst. "Darwin and the evolutionary theory." In *Evolution and Anthropology: A centennial appraisal*, edited by Betty J. Meggers, 1-10. Washington: The Anthropological Society of Washington, 1959.

Mayr, Ernst. 1990. "The myth of the non-Darwinian revolution." *Biology and Philosophy* 5 (1): 85-92.

Morgan, Thomas H. 1908. *Evolution and Adaptation*. New York: Macmillan.

Nägeli, Carl. 1914. *A mechanical–physiological theory of organic evolution*. Translated by V. A. Clark. Chicago: Open Court.

Ochoa, Carlos. 2017. *El eclipse del antidarwinismo: La historia detrás de la síntesis moderna*. Toledano: Centro de Estudios Filosóficos, Políticos y Sociales Vicente Lombardo Toledano.

Osborn, Henry F. 1905. *From Greeks to Darwin. An Outline of the development of the evolution idea*. New York: Macmillan.

Osborn, Henry F. 1921. *The Origin and Evolution of Life. On the theory of action reaction and interaction of energy*. New York: Charles Scribner's Sons.

Osborn, Henry F. 1911. "Biological conclusions drawn from the study of the titanotheres." *Science* 856 (32): 825-828.

Osborn, Henry F. 1933. "Aristogenesis, the observed order of biomechanical evolution." *Paleontology* 19 (7): 699-703.

Osborn, Henry F. 1934. "Aristogenesis, the Creative Principle in the Origin of Species." *The American Naturalist* 68 (716): 193-235.

Packard, Alpheus S. 1894. "On the inheritance of acquired characters in animals with complete metamorphosis." *Proceedings of the American Academy* (29): 331-370.

Packard, Alpheus S. 1904. "Origin of the markings of organisms (poecilogenesis) due to the physical rather than biological environment; with criticisms of the Bates-Muller hypothesis." *Proceedings of the American Philosophical Society* 43 (178): 393-450.

Popov, Igor. 2018. *Orthogenesis versus Darwinism*. Cham: Springer.

Ryder, John A. 1878. "On like mechanical (structural) conditions as producing like morphological effects." *The American Naturalist* 12 (3): 157-160.

Ryder, John A. 1893. "Energy as a Factor in Organic Evolution." *Proceedings of the American Philosophical Society* 31 (141): 192-203.

Ryder, John A. 1895. "A dynamical hypothesis of inheritance." *Science* 22 (1): 597-605.

Wallace, Alfred R. 1900. *Studies scientific & social. In two volumes. Vol. I.* London: Macmillan & CO., Limited.

Whitman, Charles O. 1919. *Orthogenetic evolution in pigeons. Vol.1.* Washington: The Carnegie Institution of Washington.

Winsor, Mary P. 2013. "Darwin and Taxonomy." In *The Cambridge Encyclopaedia of Darwin and Evolutionary Thought*, edited by Michael Ruse, 72-79. New York: Cambridge University Press.

Winsor, Mary P. 2006. "The Creation of the Essentialism Story: An Exercise in Metahistory." *History and Philosophy of the Life Sciences* 28 (2): 149-174.

Witteveen, Joeri. 2018. "Typological thinking: Then and now." *JEZ-B: Molecular and Developmental Evolution*: 1–9. Doi: 10.1002/jez.b.22796.