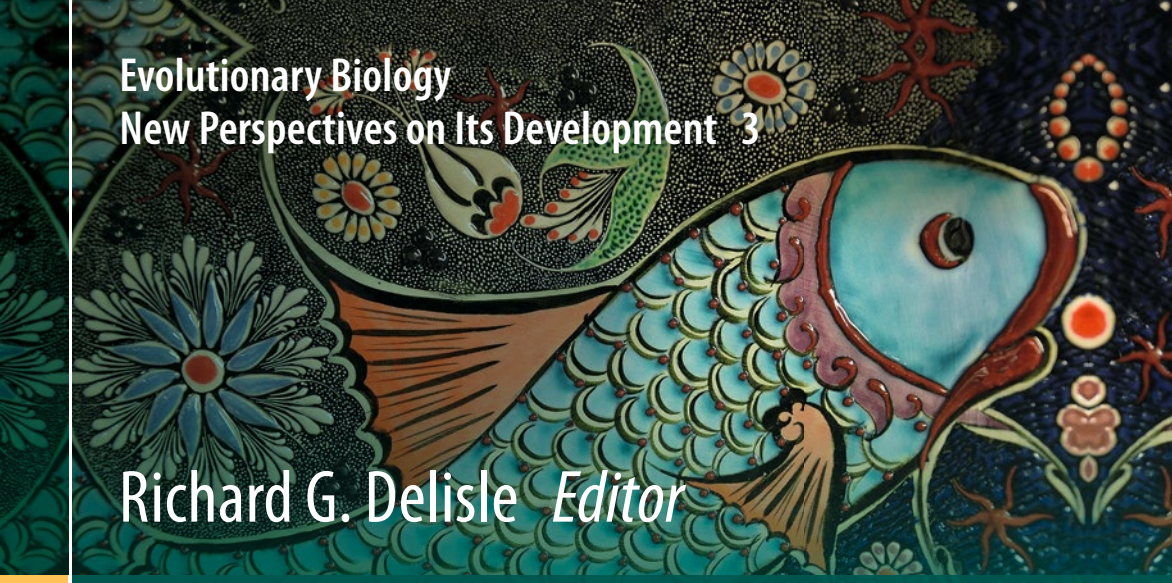

Evolutionary Biology
New Perspectives on Its Development 3

Richard G. Delisle *Editor*

Natural Selection

Revisiting its Explanatory Role in Evolutionary Biology

Springer

Chapter 5
Natural Selection in Ernst Haeckel's Legacy

Georgy S. Levit and Uwe Hossfeld

Abstract The "German Darwin" Ernst Haeckel was very influential not only in Germany but in non-German-speaking countries as well. He was a key figure during the "first Darwinian revolution," a period when the foundation for the modern evolutionary theory was laid. Haeckel defended and developed the Darwinian theory with unparalleled passion and energy. He created a conceptual framework within which the majority of Darwinians worldwide worked over decades. Contemporary evolutionary theory is unthinkable without notions coined by Haeckel such as "phylogeny," "ontogeny," "phylogenetic tree," or "ecology." Moreover, his theories were encouraged and admired by Darwin himself. It was Haeckel who crucially contributed to the visualization of the Darwinian theory and who tried to convert Darwinism into a universal worldview. Yet it remains controversial to what extent Haeckel's view of evolutionary mechanisms corresponded to those in Darwin's own theory. In this chapter, we will examine this issue and demonstrate that although Haeckel championed natural selection throughout his whole career, his neo-Lamarckian concept of variation made his grasp of natural selection different from that of Darwin. As paradoxical as it may sound from the modern viewpoint, Haeckel made these neo-Lamarckian adjustments in order to render the Darwinian theoretical system more straightforward.

Keywords Ernst Haeckel · Darwinian theory · Natural selection · Lamarckism · Evolutionary mechanisms

5.1 Introduction

Ernst Haeckel is, without doubt, a crucial figure in the growth of Darwinian thought in the nineteenth century (Hossfeld et al. 2019; Levit and Hossfeld 2017, 2019). As Robert Richards has emphasized, "More people at the turn of the century learned of

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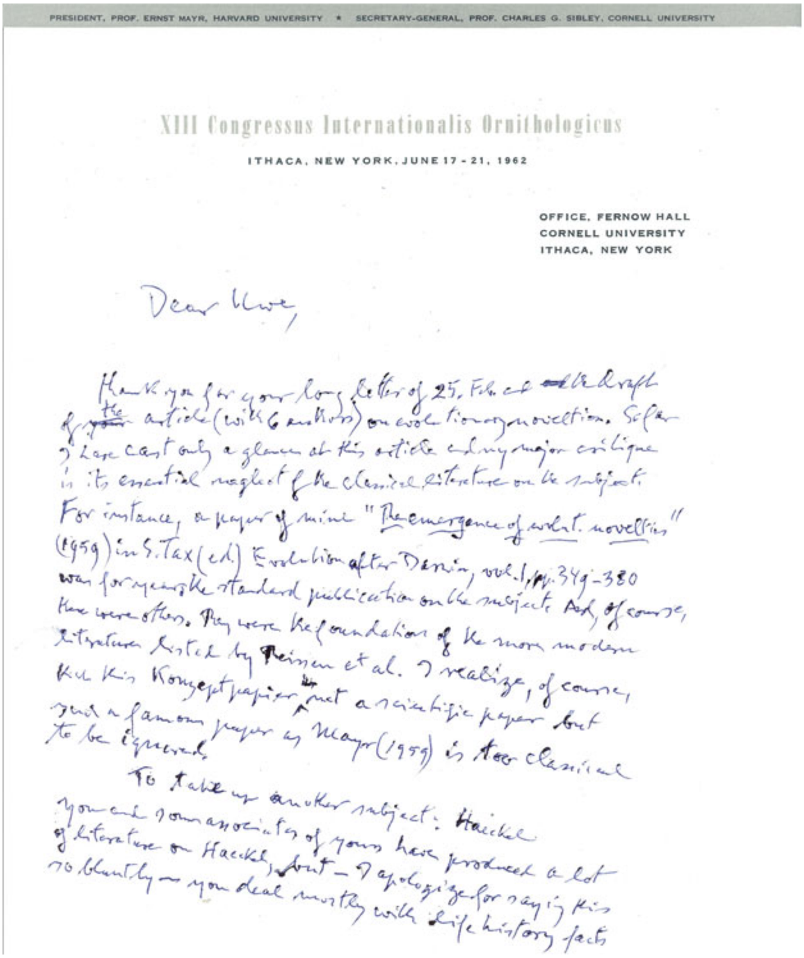
Fig. 5.1 Ernst Haeckel (portrait) from "Challenger Report" (1884, Courtesy: Günther-Berlin)

evolutionary theory from his pen than from any other source, including Darwin's own writings" (Richards 2018). Considering Haeckel's significance and level of influence, the question whether his version of Darwinism differed from that of the British genius himself is of key importance (Fig. 5.1). There is a widespread tendency among contemporary historians of biology to regard Haeckel as Darwin's supporter in terms of general evolutionism but to deprive him the priority of being one of the earliest champions of natural selection. Richards has made a clear statement on the role of natural selection in Haeckel's theoretical system: "His *Generelle Morphologie der Organismen* (1866) sought to explain those relationships through the devices that Darwin had advanced: namely, natural selection and the inheritance of acquired characteristics. Depending on the traits and the situation of the organism, one of these devices might be emphasized more than the other. Through the course of Haeckel's career, he tilted to the Lamarckian notion, but kept natural selection at the ready" (Richards 2018). Ernst Mayr has argued along similar lines, stating that Haeckel accepted natural selection only "in part" (Mayr 1991, p. 37). At the same time, Mayr was convinced that the place of natural selection in Haeckel's thought was under-researched. In a letter to one of us (UH), Mayr emphasized the necessity of estimating the exact role of natural selection and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XIII Congressus Internationalis Ornithologicus

ITHACA, NEW YORK, JUNE 17 - 21, 1962

OFFICE, FERNOW HALL
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ITHACA, NEW YORK

Dear Uwe,

Thank you for your long letter of 25. Feb. and the draft of the article (with 6 authors) on evolutionary novelties. So far I have cast only a glance at this article and my major critique is its essential neglect of the classical literature on the subject. For instance, a paper of mine "The emergence of evol. novelties" (1959) in S. Tax (ed.) Evolution after Darwin, vol. 1, pp. 349–380 was for years the standard publication on the subject. And, of course, there were others. They were the foundation of the more modern literature listed by Reinsen et al. I realize, of course, that this Konzeptpapier is not a scientific paper but such a famous paper as Mayr (1959) is too classical to be ignored.

To take up another subject: Haeckel. You and some associates of yours have produced a lot of literature on Haeckel, but – I apologize for saying this so bluntly – you deal mostly with life history facts

Fig. 5.2 Ernst Mayr's letter, Bedford, Massachusetts, 5 March 2004

alternative evolutionary mechanisms in Haeckel's works, especially in his early publications: "What we now need is a careful analysis of all of Haeckel's statements on natural selection. Did he accept it without reservations? Did he suggest that natural selection was not sufficient to explain all evolutionary phenomena? [. . .] Was selection for Haeckel a selection of the best or an elimination of the worst? Did Haeckel appreciate the importance of sexual selection?"[1] (Fig. 5.2).

Mario di Gregorio has investigated these issues extensively and formulated original views on Haeckel's understanding and use of natural selection. Haeckel, he claimed, hardly applied natural selection to individuals, but rather to groups,

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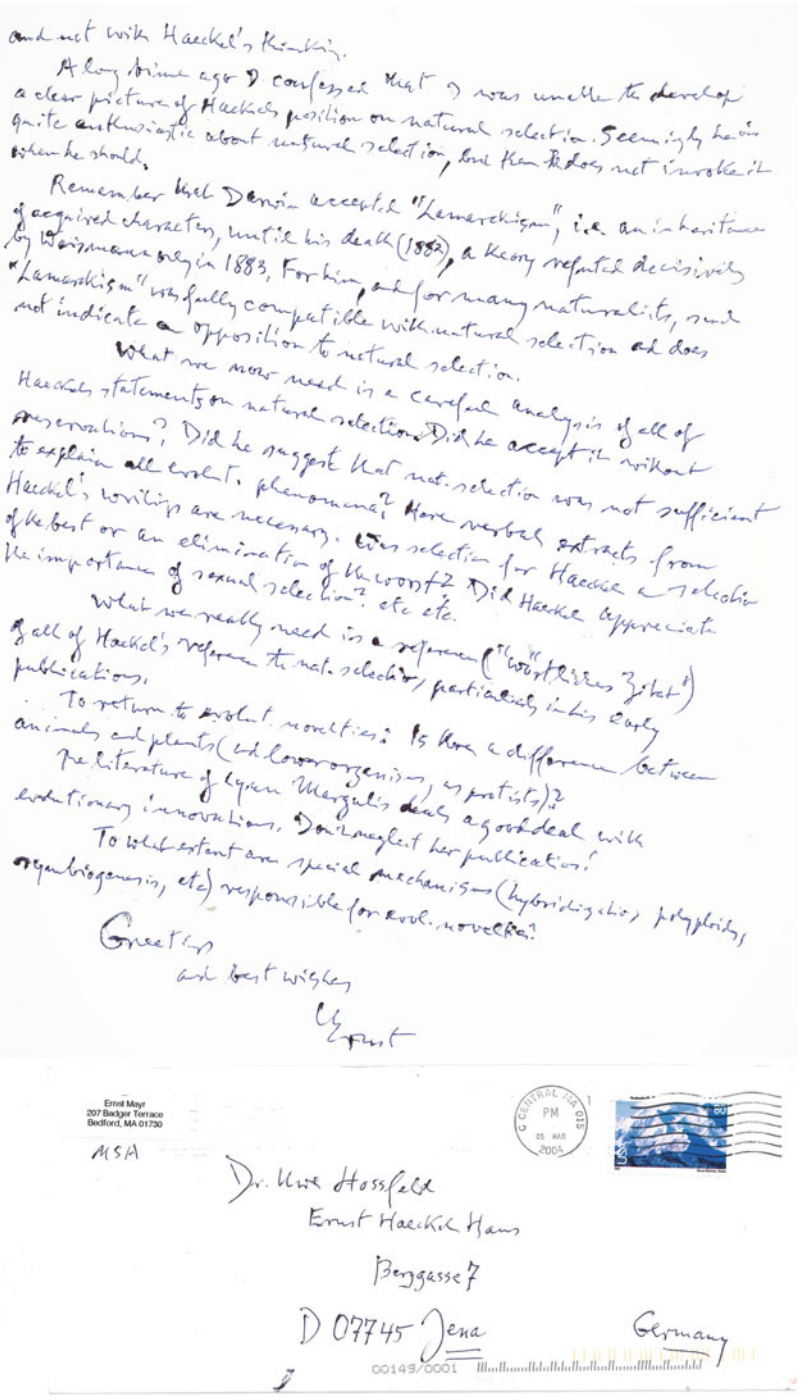
[1]E. Mayr to U. Hossfeld, Bedford, MA, 5 March 2004.



and not with Haeckel's thinking.

Along time ago D. confessed that I was unable to develop a clear picture of Haeckel's position on natural selection. Seemingly he is quite enthusiastic about natural selection, but then he does not invoke it when he should.

Remember that Darwin accepted "Lamarckism", i.e. an inheritance of acquired characters, until his death (1882), a theory refuted decisively by Weismann only in 1883. For him and for many naturalists, and "Lamarckism" was fully compatible with natural selection and does not indicate a opposition to natural selection.

What we more need is a careful analysis of all of Haeckels statements on natural selection. Did he accept it without reservations? Did he suggest that nat. selection was not sufficient to explain all evolut. phenomena? Were verbal extracts from Haeckel's writings are necessary. Was selection for Haeckel a selection of the best or an elimination of the worst? Did Haeckel appreciate the importance of sexual selection? etc etc.

What we really need is a reference ("Wortlaut") of all of Haeckel's reference to nat. selection, particularly in his early publications.

To return to evolut. novelties: Is there a difference between animals and plants (and lower organisms, protists)? The literature of Lynn Margulis deals a good deal with evolutionary innovations. Don't neglect her publications!

To what extent are special mechanisms (hybridization, polyploidy, symbiogenesis, etc) responsible for evol. novelties?

Greetings
and best wishes
Ernst

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Fig. 5.2 (continued)

"because groups were better suited to his concept of morphological levels of individuality" (Di Gregorio 2008). All these views are at odds with Darwin's own estimation of Haeckel. In as early as 1864, after receiving Haeckel's copy of *Neue Stettiner Zeitung* (20 September 1863) with a report on Haeckel's "Speech of Stettin" and Haeckel's paper on marine zooplankton (Haeckel 1864), Darwin wrote: "I am delighted that so distinguished a naturalist should confirm & expound my views; and I can clearly see that you are one of the few who clearly understands Natural Selection."[2] Darwin was delighted not only by Haeckel's grasp of natural selection; right in the introduction to the first edition of *The Descent of Man*, Darwin claimed that Haeckel was the only major evolutionist who immediately realized the significance of sexual selection: "Prof. Häckel is the sole author who, since the publication of the 'Origin,' has discussed, in his various works, in a very able manner, the subject of sexual selection, and has seen its full importance" (Darwin 1871, p. 5). In the 1882 edition of the book, Darwin repeated this passage even in a little bit extended form (Darwin 1882, p. 3). Certainly, as noted by Richards elsewhere, some historians of science would argue that if Darwin's German were better, "he would have detected deviant tendencies in the work of his new disciple" (Richards 2004). But Darwin was not as quick and superficial in his judgments as one might suppose. His letters suggest that when having difficulties with German (as he did, for example, in the work of Fritz Müller) he employed assistants to help him acquire an accurate grasp of German-language concepts.[3]

The major objective of this chapter is to evaluate Richards's thesis (Richards 2018) which can be broken down to two statements: (1) In the *Generelle Morphologie*, Haeckel advocated both natural selection and the inheritance of acquired characters; (2) over the course of his career, Haeckel became more and more neo-Lamarckian, tending to downplay the role of natural selection as an actual explanatory pattern, although he did not abandon it completely. We will proceed as follows. First, we will explicate Darwin's own views on evolutionary mechanisms as Darwin was Haeckel's major inspiration and Haeckel's initial objective was to substantiate Darwin's insights by doing extensive empirical research. Second, we ask whether Haeckel gives fair due to all evolutionary mechanisms suggested by Darwin, as Darwin never understood natural selection to be the sole mechanism of evolutionary advancement. Third, we will demonstrate the role of natural selection in Haeckel's works along with auxiliary evolutionary mechanisms beginning with *Generelle Morphologie (GM)* and ending with his final publications. We will try to concentrate on Haeckel's purely scientific, technical (as opposed to popular) works as they remained untranslated and are little known to English-speaking audiences.

Our evidence suggests that Haeckel tried to exactly follow Darwin and to make his doctrine more straightforward. Haeckel introduced into his works all the major

[2]Darwin to Ernst Haeckel, 9 March 1864. https://www.darwinproject.ac.uk/letter/DCP-LETT-4422.xml.

[3]Darwin to Haeckel, 21 November 1864. https://www.darwinproject.ac.uk/letter/?docId=letters/DCP-LETT-4676.xml.

evolutionary mechanisms Darwin mentioned, i.e., use/disuse, direct impact of the environment, macromutations, and natural selection. As our qualitative and quantitative studies demonstrate, natural selection never disappeared from Haeckel's vocabulary, yet his understanding of it differed crucially from that of Darwin, with the core issue being Haeckel's interpretation of variation. If Darwin's variation was predominantly random (isotropic), Haeckel's variation was predominantly definitely directed, i.e., immediately adaptive. Therefore, Haeckel embedded neo-Lamarckian inheritance, by which we mean the inheritance of acquired characters, right into his theory of natural selection.[4] Haeckel's successor in Jena (and prominent "old-school-Darwinian"), Ludwig Plate, saw no problem in this approach: "Definitely directed variation and selection are not mutually exclusive, but can work together. It does not matter to selection, if a certain change is in the same direction as the one before or not, if the change continues in the same direction or not" (Plate 1913, p. 510; Levit and Hossfeld 2006).

Haeckel's theory of heredity (perigenesis), which he coined in the mid-1870s, only strengthened his neo-Lamarckian view of variation. Thus, Haeckelian natural selection was not opposed to neo-Lamarckism but peacefully coexisted with it. Furthermore, we argue that Darwin's own theory of pangenesis is better suited to neo-Lamarckian interpretations than to strict Darwinian selectionism (as paradoxical as this may sound).

5.2 Darwin on Evolutionary Mechanisms

Darwinism is a dynamic and complex theoretical system consisting of several tightly interconnected postulates and numerous auxiliary hypotheses. The difficulty with defining Darwinism is connected with the fact that the theory of natural selection only achieved logical consistency and conceptual maturity decades after Darwin's death (Levit et al. 2008b, 2011). The first step toward Darwinism as we know it came with the synthetic theory of evolution (STE), which proposed a logically coherent and empirically well-substantiated theoretical system which become "Darwinian" in the modern sense (Reif et al. 2000; Granovitch 2021). That is why an appeal to Darwin's own writings is not the best argument in favor of the "Darwinian" character of a concept.[5] Contemporary "post-synthetic" Darwinism possesses a prerogative of retrospective classification of concepts as "Darwinian" or "anti-Darwinian" irrespectively of Darwin's own views. This prerogative has been legitimized by the almost perfect logical consistency of this complex theoretical system,

[4]Although the genuine nature of Lamarck's original theory is a topic of debate, the term neo-Lamarckism (Lamarckism) "has come to mean the inheritance of acquired characteristics" (Bowler 2003, p. 90).

[5]Comparatively, an appeal to Einstein's writings on general relativity constitutes a strong argument in favor of the "Einsteinianism" of a particular concept.

elaborated by generations of experimental biologists and theoreticians during the second half of the twentieth century. That is why Haeckel's Darwinism must be compared to Darwin's very own Darwinism without references to "synthetic" or "post-synthetic" doctrines. This is the only way to determine the "Darwinian" nature of Haeckel's theory as viewed through the "Down House" window (Levit and Hossfeld 2019).

Darwin's own theory, which advanced the notions of organic evolution and common descent, introduced the principle of natural selection within a broader theoretical context. First of all, Darwin championed sexual selection which drastically increased the explanatory power of his theoretical system. Furthermore, already in the first edition of the *Origin* (1859), this context encompassed a multiplicity of evolutionary mechanisms including neo-Lamarckian variation: "Lamarckian variation is there, under the terms 'direct action of the conditions of life' and the inheritance of 'habit,' and hence 'use and disuse'" (Olby 2009). Although these neo-Lamarckian alternatives to natural selection played a minor role in his explanatory pattern, Darwin always accepted these alternative mechanisms (Olby 2017). The same is true for Darwin's mutationism (famous Darwin's "sports," i.e., macromutations). The founder of mutationism, Hugo de Vries, who claimed that sudden and non-reverting saltations bring about new species, even "portrayed Darwin as the father of macromutationism" (Gould 1983). Besides, this initial version of Darwinism incorporated the germs of a concept of evolutionary constraints expressed, for example, as the concept of correlation. These ideas later gave rise to a theory of orthogenesis, i.e., a theory of directed evolution (Levit and Olsson 2006; Levit et al. 2008b).

The role of these "alternative" evolutionary mechanisms in Darwin's theory probably even increased over time, a fact which becomes apparent when comparing the first and sixth editions of *On the Origin of Species* (Darwin 1859, 1872) as "in the last two editions non-selective forces come into play" (Liepmann 1981). Some scholars have opposed this "Darwin's Lamarckianization" thesis: "From Darwin's own perspective, nothing has changed: he is just trying to make clearer a point that he has always made but that has been constantly overlooked" (Hoquet 2017). In Hoquet's view, instead of becoming more and more Lamarckian, "Darwin stresses the power of variations, something acting simultaneously with the power of natural selection" (Hoquet 2017). If it is so, it fits our hypothesis that Haeckel decided to coin his own theory of variation and heredity in order to make the whole theoretical system more straightforward even better than the "Lamarckianization" thesis.

Historians of science disagree about the role of various evolutionary mechanisms in Darwin's explanatory paradigm. For example, Winther claims that "Darwin was caught in the logical bind [. . .]" as "he attempted to champion the importance of natural selection in producing adaptations while also accentuating systematic and necessarily adaptive somatically-mediated variations" (Winther 2000). Any emphasis he placed on non-selectionist mechanisms of adaptation necessarily decreased the standing of his major discovery, namely, the importance of natural selection. By contrast, Ernst Mayr saw no conflict between various evolutionary mechanisms

within Darwin's own theoretical system: "For Darwin inheritance of acquired characters and a direct effect of the environment were compatible with natural selection" (Mayr 1997). Winther (2000) seems to be right if we view Darwin's theory through the lens of the modern synthesis, whereas Mayr is absolutely right if we see the theory with Darwin's own eyes. Twenty-three years after the first publication of *Origin* (1859), in the last edition of *The Descent of Man* prepared during his lifetime, Darwin listed all the major evolutionary mechanisms practically on one page (Darwin 1882, pp. 607–608). Expectedly, he considered the primary mechanism to be the struggle for existence and natural selection. Sexual selection is another powerful driving force of evolution. Darwin's neo-Lamarckian "long-continued use or disuse of parts will have done much in the same direction with natural selection" (the view passionately supported by Haeckel, as we will see below). At the same time, Darwin also asserted that various parts of the organism are modified in accord with the "principle of correlation," i.e., he admitted some constraints on the independent variation of features. Finally, Darwin claimed that "something may be attributed to the direct and definite action of the surrounding conditions of life" (the second neo-Lamarckian mechanism). Darwin also included in his list of evolutionary mechanisms the "occasional modifications" bringing about "structures" which "cannot be accounted for by any form of selection, or by the inherited effects of use and disuse of parts" (Darwin 1882, p. 608). Darwin described macromutations (sports) as one more auxiliary evolutionary mechanism, but did so only tentatively, therefore excluding it from the list of "regular" evolutionary mechanisms. "Sports" are more commonly found under domestication, Darwin argued, than in nature, where they are "extremely rare" (Largent 2009). As to the general dynamics of all these factors in Darwin's own theoretical system, his tendency toward either admitting the increasingly important role of non-selectionist mechanisms or to better articulating their role (depending on our interpretation of Darwinian texts) is clearly detectable through the six editions of the *Origin* and in some of his other publications. Independently of how exceptional non-selectionist mechanisms were from Darwin's own viewpoint, external observers were entitled to take them seriously and to consider their role in the general concert of evolution.

Darwin was Haeckel's scientific icon, and our analysis suggests that Haeckel followed Darwin quite closely in his description of evolutionary mechanisms (Levit and Hossfeld 2019). Indeed, it would be surprising if he did not. Haeckel elaborated on both natural selection and non-selectionist mechanisms and tried to build them into a noncontradictory theoretical system. But he demonstrated a tendency to convert Darwin's tentative concepts and cautious assumptions into strong beliefs. As Darwin remarked in his typical gentle manner after reading *Generelle Morphologie*, "Your reviewer will say you have spoken much too strongly."[6] This strength of conviction is the principal difference between Haeckel and Darwin.

[6]Letter 5293 (Darwin to Haeckel, 18 August 1866).

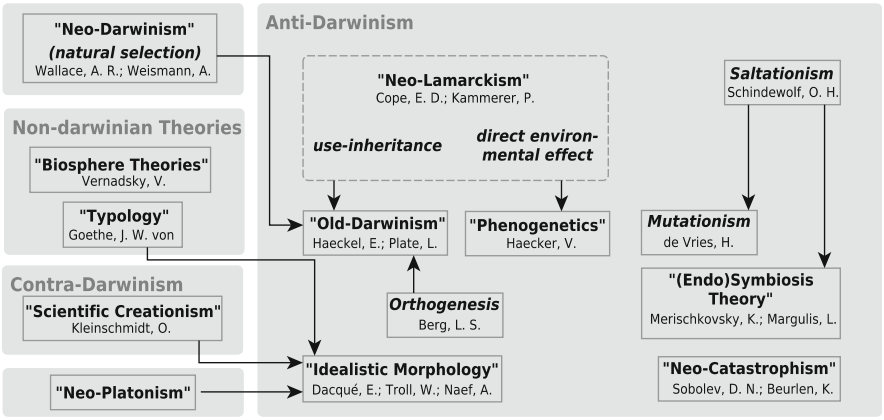

Fig. 5.3 Natural selection and the alternative evolutionary mechanisms at the turn of the centuries (nineteenth to twentieth)

One's interpretation of Darwin's texts depended much on the school one belonged to. Haeckel (old-school-Darwinism) and Weismann (neo-Darwinism) picked up different ideas from Darwin's heritage. This split into two major rival selectionist movements—namely, old- and neo-Darwinism—was determined by each movement's position toward the supposed pluralism of evolutionary mechanisms in Darwin's texts (Levit and Hossfeld 2006). Haeckel was certainly on the site of the pluralists and therefore followed Darwin's intention to create an "open-ended" theory escaping monolithic explanations (Fig. 5.3).

5.3 Natural Selection and Sexual Selection in the *Generelle Morphologie*

The two-volume *Generelle Morphologie* (*General Morphology of Organisms*) (hereafter *GM*) is Haeckel's first major Darwinian work, which appeared in 1866 and embraced almost all aspects of Darwin's theoretical system beginning with detailed phylogenetic trees and ending with the philosophy of monism (Haeckel 1866). Significant space is also devoted to natural selection. Below we outline Haeckel's understanding of natural selection in the *GM*, a task aided by the authors' new translations of several full-length quotations (as *GM* is unavailable in English).

Haeckel devoted specifically to natural selection sections III and VII of the 19th chapter of the so-called fifth book, which is a part of the second volume. But strong claims regarding natural selection can be found also in other parts of the text.

Three claims are of special importance for our objectives.

First, Haeckel unequivocally stated that the discovery of natural selection belongs to the most significant events in the history of knowledge, i.e., in science and philosophy: "The discovery of natural selection via struggle for existence, published by Darwin in 1859, is one of the greatest discoveries of the human research urge.[7] It shed at once such an overwhelming and elucidating light on the dark chaos of a huge collection of biological data, that it made it impossible even for glaring empirics (if they want to come along with modern science at all) to escape the new natural philosophy growing on its foundation [of natural selection]" (Haeckel 1866, Bd. I, p. 71).[8]

Second, Haeckel emphasized that natural selection is a universal evolutionary mechanism acting on all organisms of all three kingdoms, i.e., Animalia, Plantae, and Protista (unicellular organisms), through the whole history of the Earth: "All the large numbers of species of all three kingdoms, which ever existed on our Earth, came about this way, originating from a few autogenous species, under the influence of natural selection discovered by Darwin" (Haeckel 1866, Bd. II, p. 30).[9]

Third, Haeckel insisted that natural selection constitutes the crucial argument "for the exclusive validity of mechanically acting causes in the whole field of biology," i.e., the ultimate evidence for the necessity of naturalistic-causal explanations, thereby whisking away all kinds of teleology (Haeckel 1866, Bd. I, p. 100). In other words, natural selection was for Haeckel not only an ultimate explanatory pattern of biological phenomena but the cornerstone of the new naturalistic worldview opposed to religious prejudices.

Haeckel gave examples of adaptations which could appear only by natural selection. In the already mentioned section VII of the 19th chapter, he discussed the "pelagic fauna of crystal animals" (Haeckel 1866, Bd. II, p. 242). By "crystal animals" or "glass-like animals" (Glasthiere), Haeckel was referring to transparent marine fauna like *Ctenophora* or *Pyrosomatida*. He proceeded from the assumption that "crystal animals" existed in the past in varieties with different levels of transparency and colorlessness (Fig. 5.5). The most transparent and colorless had an advantage in the struggle for existence in clear waters. These individually

[7] "Forschungstrieb," a term akin to Blumenbach's *Nisus Formativus*.

[8] *All citations from GM are given in our translation*. German original: "Die 1859 von Charles Darwin veröffentlichte Entdeckung der natürlichen Zuchtwahl im Kampfe ums Dasein, eine der grössten Entdeckungen des menschlichen Forschungstriebes, hat mit einem Male ein so gewaltiges und klärendes Licht in das dunkle Chaos der haufenweis gesammelten biologischen Thatsachen geworfen, dass es auch den crassesten Empirikern fernerhin, wenn sie überhaupt mit der Wissenschaft fortschreiten wollen, nicht mehr möglich sein wird, sich der daraus emporwachsenden neuen Naturphilosophie zu entziehen."

[9] "Alle die zahlreichen Arten der drei Reiche, welche jemals auf unserer Erde gelebt haben, sind in dieser Weise, unter dem Einflüsse der von Darwin entdeckten natürlichen Zuchtwahl, im Laufe der Zeit aus einer geringen Anzahl autogener Species hervorgegangen."

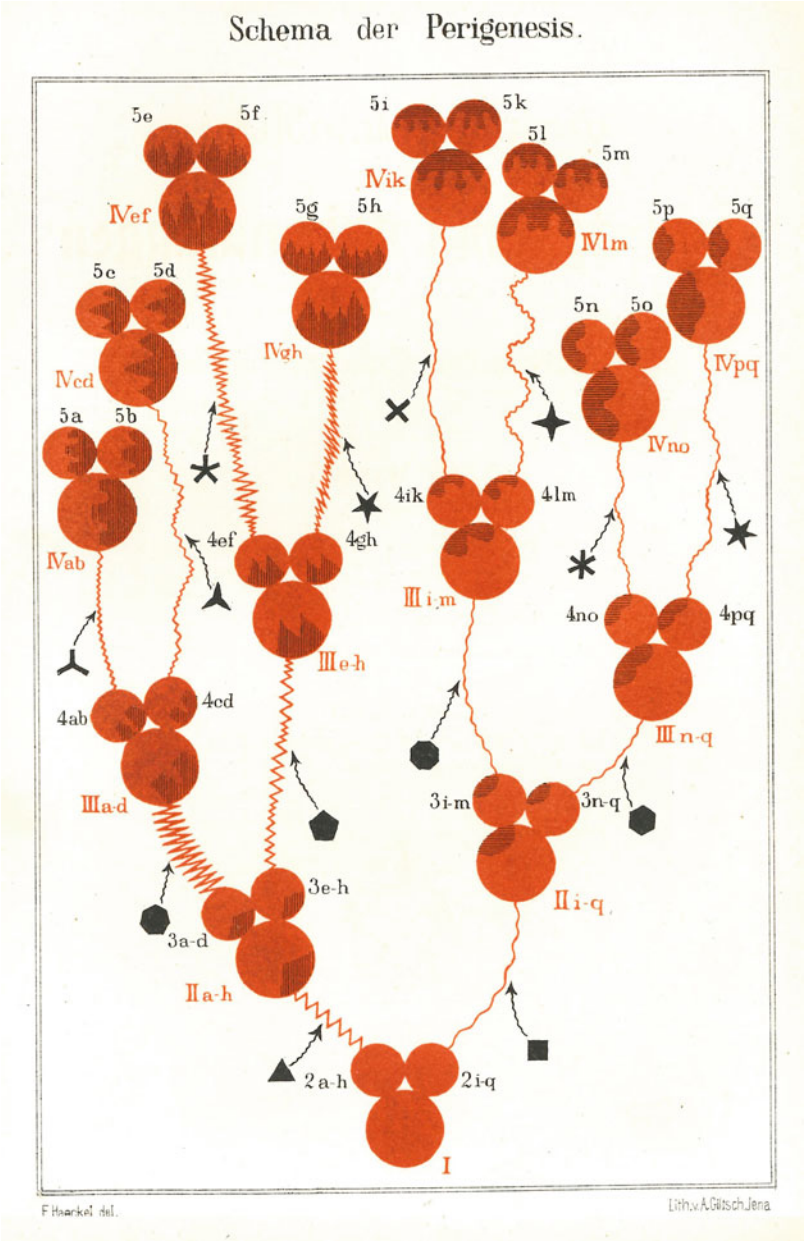

Fig. 5.4 Haeckel's illustration of his perigenesis hypothesis (from Haeckel 1876, pp. 80–81). Haeckel's scheme of perigenesis reflects his idea of interaction between inheritance and adaptation. It presents a transmission of hereditary information in five generations. Four generations indicated as (I–IV) and the last fifth generation as (5a–5q). The plastidule movements transmitting hereditary information are depicted as the red wave lines (pure hereditary information without external influences). Environmental influences are presented as the black wave lines. Environmental

advantageous features were strengthened and secured over many generations so that eventually, completely transparent (glass-like) organic structures came into being. There can be no doubts, Haeckel argued, that these glass-like structures appeared as a result of natural selection as their close non-pelagic relatives dwelling on the seabed or on the coast demonstrate no glass-like body composition, but are opaque and colored (Ibid., p. 243). The transparency of the "crystal animals" gave advantages to both predators and prey, which in the hypothetical past existed in different "varieties." Haeckel brings in this connection also a "very special argument" that many sea animals are colorless and transparent only as pelagic living larvae, but later, when dwelling on the sea bottom or on the coast acquire colors and become opaque as with most Echinodermata (Ibid., pp. 243–244).

Thus, for the three above reasons, natural selection appears to be the most important evolutionary mechanism for Haeckel. This view is also underpinned by our quantitative analysis as, in the *GM*, Haeckel employed the term "natural selection" in various word combinations (see Table 5.1) more than 160 times.[10] If we consider that Haeckel mentioned sexual selection 20 times (see Table 5.2), along with an intensive discussion of artificial selection (which he mentions 32 times; see Table 5.3), we come to more than 200 references to selectionist mechanisms in both volumes of *GM*.

The above three claims suggest the following. First, natural selection was for Haeckel not only a purely biological concept but the foundation of a new "natural philosophy." To fully appreciate this claim, one should consider that for Haeckel, "all true natural science is philosophy, and all true philosophy is natural science. All true science (*Wissenschaft*), therefore, is natural philosophy" (Haeckel 1866, Bd. II, p. 447). Natural selection therefore was crucial for Haeckel's "universalism," i.e., for his attempts to offer all-embracing "scientific" explanations of the universe driven by an aspiration to convert Darwinism into a worldview. Natural selection was *the* universal evolutionary mechanism within a universalist theoretical system, which Haeckel presented already in the *GM*.

Fig. 5.4 (continued) influences modify plastidules' movements and in that way function as adaptations: "In this way, variations are introduced into the germ line in accordance with Haeckel's neo-Lamarckian theory" (Allen 2014). Various black geometric figures symbolize a diversity of environmental conditions an organism is exposed to. These varying environmental conditions cause various modifications in the internal motions within the plastidules, which is graphically reflected as a black hatching on the red balls. The "Micky-Maus-like" triple-balls consist each of one big circle and two small circles. The two small circles are the result of the division of the big one, i.e., they symbolize the division of the plastidules. The scheme is valid for both unicellular and multicellular organisms

[10]German allows many synonymous expressions for natural selection—*natürliche Auslese*, *natürliche Zuchtwahl*, *natürliche Selektion*, etc.—and therefore it is difficult to conduct very exact calculations, but the number we give provides a rough estimate (see Table 5.1).

Fig. 5.5 Haeckel's own drawing of Medusae (*Floresca parthenia*) (Ernst-Haeckel-Haus, Jena)

Second, Haeckel considered natural selection to be the most important element within Darwin's own theory. It is not an accident that Haeckel named section II of the *GM*, "The Theory of Selection," and equated the latter to Darwinism writ large (Ibid., p. 166). And, again, one should bear in mind that Haeckel considered himself a true Darwinian.

Third, natural selection was, for Haeckel, a pattern-making *method* of approaching natural phenomena. His threefold parallelism of ontogeny, phylogeny, and classification not only generally "provided the strongest proof for Darwin's theory of descent with modification" (Rieppel 2019) but coupled with natural selection established the core of the causal explanation of evolution.

So natural selection was crucial for Haeckel. As Di Gregorio (2008) claims, Haeckel clearly distinguished various theories within Darwin's conceptual construction. Thus, Haeckel separated the theory of natural selection from a general evolutionism (evolution as such), for which he suggested the term "Lamarckism," as Lamarck was the first to develop a scientific "theory of descent" (Haeckel 1866, Bd. II, p. 166). This must be considered when analyzing Haeckel's position toward "Lamarckism" within his works, as it has little to do with its current meaning.

Some words need to be said about the context in which Haeckel discussed natural selection within *GM*. Natural selection is mostly analyzed in the second volume of the *GM* devoted to the "general theory of evolution [Entwickelungslehre]" and organized into eight "books" (major chapters). He begins the volume by presenting systematics of various organismic groups and then goes on to ontogeny and phylogeny. The last two "books" of the volume are devoted to the significance of evolutionary theory for anthropology and cosmology. The fifth "book," titled, "First part of the general introduction to evolutionary theory [Entwickelungsgeschichte]" is divided into five subchapters (16–20): "The notion and the tasks of ontogeny" (16), "evolutionary history of physiological individuals" (17), "evolutionary history of morphological individuals" (18), "the theory of descent and the theory of selection" (19), and finally "the ontogenetic theses" (20). Natural selection is mostly discussed in the 19th chapter within a wider discussion about the overall significance of the theory of descent (Haeckel 1866, Bd. II, pp. 166–170). Haeckel starts with the general statement that all organisms on Earth originate from a few (or even a single) "most simple" species, the so-called Monera (unicellular organisms, roughly corresponding to the current notion of bacteria), which, in their turn, evolved from inert matter. This theory was not the sudden discovery of a single author, Haeckel argued. Rather, there were several scholars who advanced similar views, most importantly Lamarck, Geoffroy St. Hilaire, Goethe, Lorenz Oken, Darwin, and Wallace (Ibid., p. 153). Within this pantheon, Darwin had for Haeckel a very special place, because Darwin had begun an unprecedented "reformation" of the theory of descent and 1859 marked a new period in the history of life sciences. Haeckel considers Darwin a true "hero," combining broad empirical knowledge and a deep philosophical grasp of nature (Ibid., p. 163). Darwin's merits, Haeckel argues, include two major elements. First, Darwin made the "doctrine of descent" into a strict and deep theory embracing all biological disciplines. Second, Darwin invented the theory of natural selection which provided a causal explanation of evolution (the theory of transformation—*Umwandlungslehre*). Haeckel also mentions Wallace who independently came to "the same basic ideas" (*zu den selben Grundideen*), foremost among these being the concept of natural selection. For Haeckel, natural selection "follows with necessity the natural tendency of organisms to multiply in geometrical progression, whereas their required existence conditions (and especially nourishments) grow only in arithmetic progression" (Ibid., p. 164). Under these circumstances, the struggle for existence operates as "a breeder" (*züchtend*) and brings about new species. The significance of the discovery of natural selection, Haeckel continued, cannot be overestimated as evolutionary theory (*Transmutationstheorie*) becomes a true and complete theory on the top of all biological sciences only due to the theory of natural

selection. Natural selection is *causae efficientes* of evolution (Haeckel opposed *causae efficientes* as natural acting causes (*Werk-Ursachen*) to *causae finales* corresponding to supranatural teleology (Zweck-Ursachen) (Ibid., p. 26) based on the interaction of two functions immanent to all living organisms: heredity and adaptation (Ibid., pp. 167–168). All organismic features are either the result of adaptation or heredity. As organisms adapt to various environments and inherit new features, one can observe a process of differentiation having no constraints because variability has no limits. In this way "from one and the same species, due to adaptation to very different life conditions, occur very different species" (Ibid., p. 168). Describing the process of adaptation, Haeckel uses the term "the inheritance of characters acquired through adaptation [*Anpassung*]."[11] Now, since the individuals of the same species do not vary in exactly the same manner, the struggle for existence comes into being. Thus, natural selection selects individuals best adapted to their environments. These better adapted organisms are also more perfect (*vollkommen*) than their predecessors, and therefore the whole process of evolution runs toward perfection or progress (*Vervollkommnung*, *Fortschritt*) in the Earth's organisms organization. Perfecting (getting more perfect, advanced, or complete) is for Haeckel an everlasting process and one of the major characteristics of evolution. The struggle for existence ceases by an increasing divergence of traits.

All the above sounds quite Darwinian, maybe with the exception of Haeckel's straightforward progressionism as, for Darwin, natural selection was not a universal law of advancement (Hoquet 2017).[12]

The difference between Darwin and Haeckel becomes apparent when the latter explicates his understanding of heredity. Haeckel provided a detailed account of his concept of heredity and adaptation already in the *GM*. He distinguished "progressive" and "conservative" heredity as organisms may inherit ancestral (conservative) or newly acquired (progressive) features. In this context, he introduced "the law of progressive heredity" or "the law of inheritance of acquired characters," proving that "all descendants of their parents inherit not only old characters inherited by these parents [from their ancestors], but (as a minimum partly) also new characters acquired by them [parents] during their lifetimes" (Haeckel 1866, Bd. II, p. 178). Haeckel clearly stated that these new characters are acquired via adaptation. These adaptive features may be due to use/disuse, habit, or developmental interaction with an environment, but ultimately can be all reduced to nutrition (Ibid., p. 192), since the persistence of all organisms is only possible on the foundation of nutrition-based metabolism. This metabolism is *the* cause and the fundamental condition of changes leading to adaptation (Ibid., p. 193). New substances (molecules) can also be assimilated from the external world. In this way, environmental substances (*Materien der Aussenwelt*) have a chance to influence the protein structures (*Eiweiss-Verbindungen*) of changing organisms. At the same time, Haeckel distinguished direct and indirect adaption (Ibid., p. 196). A direct (or actual) adaptation is

[11]"Vererbung der durch Anpassung erworbenen Abänderungen."

[12]Cf. "Haeckel was indeed a progressionist, but then so was Darwin" (Richards 2009, p. 147).

an immediate adaptation of an organism to its environment during its lifetime. Indirect (or potential) adaptation means that only the next generation will enjoy the fruits of adaptive changes. In this theory, individual changes are, however, never completely congruent and, depending on the character of environmental influences they experience, may even look random. So there is always space for natural selection to act on subtle differences.

To sum up, in the *GM*, Haeckel gave natural selection an absolutely central role in his evolutionary theory. He considered natural selection the most essential Darwinian concept and even equated the term "Darwinism" with the term "natural selection." Furthermore, he maintained that the discovery of natural selection was one of the most significant events in the history of knowledge since it offered a pattern-making method of establishing scientific worldviews.

Yet Haeckelian natural selection is not equivalent to Darwinian natural selection. The crucial difference between the two authors' theories lies in their respective interpretations of variation.

Darwin held that the environment was necessary for both adaptation and variation. He provided an external mechanism for adaptation: natural selection. He also proposed an external mechanism for variation: changes in the environment (Winther 2000). Darwin as well as Haeckel believed that the environment produces variation by acting both on the reproductive system and soma: "[. . .] the conditions of life appear to act in two ways, - directly on the whole organisation or on certain parts alone, and indirectly by affecting the reproductive system" (Darwin 1872, p. 5). Variations induced by environmental "disturbance" of soma could sometimes be definitely directed and adaptive in Darwin's view. But as a rule, Darwin's variation is random (isotropic):

> With respect to the direct action, we must bear in mind that in every case, as Professor Weismann has lately insisted, and as I have incidentally shown in my work on 'Variation under Domestication,' there are two factors: namely, the nature of the organism, and the nature of the conditions. The former seems to be much the more important; for nearly similar variations sometimes arise under, as far as we can judge, dissimilar conditions; and, on the other hand, dissimilar variations under conditions which appear to be nearly uniform. The effects on the offspring are either definite or indefinite. (Darwin 1872, p. 6)

Haeckel's variation, by contrast, is predominantly definitely directed.[13] Thus, the principal difference between Darwin and Haeckel here is that for Darwin, "the nature of the organism" was stronger than "the nature of the conditions," whereas for Haeckel, the environment was an immediate force directing "the nature of the organism." Consequently, Haeckelian natural selection is even more severe than Darwin's as organisms vary in a similar direction and thereby compete for similar resources. Haeckel's understanding of variation creates a certain theoretical difficulty in separating his "Darwinism" from his "neo-Lamarckism," because his

[13]Richards maintains that Haeckel advocated "accidental variations" to a much greater extent than we think as *Anpassung* in Haeckel's texts does not necessarily mean (pre)adaptation to environmental circumstances (Richards 2009, p. 145).

neo-Lamarckism appears to be built-in into his concept of natural selection as a necessary component.

5.4 Haeckel on Natural Selection in the Late Publications

In the period post-*GM*, Haeckel's interest in biological anthropology and embryology visibly strengthened, though sometimes at the cost of detailed discussions of evolutionary mechanisms. In the 1870s and thereafter, Haeckel continued to publish manuscripts with both low and high frequency of references to natural selection, sometimes ignoring this concept in the works where it would be highly expected and mentioning it in seemingly surprising contexts. For example, in 1872, he published a seminal three-volume monograph on calcareous sponges, *Kalkschwämme*, which included two volumes of text and one atlas with illustrations (Haeckel 1872). In this monograph, Haeckel coined his famous "biogenetic law" (ontogeny recapitulates phylogeny) as sponges expressed in their whole being "the profound meaning of this biogenetic fundamental law [*biogenetischen Grundgesetzes*]" (Haeckel 1872, Bd. I, p. 215; Olsson et al. 2017; Porges et al. 2019). The entire organization of these animals, Haeckel emphasized, becomes clear to us only through their ontogeny, "through which we are led directly to their phylogeny" (Haeckel 1872, Bd. I, p. 215). The biogenetic law, being in the *GM* only a hypothesis, gained a strong empirical foundation in the *Kalkschwämme* (Reynolds 2019). Since the "biogenetic law" initially evolved within the pages of *GM* (Porges et al. 2019) and proved central to Haeckel's evolutionary theory, one would expect to see natural selection in the *Kalkschwämme* as well. Yet there is not a single reference to this evolutionary mechanism in the entire monograph.

By contrast, in a 100-page, rather ideologically motivated paper called *Freedom in Science and Teaching*, originally published in German in 1878 and a year later appearing in English translation, Haeckel referenced natural selection 20 times (Haeckel 1879). In this paper, Haeckel argued against his teacher, Rudolf Virchow, who maintained that science was essentially esoteric in character and who reasoned against the attempts of Darwinians to appeal directly to a broad audience, i.e., to popularize Darwinism and "materialism." Virchow placed special attention on Darwinian biological anthropology, which was, according to him, only a vague hypothesis. Contrarily, Haeckel advocated a limitless freedom of science and, as one would expect, argued in favor of the descent of man from apes. In this paper, he repeated his thesis that Darwinism equals natural selection: "This theory of elimination was first clearly recognized and appreciated in its full significance by Charles Darwin in 1859, and the selection-hypothesis which he founded on it is Darwinism properly so called" (Haeckel 1879). He emphasized that the theory of natural selection was "the immeasurable step" in establishing the idea of evolution and in combating the immutability of species (a fundamental teleological idea, in Haeckel's terms) and creationism. It was the theory of selection that annihilated the doctrine of isolated creation "in one blow" and "suddenly opened" Haeckel's eyes "to a

comprehension of that greatest of all biological riddles," the origin of specific biological forms. He also emphasized that the theory of selection is applicable to human evolution: "The theory of selection teaches that in human life, as in animal and plant life everywhere, and at all times, only a small and chosen minority can exist and flourish, while the enormous majority starve and perish miserably and more or less prematurely" (Haeckel 1879). Phrases like "animal and plant life everywhere" and "at all times" in the above quotation suggest that Haeckel still believed in the universal character of natural selection as an evolutionary mechanism. In fact, he stressed in the paper that "most organic species have originated by a process of selection." In sum, there is nothing to suggest that Haeckel had begun to have doubts about natural selection at the time of writing this paper, which was actually a public address. Surely, Haeckel's emphasis on the significance of natural selection can be explained by the polemic nature of the paper as its major objective was protecting Darwinism from accusations of it being just a hypothesis. But, from another side, in these polemics, Haeckel was forced to outline the immutable hard core of Darwinism, to use Lakatosian terms, and this hard core was for him constituted by the theory of natural selection.

In more technical publications of the mid-1870s, Haeckel continued to praise natural selection as the core of evolutionary theory. For instance, in a pamphlet devoted to Haeckel's very own theory of heredity (see next chapter for details), Haeckel emphasized that "Darwin's theory of selection and the theory of descent justified by it, in accord with my deepest conviction, remains unshakable" (Haeckel 1876, p. 18).

Haeckel continued to employ the concept of natural selection also in very late publications. In his major late three-volume technical work, *Systematische Phylogenie* (*Systematic Phylogeny*) (Haeckel 1894–1896), he reiterated his commitment to natural selection as a major evolutionary mechanism and referenced the term natural selection 39 times, accompanied by several references to sexual selection. He also made several strong claims about natural selection; thus, in the first volume, devoted to the phylogeny of protists and plants, Haeckel claimed that both major evolutionary laws, "the law of progressive differentiation" and "the law of perfectioning" (Vervollkommnung), logically follow from the theory of natural selection.

The following extensive quotation effectively illustrates both Haeckel's grasp of phylogeny and his understanding of the role of natural selection in it:

> The natural process of phylogeny is on the whole a process of progressive development.[14] In the history of the organic world, the number, the diversity and the perfection of organic forms increases in the course of time; this historical progress is the more evident, the more we approach the present day. The principal fact of this progressive development finds its explanation in the theory of selection. As natural selection, due to the struggle for existence, takes an effect incessantly and anytime by way of adaptation and inheritance, it has as its

[14]Haeckel used the term "Entwickelung" (development) in the sense of contemporary term "evolution."

> necessary result a continual multiplication, differentiation and perfecting of organisms. (Haeckel 1894, p. 11)[15]

It is easy to see that in this last voluminous technical work Haeckel is still a champion of natural selection and regards it as a major evolutionary mechanism. He still believed that progressive development "generally occurred through the continuous operations of natural selection," a belief highlighted by Richards in his writings on the *Generelle Morphologie* (Richards 2009, p. 147). As in the early works, Haeckel insisted that natural selection is a universal evolutionary mechanism acting at all times and in all places. Elsewhere, when discussing the age of the Earth, he mentioned natural selection as the major directing evolutionary force (Haeckel 1894, p. 17).

Haeckel's popular writings of the end of the nineteenth century reflect his adherence to natural selection as well. Thus, in what is probably his best-known book, *The Riddle of the Universe*, originally published in German as *Die Welträthsel* in 1899 and thus belonging to his very late publications, one can find 32 mentions of selectionist mechanisms (27 directly to natural selection). Most importantly, he repeats the idea initially formulated in the *GM* that the core of Darwin's discovery is the theory of natural selection: "Darwin, however, had not only the signal merit of bringing all the results of the various biological sciences to a common focus in the principle of descent, and thus giving them a harmonious interpretation, but he also discovered, in the principle of selection, that direct cause of transformism which Lamarck had missed" (Haeckel 1934, p. 64). Haeckel would certainly oppose the view presented by Richard Delisle in this volume that natural selection was only an "auxiliary hypothesis" for Darwin (Delisle 2021).

In other words, in his late and very late publications, Haeckel emphasized the role of natural selection as strongly as he did in the early works. A relatively low frequency of references to natural selection in *Systematische Phylogenie* can be explained by the overall lower level of attention he gives to the mechanisms of evolution in the text, instead devoting himself to lengthy discussions of the exact pathways of evolution (phylogenetic reconstructions). The generally lower frequency of natural selection in later works compared to *Generelle Morphologie* is due to the plain fact that Haeckel never again composed a work of comparable comprehensiveness by keeping a very high level of technicality (as opposed to popular publications with less technical details). There was no second edition of the *GM* either, whereas his popular works usually had many editions.

[15]German original: "Der phylogenetische Naturprocess ist im Grossen und Ganzen ein Process der fortschreitenden Entwickelung. In der Geschichte der organischen Welt nimmt von Periode zu Periode die Zahl, Mannichfaltigkeit und Vollkommenheit der organischen Formen zu; dieser historische Fortschritt wird in der Palaeontologie um so auffallender, je mehr wir uns der Gegenwart nähern. Die grosse Thatsache dieser progressiven Entwickelung findet ihre Erklärung durch die Selections-Theorie; denn die natürliche Zuchtwahl durch den Kampf um's Dasein, welche jederzeit und unaufhörlich mittelst der Anpassung und Vererbung wirksam ist, hat zur notwendigen Folge eine beständige Vermehrung, Differenzirung und Vervollkommnung der Organismen."

5.5 Non-selectionist Mechanisms in Haeckel's Works

As already mentioned, Haeckel advocated the whole range of non-selectionist mechanisms as well. The major difficulty with detecting and statistically analyzing these mechanisms in his texts is the great number of synonymous expressions he used for the same phenomenon.

Haeckel undoubtedly championed the best-known mechanism of neo-Lamarckian evolution, i.e., the "use and disuse of organs" (*Gebrauch und Nichtgebrauch der Organe*) accompanied by the inheritance of acquired characters. He also believed that the environment had a direct impact on organisms' heredity (*direkte oder universelle oder actuelle Anpassung*). Both of these neo-Lamarckian evolutionary mechanisms, advocated by Darwin as well, appear already in the *Generelle Morphologie* (e.g., Haeckel 1866, Bd. II, pp. 168, 196, 205, 364) and then never disappear from Haeckel's publications.

The idea that large mutations or "sports" bring about evolutionary "monsters" (*monströse Abänderung, sprungweise Abänderung, plötzliche Ausartung, monströse Entwickelung*) (terminologically close to the famous "hopeful monsters" of the twentieth-century geneticist Richard Goldschmidt) is also to be found already in the *Generelle Morphologie* (Haeckel 1866, pp. 204, 205). These large-scale, one-step mutations obey "the law of monstrous variation" (*lex variationis monstrosae*) and apply to all known kinds of organisms: "All organisms, under certain very unusual and deviant nutritional conditions, are able to produce offspring deviating from the characters of their parent organisms to such an extraordinary and unusual extent (and not in a usual low degree) that man can label them monsters or malformations" (Haeckel 1866, Bd. II, p. 204). Haeckel was of the opinion that "monsters" are relatively common among the offspring of humans, domesticated animals, and plants. These monster mutations can beget not only new species but also new families and orders. Although Darwin also admitted the existence of "sports" and monsters, Haeckel went much further than his scientific idol and advocated for the validity of this concept "too strongly."

Haeckel also championed Darwin's idea of correlation in both his early and late publications (e.g., Haeckel 1866, p. 218; 1874, p. 133; 1896, p. 231). Darwin defined correlated variation as an interconnectedness of various parts of an organism from the evolutionary perspective: "I mean by this expression that the whole organisation is so tied together, during its growth and development, that when slight variations in any one part occur and are accumulated through natural selection, other parts become modified" (Darwin 1872, p. 114). Haeckel, as in other cases, elevated Darwin's idea of correlation to the rank of a law (Haeckel 1866, Bd. II, p. 216). Although the idea of correlation is not necessarily non-selectionist in nature, it can be associated with both orthogenesis (the idea that macroevolution is linear and determined by definite variations; Ceccarelli 2021) and neo-Lamarckism.

Although Haeckel traced the law of correlation back to Goethe, he defined it in terms reminiscent of Darwin's original concept and emphasized that correlation can lead to nonadaptive organismic features. All organismic changes occur as adaptive

reactions, Haeckel argued, but considering that an alteration of an individual character may affect the whole organism, the latter may demonstrate nonadaptive features as well (*Abänderungen welche nicht unmittelbar durch jene Anpassung bedingt sind*) (Haeckel 1866, Bd. II, p. 216). In that sense, Haeckel revolted against the adaptationist fallacy (the idea that nearly all evolutionary changes are adaptive) early on. Remarkably, he saw the ultimate cause of correlation in the "nutritive interaction" between all parts of an organism.

Haeckel advocated for non-selectionist mechanisms also in the later works, but he had no clearly detectable bias toward them. For Haeckel, it was important to demonstrate that evolution is a consistently causal process, that no "wonder" is in play, and that all evolutionary events occur in the continuous theoretical space, where various phenomena and their explanations are not opposed to each other, but complement each other. For example, in *The Evolution of Man*, he devoted several pages to "sudden variation" bringing about new fixed species (e.g., a common two-horned he-goat begets a four-horned goat) but insisted that this phenomenon can be ultimately reduced to the Darwinian idea of gradual evolutionary changes: "All these functions of evolution which 'suddenly and by a leap' produce this four-horned form of goat are in reality perfectly 'gradual and continuous' changes in the evolution of those masses of cells of which we have spoken: they depend on a change in the nutrition of the tissue at these two points in the frontal bone and skin" (Haeckel 1879, p. 169). Haeckel also narrowed the scope of possible evolutionary changes caused by sudden mutations over the course of his scholarly career. If in early works sudden mutations could bring about new families in one jump, in later works he tended to limit their range to the level of species.

Haeckel subordinated other non-selectionist evolutionary mechanisms to Darwinian ones as well. In *The Evolution of Man* (1879), one can find all the major mechanisms Haeckel suggested in the *Generelle Morphologie* (1866): use and disuse, direct adaptation, saltations, and correlative adaptation (e.g., Haeckel 1879, pp. 86, 158). At the same time, the frequency of their use is comparable with his early publications. Thus, he employed the notion of natural selection 25 times in *The Evolution*, accompanied by 11 references to sexual selection. By contrast, the expression "direct or actual adaptation" is used only once, and "use or disuse of organs" is employed two times. Most importantly, Haeckel labels "use and disuse" (which he also calls "adaptation through practice and habit") as "Lamarck's theory" and asserts that Lamarck failed to grasp the most important factor of evolution, namely, natural selection:

> [. . .] but Lamarck did not reach the principle which Darwin subsequently introduced as the most important factor in the Theory of Transmutation, namely, the principle of Natural Selection in the Struggle for Existence. Lamarck failed to discover this most important causal relation, and this, together with the low condition of all biological sciences at that time, prevented him from more firmly establishing his theory of the common descent of animals and man. (Haeckel 1879, p. 86)

In other words, in *The Evolution of Man* (1879), Haeckel advocated neo-Lamarckian mechanisms but clearly subordinated them to the "major causal principle," i.e., to the principle of natural selection.

The same tendency can be found in the two volumes of *The History of Creation* (1880, 1887), although Haeckel mentions neo-Lamarckian mechanisms far more frequently therein (in comparison to the *GM* and *The Evolution*). Direct (or actual) adaptation is mentioned in the text 12 times, and use/disuse 5 times (e.g., Haeckel 1880, pp. 225, 225, 227, 231, 231, 245). Comparatively, however, "natural selection" appears quite frequently—a total of 69 times in the text. Altogether there are 146 references to selectionist processes in both volumes of *The History of Creation* (Haeckel 1880, 1887). The preference for selectionism is evident in this quite late Haeckelian text.

In the three volumes of his *Systematische Phylogenie* (1894, 1895, and 1896), which were not primarily devoted to the discussion of evolutionary mechanisms, selectionist processes, as already mentioned, were referenced 39 times altogether (Table 5.4). The same three volumes contain only three references to direct (or actual) adaptation and four references to use/disuse, i.e., only seven total references to Lamarckian mechanisms. One can certainly find less direct discussion of neo-Lamarckian mechanisms in this text, but his tendency of highlighting selectionism and bringing it into conceptual communication with neo-Lamarckism is apparent.

Haeckel does not neglect natural selection in his post-*Generelle Morphologie* texts, nor does he increasingly prefer non-selectionist evolutionary mechanisms, even considering his very late fundamental treatise, *Systematische Phylogenie*. The core issue with Haeckel's original interpretation of evolutionary mechanisms was not his alleged departure from natural selection over the course of time, but his view of the nature of variation, which rendered his understanding of natural selection partly incompatible with Darwin's and completely incompatible with that proposed by the modern synthesis.

5.6 Haeckel's View of Variation and His Theory of Heredity

Haeckel remained a champion of natural selection throughout his whole career as a Darwinian biologist, yet his version of the theory of natural selection was incongruent with Darwin's. The major difference between the two theories laid in their interpretations of the nature of variation. Darwinian variation was mostly isotropic and only partly definitely directed (Winther 2000). Haeckel's variation was mostly directed and adaptive and only isotropic to a minor extent. The directedness of variation was due to the ability of an environment to influence developmental processes on a molecular-biological level.

As to the question why Haeckel tilted toward definitely directed variation, our analysis proves that Haeckel's approach made the whole explanatory pattern more logical and consistent than Darwin's conceptual system. Darwin, as is well known, tentatively proposed the hypothesis of pangenesis, according to which animal and plant cells threw off so-called gemmules (particles) circulating within the organism (Darwin 1868). These gemmules were supposed to be the bearers of hereditary

information, including information on an organism's environment, and to transmit this information from parents to offspring. The blending of gemmules occurring in the progeny (blending inheritance) guaranteed the transmission of information from both parents in the case of sexual reproduction. Darwin's pangenesis hypothesis, first coined in *The Variation of Animals and Plants Under Domestication* in 1868 (2 years later than Haeckel's *GM*), was quite a Lamarckian one (Darwin 1868). As Olby puts it, "As for the inheritance of acquired characters, Pangenesis accommodates it, for altered organs will send their kind of gemmules to the reproductive system" (Olby 2017). Independently of the question of how Darwin himself combined the ideas of isotropic variation and pangenesis, there are numerous places in *The Variation* where he appears to allow a Haeckelian interpretation of variation:

> In variations caused by the direct action of changed conditions, whether of a definite or indefinite nature, as with the fleeces of sheep in hot countries, with maize grown in cold countries, with inherited gout, &c. conditions, whether acting on the embryo, the young or adult animal, can cause inherited modifications. It is equally or even more unintelligible on any ordinary view, how the effects of the long-continued use or disuse of any part, or of changed habits of body or mind, can be inherited. A more perplexing problem can hardly be proposed; but on our view we have only to suppose that certain cells become at last not only functionally but structurally modified; and that these throw off similarly modified gemmules. (Darwin 1868, pp. 394–395)

Darwin was certainly far from the idea of making variation completely neo-Lamarckian. Rather, he just "wanted to include in his scheme the possibility of the inheritance of some limited acquired characters" and "pangenesis gave him the chance to be Lamarckian without any of Lamarck's inner strivings" (Browne 2002, pp. 283–284). Haeckel's hypothesis of definitely directed variation reflected on this part of Darwin's intuition regarding the nature of heredity and rendered the whole theory more straightforward and less self-contradictory for an external viewer. Haeckel, as always, spoke "too strongly." He argued that the very possibility of natural selection was guaranteed by the unequal abilities of various organisms (of the same population) to immediately adapt to certain environmental conditions. Commenting on the "causes" of heritability (*Erblichkeit*) as a "virtual power" (as opposed to heredity as an actual characteristic), Haeckel asserted that although little is known about its mechanisms, with all probability some material particles are transferred from the parental organism to the descendants and these particles transmit both parental and environmental information. In that sense, Haeckel followed Darwin's "pangenesis" theory in his early publications (Levit et al. 2008a).

In an 1875 lecture presented to the *Medical-Scientific Society of Jena*, Haeckel propounded his own theory of heredity, the so-called perigenesis theory, which was consequently published as a separate pamphlet (Haeckel 1876; Di Gregorio 2005, p. 224; Reynolds 2008) (Fig. 5.4). Haeckel emphasized that the rudiments of this hypothesis were to be found already in the *GM* (Haeckel 1876, p. 17). The objective of the theory was to explicate the predominantly neo-Lamarckian nature of variation: "Like Darwin, Haeckel maintained an important role for the inheritance of acquired characteristics, and his theory of heredity provided a mechanism for how it might work" (Allen 2014). At the core of the theory was the idea of "the plastidules,"

molecules constituting protoplasm and consisting only of atoms. In accordance with his monism, Haeckel argued that all atoms are ensouled (*beseelt*) (Haeckel 1876, p. 39) and therefore that the plastidules possess an "unconscious memory" determining their wavelike motions. These motions Haeckel described as "ramified undulation" (*verzweigte Wellenbewegung*) (Ibid., p. 65). This "ramified undulation" is the essence of the "perigenesis theory" and the *causa efficiens* of any biogenetic process. The perigenesis hypothesis was, for Haeckel, a "genetic molecular theory" (*genetische Molekular-Theorie*) (Ibid., p. 17) bringing together inheritance as an internal organismic characteristic and adaption as modification in accordance with immediate external conditions. As the plastidules do have a "memory," they transmit hereditary information from one generation to another, at the same time "being liable to have their undulations affected by external forces" (Di Gregorio 2005, p. 226). In other words, the wave dynamics of the plastidules guaranteed the intergenerational transmission of hereditary information including newly acquired environmental information. As Fig. 5.4 explicates, various external influences induce various wavelike motions of the plastidules, and these changes are inherited by following generations (e.g., IVef to 5e, 5f). Since, for example, IVpq saved a memory of different external conditions than IVef, it gave different hereditary information to the next generation: 5p, 5q.

Despite the neo-Lamarckian nature of the perigenesis theory, there was a room for natural selection within it: "Like Darwin's gemmules, Haeckel's theory of perigenesis provided a mechanism—in his case a quasi-molecular one—for the origin of variations, and thus for creating the raw material on which selection could act" (Allen 2014).

It was evident already to Haeckel's contemporaries that his theory "does not furnish a clearer explanation than does Mr. Darwin's pangenesis" (Lankester 1876). Some of Haeckel's and Darwin's colleagues such as George John Romanes and Edwin Ray Lankester (Lankester 1876) saw great similarities between Darwin's and Haeckel's views. Romanes maintained that Darwin's theory was superior to Haeckel's because Haeckel's "terms are so much more general" (Burkhardt 2017, p. 26). At the same time, Lankester argued that both Darwin and Haeckel were "students of Mr. Herbert Spencer's works" and that both theories had their roots in Spencer's neo-Lamarckian concept of "life units." Lankester concluded that Darwin and Haeckel's theories were similar but equally obscure. Reacting to news of the perigenesis theory, Darwin himself wrote to Haeckel in 1876: "With respect to Pangenesis, I am sorry that you dissent so strongly from it, as it has lately risen in my estimation; but you are thoroughly right to explain in the clearest & strongest terms, your dissent."[16] Although Darwin himself was unhappy with Haeckel's departure from pangenesis, and although Haeckel stressed that perigenesis is his only fundamental disagreement with Darwin, both theories are fundamentally similar insofar as they both posit the existence of hypothetical "particles" having a kind of a "memory" which are able to transmit information in a neo-Lamarckian way.

[16]Letter no. DCP-LETT-10506 (Darwin to Haeckel, 14 May 1876).

Indeed, both theories are neo-Lamarckian enough to be more compatible with the idea of directed variation than with isotropic variation. Making his theory of natural selection fully compatible with neo-Lamarckism, Haeckel rendered the whole theoretical system more consistent with the proposed mechanisms of heredity. Haeckel's model enabled improved congruity between selectionist and neo-Lamarckian elements of the theory.

5.7 Conclusion

Considering Haeckel's extraordinary importance for the development of continental Darwinism, and that the level of his influence sometimes surpassed that of Darwin himself up until the end of the nineteenth century, Haeckel's understanding of natural selection sheds light not only on his own theory but also on the very essence of Darwinism around the time when Darwin was working. One should not forget that Haeckel and Darwin were in contact and that Darwin vividly reacted to Haeckel's achievements, either encouraging them or remaining reserved, as in the case of the perigenesis theory.

Our quantitative analysis of Haeckel's Darwinian texts and the review of his selected theoretical claims demonstrates that Haeckel considered natural selection through his whole career. The crucial issue was, however, his grasp of the very nature of natural selection. Insofar as Haeckel championed the idea of predominantly definitely directed variation, his version of natural selection differed essentially from that of Darwin. Although Darwin also developed a fairly neo-Lamarckian theory of heredity (pangenesis), he simultaneously championed predominantly isotropic variation and only accepted adaptive (directed) variation in a limited way. Haeckelian variation is, on the contrary, predominantly adaptive, and this provides the Haeckelian concept of natural selection with a different emphasis. Paradoxically, for a contemporary reader, the concept of adaptive variation makes Haeckelian natural selection seem more harsh as, if it were true, competing individuals would vary in a similar direction and experience selective pressure on their very subtle differences.

Our analysis also demonstrates that Haeckel advocated (purely) non-selectionist evolutionary mechanisms as well. Along with neo-Lamarckian direct environmental impact and use/disuse, Haeckel considered large mutations (jumps, sports, monstrosities) to be legitimate mechanisms of evolution, and he also supported the Darwinian idea of correlation.

In sum, Haeckel used Darwin as an inspiration and his understanding of evolutionary mechanisms can be traced back to Darwin's texts. However, Haeckel provided Darwin's ideas with new content and reformulated them within a different theoretical context. Although this reformulation did not necessarily bring him into intractable conflict with Darwin's own Darwinism (as Darwin was not in principle against neo-Lamarckian explanations), it renders his version of Darwinian selectionism even further from contemporary understandings thereof.

Haeckel's consistent support of natural selection as an evolutionary mechanism can be explained by his fidelity to Darwin's ideas, but more importantly by natural selection's ability to explain the whole range of biological phenomena from *monera* to man. Natural selection was, for Haeckel, *the* causal mechanism of evolution which allow us to explain evolutionary progress in naturalistic terms. Paradoxically, it was a neo-Lamarckian natural selection.

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Archival Sources

Letters of Ernst Mayr to Uwe Hossfeld (private archive of Uwe Hossfeld)
Letters of Darwin to Haeckel (www.darwinproject.ac.uk)

Supplementary Materials

Table 5.1 Selectionist terms in Haeckel's *Generelle Morphologie* (1866)

Notions	Frequency	English translation
Selections-Theorie	37	Selection theory
Selection	9	Selection
Selection-Gesetz	1	Law of selection
Natural selection	3	Natural selection
Natürliche Selection	2	Natural selection
Auslese	11	Selection
Natürliche Auslese	4	Natural selection
Auswahl	9	Selection
Natürlicher Auswahl-Process	1	Process of natural selection
Natürlichre Züchtungs-Process	1	Process of natural selection
Zweckmäßige Auswahl	1	Purposeful selection
Zuchtwahl	8	Selection
Zuchtwahl-Lehre	2	Selection doctrine
Zuchtwahllehre	1 (3)	Selection teaching
Natürliche Zuchtwahl	14	Natural selection
Gleichfarbige Zuchtwahl (selectio concolor)	1	Selection of a certain color to adapt to the environment
Natürliche Züchtung	60	Natural selection
In sum	= 165	

Table 5.2 "Sexual selection" in the *Generelle Morphologie*

Notions	Frequency	English translation
Sexuelle Selection	2	Sexual selection
Geschlechtliche Auslese	1	Sexual selection
Sexuelle Auslese	3	Sexual selection
Weibliche Zuchtwahl	3	Female choice
Männliche Zuchtwahl	3	Male choice
Sexuelle Zuchtwahl	7	Sexual selection
Sexuelle Züchtung	1	Sexual selection
In sum	= 20	

Table 5.3 "Artificial selection" and "the process of (artificial) selection" in the *Generelle Morphologie*

Notions	Frequency
Künstliche Züchtung	26
Künstliche Auslese	1
Künstliche Zuchtwahl	1
Züchtungs-Vorgang	2
In sum	= 30

Table 5.4 References to the selectionist mechanisms in three volumes of Haeckel's *Systematische Phylogenie* (1894, 1895, and 1896)

Notions	Frequency	English translation
Selection	4	Selection
Selections-Theorie	13	The theory of selection
Selections-Princip	1	The principle of selection
Selection-Process	1	Selection process
Natural-Selection	6	Natural selection
Cellular-Selection	3	Cellular selection
Personal-Selection	1	Individual selection
Kosmetische Selection	1	Cosmetic selection
Natürliche Zuchtwahl	5	Natural selection
Züchtung	2	Selection
Natürliche Züchtung	2	Natural selection
In sum	= 39	

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