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ORIGINAL PAPER

Psychoontogeny and psychophylogeny: Bernhard Rensch's (1900–1990) selectionist turn through the prism of panpsychistic identism

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Abstract Toward the end of the 1930s, Bernhard Rensch (1900–1990) turned from Lamarckism and orthogenesis to selectionism and became one of the key figures in the making of the Synthetic Theory of Evolution (STE). He contributed to the Darwinization of biological systematics, the criticism of various anti-Darwinian movements in the German lands, but more importantly founded a macroevolutionary theory based on Darwinian gradualism. In the course of time, Rensch's version of the STE developed into an all-embracing metaphysical conception based on a kind of Spinozism. Here we approach Rensch's "selectionist turn" by outlining its context, and by analyzing his theoretical transformation. We try to reconstruct the immanent logic of Rensch's evolution from a "Lamarckian Synthesis" to a "Darwinian Synthesis". We will pay close attention to his pre-Darwinian works, because this period has not been treated in detail in English before. We demonstrate an astonishing continuity in topics, methodology, and empirical generalizations despite the shift in Rensch's views on evolutionary mechanisms. We argue that the continuity in Rensch's theoretical system can be explained, at last in part, by the guiding role of general methodological principles which underlie the entire system, explicitly or implicitly. Specifically, we argue that Rensch's philosophy became an asylum for the concept of orthogenesis which Rensch banned from evolutionary theory. Unable to explain the directionality of evolution in terms of empirically based science, he "pre-programmed" the occurrence of human-level intelligence by a sophisticated philosophy combined with a supposedly naturalistic evolutionary biology.

Keywords Macroevolution · Lamarckism · Modern Synthesis · Rensch · Ontogeny and phylogeny

> The paradox of the moderns is that from the outset they have accepted massive cognitive or psychological explanations in order to explain equally massive effects, whereas in all other scientific domains they seek small causes for large effects.
>
> Bruno Latour (1993) (We Have Never Been Modern)

Introduction

Bernhard Rensch was, arguably, one of the most prominent and controversial figures on the international scene of what is known as the Modern or Evolutionary Synthesis. On the one hand, due to the efforts of Ernst Mayr (1904–2005) and professional historians of science (e.g., Mayr and Provine 1980; Junker 2004), Rensch became the figurehead of the German-language Synthesis. On the other hand, until the late 1930s Rensch was one of the strongest and most original anti-Darwinians, who then suddenly changed into the selectionist camp. In addition, Rensch created an exotic and sophisticated evolutionary metaphysics that seems, from a modern viewpoint, unrelated to his sound evolutionary biology and hardly compatible with the worldviews of the other major figures in the Synthetic movement, and especially not with Mayr's philosophy of biology. Mayr is of the primary interest in this respect, because he appears in the

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Synthesis both as one of the players, and as a historian and philosopher of the Synthesis. Yet Rensch's evolutionary biology is an integrated part of his theoretical work, as is also the case with Mayr's biology and philosophy.

The question of Rensch's turn to selectionism, and the role of his general philosophy in this development, appears to be of crucial importance. In the present paper, we approach this issue by outlining the evolution of his theoretical views with only a short excursion into the biographical circumstances that accompanied his selectionist turn. We will try to reconstruct the immanent logic, which turned him from the attempts to create a "Lamarckian Synthesis" into a Darwinian way of thinking. We will describe his pre-Darwinian views in some detail, because there are no English-language works elucidating his theorizing in this period in any detail. Although Rensch's services to evolutionary biology are widely known, we summarize below very briefly his main contributions (Fig. 1).

Rensch is first of all known as a biologist, who along with Erwin Baur (1875–1933), Walter Zimmermann (1892–1980), Nikolai V. Timofeev-Ressovsky (1900–1981), and Gerhard Heberer (1901–1973) and others contributed to the growth of the Modern Synthesis in the German-speaking countries (Reif et al. 2000; Junker 2004; Kutschera and Niklas 2004, 2008). His most well-known book in this respect is *Neuere Probleme der Abstammungslehre—Die Transspezifische Evolution* (1947), which became known in the Anglo-Saxon world under the title *Evolution above the Species Level* (Rensch 1960). The rest of his scientific legacy is less known with the exception of his historical paper published in the seminal collective monograph edited by Mayr and Provine (1980), which shaped the mainstream retrospective view of the history and borderlines of the Synthesis. Rensch was praised by Mayr as the only German co-architect of the Modern Synthesis. Following Mayr many other English-speaking authors also reduce the Synthesis in the German lands to the contributions by Rensch. This is, however, an evident simplification of the history (Reif et al. 2000). As recently pointed out (Junker and Hoßfeld 2001) the Darwinian synthetic movement in Germany was a joint venture of scientists from different disciplines as the multi-author book *Die Evolution der Organismen* (Heberer 1943) shows. At the same time, the chapter *Die biologischen Beweismittel der Abstammungslehre* (The biologcal proofs of evolutionary theory) written by Rensch for this volume was an essential contribution to the early German-language Synthesis.

Fig. 1 Bernhard Rensch, Aufnahme 1954; Gerhard Heberer von Rensch zum 60. Geburtstag erhalten (Gerhard Heberer's legacy, courtesy of Uwe Hoßfeld)

Rensch himself retrospectively saw his scientific work as a part of a German and international interdisciplinary synthetic lobby (Rensch 1980, p. 298). His specific contribution to the Synthesis was not restricted by the incorporation of systematics into the general theory, but also involved the fields of paleontology and morphology. In this respect his works complements the results achieved by Mayr, Julian Huxley, and Simpson. Both Rensch and Simpson were convinced that macroevolution can be explained without appealing to saltationism and orthogenesis, and that the neo-Lamarckian mechanisms are redundant for evolutionary explanations. Instead they claimed that paleontological data should be connected with the new explanatory paradigm developing in genetics and microsystematics (Mayr 1982, p. 607) (Fig. 2).

Rensch, more than any biologist of his time, emphasized that there is a strong correlation between geographical isolation and environmental conditions. Ornithological observations played a crucial role as an empirical basis for his generalisations, just like they did for Ernst Mayr. For example, three out of seven so-called "biological rules" that Rensch suggested are applicable only to the "ring species" [Rassenkreise] of birds. For example, the "Flügelschnittregel" declares that the races of the colder regions have more narrow and acute wings if compared to the wings of birds in warmer regions. The special role of birds is connected with the life style confronting them with multiple, often contrasting environments.

Until the end of the 1930s, Rensch explained these rules in a neo-Lamarckian way (we analyze it below in detail) maintaining that the "rules" can be explained by direct adaptation of the organisms to their environment (Rensch

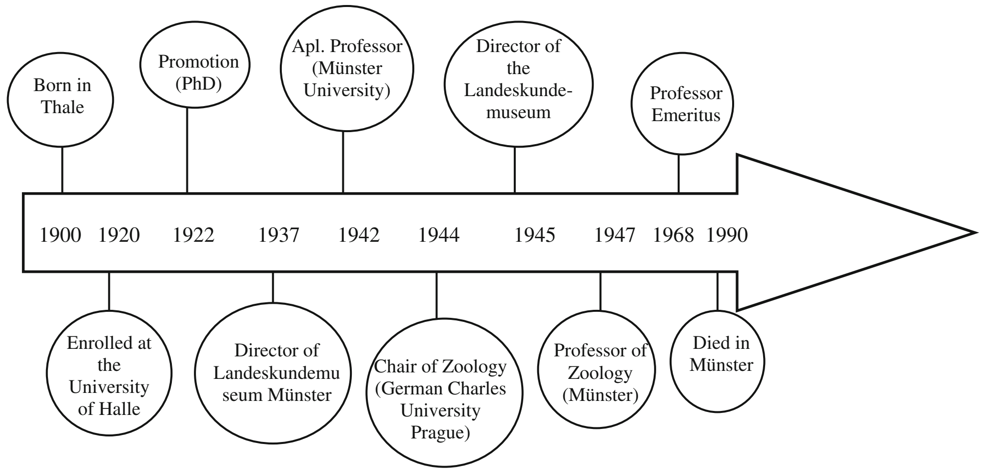


Fig. 2 Bernhard Rensch's major life stations

1933, pp. 48, 58). Natural selection was seen as an auxiliary factor of evolution, but not the only or major directing force in evolution (ibid., p. 54). The first major paper considering selectionism as a serious alternative to neo-Lamarckism was the *Typen der Artbildung* (*The Types of Speciation,* Rensch 1939). His arguments here appear to be quite "Synthetic" since he claims that random mutations and selection can be generally seen as sufficient to explain major transitions in evolution. Also when elucidating the "higher categories" and "the special regularities of paleontology" there is no need for other explanatory patterns. There is no reason, Rensch argued, for postulating other and totally hypothetic laws than those that explain microevolution.

As we shell see in more detail in due course, Rensch's writings on evolutionary biology between 1929 and 1947 demonstrate an astonishing continuity of topics, methodology, and empirical generalizations, despite the shift in his views on the mechanisms of evolution. Below we approach the problem of Rensch's "selectionist turn" by outlining the theoretical context in which it happened, and by a detailed analysis of his conceptual transformation in science and philosophy. Our conclusion is that the continuity in Rensch's theoretical system can to a certain extent be explained by the guiding role of general philosophical principles, which explicitly or implicitly underlie the entire system. We also show that Rensch's philosophy has its roots in the monist movement, which was especially strong in the German lands. We will begin, however, with an outline of Rensch's early Lamarckian works in the context of German-language Lamarckism.

Neo-Lamarckism and old-Darwinism in the early twentieth century

At the time when Rensch began his work in biology, the theoretical landscape in German evolutionary theory was dominated by the neo-Lamarckians and old-Darwinians, and it is no surprise that he became strongly influenced by these theoretical movements in the first decade of his scientific activity. To fully understand Rensch's position in the neo-Lamarckian context a short excursion into the major neo-Lamarckian trends is needed.

Lamarckism owes its name to the French naturalist Jean-Baptiste Lamarck (1744–1829). Lamarck was arguably the first scientist to propose an integral theory of biological evolution (Vorontzov 2004, p. 133). This theory was outlined by Lamarck already in 1800 in the introduction to his *Système des animaux sans vertebras* (Rothmahler 1960), but became widely known after the publication of his fundamental *Philosophie Zoologique* (1809). In the *Philosophie* Lamarck formulated his famous "two laws", the proposal, which can be found in the majority of contemporary evolutionary surveys (e.g., Bowler 2003, p. 92) that use or disuse of an organ leads either to its strengthening or to its weakening, and the claim of the inheritance of acquired characteristics. However, Lamarck presented the latest and most accurate account of his evolutionary theory in the introduction to his *Histoire Naturelle* (Lamarck 1815), as pointed out, e.g., by Löther (1976, p. 316). In this voluminous work, Lamarck also postulated his famous laws directing organic evolution. Lamarck's view of life and evolution was based on two basic ideas. He claimed that "Nature" initially produced all animal species in an imperfect state, and after that they were permanently driven toward increasing complexity and perfection (Lamarck 1809). The driving force of this progressive evolution is the "power of life" (pouvoir vivre). In the paper *Faculté* (Lamarck 1817) written for the *Nouveau dictionnaire d'histoire naturelle* (1816–1819), Lamarck distinguishes "permanent" or "essential" abilities of living beings resulting from the "power of life" and independent from the external circumstances, from abilities, which can be transformed or even disappear under novel circumstances.

The abilities of the first kind correspond to organs such as the nervous or respiratory system, whereas abilities of the second kind can be exemplified by sensory and integumentary organs. The adaptive mechanisms described above provide an adjustment of these "variable" organs to their specific environments. Altogether both "the power of life" and adaptive mechanisms determine the course of evolution and explain biodiversity.

It would be, however, wrong to interpret Lamarck's theoretical heritage exclusively in terms of causally driven processes. In the *Philosophie Zoologique* (1809) Lamarck clearly stated that "there is no doubt that nothing exists except by the will of the sublime Author of everything" (Lamarck 1809).[1] Despite his naturalism Lamarck assumed that the "order of things" was initially created by this "Supreme Author", and therefore the direction of the world's further development must have been given in concert with the initial act of creation. The specificity of Lamarck's view was the confidence that the "order of things", once it had appeared, evolved without subsequent divine interventions (Nazarov 1991; Ghilarov 1998). Lamarck's creationism paradoxically co-existed with his naturalism and is entirely compatible with the idea of progressive evolution.

In his early botanical works Lamarck definitely maintained the idea of the immutability of species ("species fixism" in modern terms, Rothmahler 1960) and his influential adaptationist and progressionist ideas were developed when Lamarck became a zoology professor in the *Musée National d'Histoire Naturelle* in Paris, which was founded under his assistance in 1793. Lamarck was officially responsible for the "lower animals" (insects and worms), while Etienne Geoffroy Saint-Hilaire (1772–1844) was responsible for the vertebrates. Two years later Geoffroy Saint-Hilaire invited Georges Cuvier (1769–1832) to collaborate in the *Musée*. These three scientists not only worked at the same institution, but also lived in the same house and all three played crucial roles in the growth of both theoretical and experimental biology, although Cuvier later became associated with species fixism, whereas Lamarck and Geoffroy developed various adaptationist research programs. The latter designed a theory partially going along with Lamarck's intuition and strictly opposed to Cuvier's creationism.

Geoffroy assumed that there is a common type or common body plan (*unite de plan*) underlying the entire animal kingdom. The same (analogous) structural units of animal bodies developed in different ways in different species, since they followed different purposes (*théorie des analogues*). Although historians of science sometimes paralleled Geoffroy's concept with Goethe's idea of the proto-plant and proto-animal (Urpflanze, Urtier, Nordenskiöld 1928, p. 297; Jahn 1985, p. 301), Geoffroy, in contrast to Goethe and his followers (Breidbach 2006; Levit and Meister 2006b) proposed a causal mechanism explaining transformations of organs over the course of time. Geoffroy looked for a possibility to escape teleological and creationist explanations that had little explanatory power for an empirical biologist. His concepts, founded on embryological data, can be found in the second volume of Geoffroy's *Philosophie Anatomique* (1818–1822), in the *Principes de Philosophie Zoologique* (Geoffroy 1830) and especially in his later works, published already after his famous discussion with Cuvier (Kanaev 1976). Amlinskij (1955, p. 314) claimed that Geoffroy came to proper evolutionism only after turning to paleontological studies. Particularly important, in this respect, is his paper *Sur le degré d'infuence du monde ambiant pour modifier les formes animales* delivered to the Academy of Science on 28 March 1831 and published 2 years later (Geoffroy Saint-Hilaire 1833). The organism, Geoffroy postulated, is inseparably linked with its environment, first of all, by means of respiration and nutrition. In the hypothetical case of a stable environment the organisms would, in parallel to the inertial movement of Newtonian bodies, develop in certain monotonous directions. Yet what we really observe, he claimed, are changing environments, where heat follows cold and humidity follows drought. The contradictive influences induce the internal struggle in the organism, which either destroy it or stimulates its development (Geoffroy Saint-Hilaire 1833, p. 68). Geoffroy gives an example with the fruit trees in a garden, which, in principle are able to give the same fruits, but, in fact, we know that the same trees can give different fruits in different seasons. He claims that the causes of variation of the adult forms can be found in the embryonic stages.

The core hypothesis of the theory is quite convertible into the terms of developmental biology and proves that new organs appear due to the stoppage, underdevelopment or overdevelopment of the offspring as compared to the initial stage of the parental organs. The resulting monstrosities can lack vital capacity and become extinct, but they can be of even greater vitality then their ancestors, as interpreted from the environmental standpoint. Thus Geoffroy's "mutations" are not necessarily a proper response to the environmental influences, and if they "produce harmful overall effects, the animals subjected to them will become extinct, and be replaced by others, endowed with forms that are slightly altered, but meet the requirements of the new circumstances" (Geoffroy 1831, p. 80; extracted and quoted from Corsi 1988, p. 262).

[1] The translation by Jan Johnston of Malaspina University-College, Nanaimo, BC, Canada, is in the public domain, released in April 2000: http://members.aol.com/evomech/index.html.

Environmental perturbations thus in Geoffroy's concept perform a crucial role, not only because they directly influence evolutionarily significant ontogenetic changes, but also because an environment is a kind of selective factor giving advantage only to the forms meeting its "requirements". With the idea of the crucial role of monstrosities, Geoffroy appeared to be at the same time a founder of a new science now known as *teratology* (the study of abnormal organic forms; Le Guyader 2004, p. 8) and of the new evolutionary theory later labeled *Geoffroyism* and subordinated to Lamarckism as one of its versions (Mayr 1982, p. 526). It was Geoffroy's version of Lamarckism that later strongly influenced Bernhard Rensch. Geoffroyism became widely known in Germany by the end of the ninteenth century and was from the very beginning tightly connected with orthogenesis (the concept of directed evolution).

The very term Lamarckism [*Lamarckismus*] was coined by the "German Darwin" Ernst Haeckel (1834–1919). In 1866, only 7 years after the publication of Darwin's (1859) "Origin of Species", Haeckel released his fundamental *Generelle Morphologie der Organismen* (General Morphology of Organisms) with a subtitle "*Allgemeine Grundzüge der organischen Formen-Wissenschaft, mechanisch begründet durch die von Charles Darwin reformierte Descendenz-Theorie*" (General principles of a science of organic forms, mechanically based on Charles Darwin's revised theory of descent). "Mechanically" meant the direct application of Darwinian causal explanations to general morphology. "Darwinian" included, in Haeckel's view, also elements that we would now refer to as Lamarckian. In the chapter *Die Selections—Theorie* (the theory of selection), when presenting his understanding of Darwinism [*Darwinismus*], Haeckel introduces the notion of Lamarckism (Haeckel 1866, pp. 166–170). He emphasizes that although it is correct to label the theory of natural selection as Darwinism to appreciate the role of its founder, the usage of "Darwinism" for labeling the entire evolutionary theory [*Deszendenztheorie*: the theory of descent] is mistaken. Already Lamarck, Haeckel argued, formulated a scientific theory of evolution, which can therefore be labeled as Lamarckism as opposed to Cuvierism as a theory demanding absolute constancy of species. The general theory of descent aims at a complete and harmonic picture of evolution by reducing all its phenomena to "the only physiological process of nature, the transmutations of species" (Haeckel 1866, p. 167). The theory of natural selection, by contrast, reveals the exact machinery, "mechanical causes," of transmutation (evolution) and explains its direction. We should appreciate Lamarck, Haeckel maintained, just for promoting general evolutionism, while Darwin must be praised for his causal explanation of the theory of descent. Haeckel stresses that although in Germany von Baer and Matthias Jacob Schleiden (1804–1881) also expressed the idea of evolution, none of them proposed "an independent theory" of descent.

Although Haeckel himself has credited to Lamarck only "the idea of evolution", from our modern viewpoint, his views on evolutionary mechanisms were strongly influenced by Lamarckian ideas. Even the terminology that Haeckel uses when trying to explain the essence of Darwinism is quite Lamarckian, although he certainly follows the initial intuition of Darwin himself, who never found a way to abandon the inheritance of acquired characters as an auxiliary evolutionary mechanism The theory of selection is based on the interplay of two "physiological functions", Haeckel claimed. The first factor is heritability, which Haeckel also labels the "internal designing power" ("*innere Gestaltungskraft*", "*Bildungstrieb*"). It is the idea of the "internal designing power" that later became central for Eimer's orthogenesis. The "internal designing power" is contrasted with the "external designing power", i.e., the adaptability of organisms. "All organismic features were acquired either due to heritability or thanks to adaptability; there is no third shaping element along these two" (Haeckel 1866, p. 168). Therefore, the inheritance of acquired features (the standard formula of Lamarckism) is explained by Haeckel as the result of the interaction of the two factors mentioned above. Haeckel continues, that what Darwin metaphorically called "the struggle for existence", takes place in parallel to the competition between various organisms "living together". The least adapted organisms perish precociously before they produce offspring. In this way natural selection makes possible a gradual but permanent progress in the organism's organization toward perfection (*Vervollkommnung*).

Commenting on the "causes" of heritability [Erblichkeit] as a "virtual power" as opposed to heredity as an actual feature, Haeckel asserted, that although little is known about the mechanisms, with all probability material particles are transferred from the parental organism to the descendants. In that sense Haeckel followed Darwin's "pangenesis" theory. The second basic organismic feature, adaptability, is a "physiological function" as well, although its ultimate causes are to be found exclusively in the organism's environment (Haeckel 1866, p. 191). The essence of adaptability consists of exchange of substances between organisms and their environments. In this process, nourishment plays an especially important role. Thus in the *Generelle Morphologie*, he combines the concept of natural selection with a Lamarckian mechanism of heredity. First, he definitely supports the idea of the inheritance of acquired features, which were common for both Lamarck and Geoffroy. Second, he clearly expresses the idea of environmental influences on the organism's heredity, emphasizing the role of nourishment. This hypothesis is quite in agreement with the model proposed by Geoffroy with his accentuation of nourishment and respiration as the most important agents of environmental influences. Astonishingly, there are no references to Geoffroy in Haeckel's work.

Since Haeckel made clear statements on evolutionary mechanisms and these mechanisms were definitely Lamarckian, the publication of the *Generelle Morphologie* can be considered as the first milestone of German Lamarckism. At the same time Haeckel succeeded in incorporating his views on evolutionary mechanisms into the general philosophical worldview known as monism, which at the beginning of the twentieth century dominated the intellectual landscape in the German lands. The general purpose of the monistic movement was to build a new worldview on strictly natural-scientific foundations. The major epistemological claim of monism is that cognition is a *natural physiological process.* The metaphysical foundation of naturalistic monism was the idea of *Substance* (World's Real Essence) including three attributes: Matter [Stoff], Energy, and Psychoma [World's Soul] (Haeckel 2008, pp. 48, 69). Monism, as a teaching contrasted to dualism, became widespread in Germany and involved many outstanding scientists, philosophers and public opinion makers. Breidbach and Hoßfeld (2008, p. 14) emphasized that a German intellectual was obliged to come up with excusing arguments, if he was not a monist. The link made by Haeckel between evolutionism and general worldview in the twentieth century became characteristic for German biosciences (Levit and Meister 2006a) and played a crucial role in Rensch's methodology as well.

An alternative hypothesis promoting Lamarckism and Geoffroy's initial intuition was developed by Haeckel's contemporary Carl von Nägeli (1817–1891). His theory played an important role in the history of Darwinian thought as well, because Nägeli was the major target of August Weismann's critics of neo-Lamarckism from a neo-Darwinian standpoint (Löther 1989, p. 79). Nägeli, in his turn, developed his theory without targeting Darwin and Darwinians as major opponents. As Th. Junker has shown, Nägeli consequently developed his ideas beginning in 1853, thus in the "pre-origin-of-species" time (Junker 1989, p. 187). The theory in the mature form is presented in the fundamental volume *Mechanisch-Physiologische Theorie der Abstammungslehre* (Nägeli 1884).

According to Nägeli, evolution is a dichotomous process following, on the one hand, the innate lawfulness determined by the structure of the organisms' "idioplasma", on the other hand, following external influences. In this notable point Nägeli follows Haeckel's initial assumption that there are two forces designing evolution, an external and an internal force. Haeckel, in his turn, credited this idea to Goethe, who discussed these matters in terms of "centripetal" and "centrifugal" forces. Ultimately the idea of internal regularities of evolution gave birth to the orthogenesis tradition (Levit and Olsson 2006), whereas the hypothesis of external influences became of crucial importance for the growth of Lamarckian thought. Below we will see that the idea of the "two forces", internal and external, also influenced Rensch's evolutionary methodology.

Nägeli's ideas has influenced Weismann's student Theodor G. H. Eimer (1843–1898) strongly. Eimer was perhaps the first Lamarckian in the German countries who unambiguously declared the inheritance of acquired characters as "experimentally proven" (Eimer 1897, p. XV). He presented his views systematically in the first tome of his monography *Die Entstehung der Arten auf Grund von Vererben erworbener Eigenschaften nach den Gesetzen organischen Wachsens* (The origin of species caused by the inheritance of acquired characters according to the laws of organic growth), which appeared 4 years after Nägeli' treatise (Eimer 1888). As the ambitious title of the book suggests Eimer, in contrast to Nägeli, held views directly opposed to Darwin and Weismann and proposed an alternative evolutionary mechanism. Weismann's Darwinism, Eimer argued, cannot explain the origin of new characters. It explains, although only partly, the progress and distribution of features that are already there. By contrast, Eimer claimed, Nägeli wanted to clarify two crucial points: the origin of new features, their early evolution and the directedness of evolutionary changes (Eimer 1888, p. 21). Eimer paid much attention to the empirical evidence in favor of Lamarckian inheritance. Along with the typical arguments based on observations such as the changes in pigmentation, Eimer attributed much significance to Dorfmeister's heat experiments butterfly cocoons (Dorfmeister 1875), which played a prototype role for much twentieth century experimental work of Lamarckians. In the later works Eimer emphasized the significance of the "direct impact theory" and thus unambiguously supported Geoffroyism (Eimer 1897, p. 15).

Hans Böker's (1886–1939) papers deliver a paradigmatic example of the mature neo-Lamarckism in Germany. Böker is also important, because his influence on Rensch was not restricted to the pre-Synthetic period, but is clearly diagnosable in the later Darwinian works as well (see below). In 1924, Böker wrote a paper *Begründung einer biologischen Morphologie* [arguments for a biological morphology], where he declared his Lamarckian research program by stating that species "vary before our very eyes by means of inheritance of acquired features" (Böker 1924, p. 20). Böker, like many biologists at his time, believed he could create a new biological Synthesis and thereby describe evolutionary mechanisms properly. He was aware of the mutationist and selectionist research programs, but maintained that they were unable to deliver the whole truth: "If somebody nevertheless claims that he can explain the origin and transformation of species by mutation and selection alone, he may only assure himself of the richness and complexity of anatomical and biological interconnections and coherences going into the finest details. He would then probably understand that the biomorphological correlations of life cannot be explained only by separate 'features' and 'properties' upon which a heredity[2] researcher put so much value" (Böker 1937, p. IV).

Böker was opposed to the search for "separate features" and proposed a holistic research program combining idealistic morphology, genetics, evolutionary morphology (Lamarckian version), functional explanations, ecology, and even ethology (Hoßfeld 2002, p. 159). He called his teaching "comparative biological anatomy" and proceeded from the assumption that the organism is a kind of "construction" that consists of parts, but it is the organism as whole that is confronted with its environment. Organisms remain in harmony with their environment until it changes. If it happens, then there are two possible pathways for an organism to react to environmental perturbations: it will go extinct or adapt to the new situation. Adaptation proceeds by means of anatomical re-construction [*Umkonstruktion*] of the whole organism or its parts, and these reconstructions are heritable (Böker 1935; 1937).

Perhaps the most modern form of neo-Lamarckism, and the one that comes closest to the Synthetic principles was "old-Darwinism". Old-Darwinism was a German theoretical synthetic (but not in the sense of Modern Synthesis) movement, which was represented mainly by Ernst Haeckel and his successor, as the Chair of Zoology in Jena, Ludwig H. Plate (1862–1937) (cf. Tort 1996; Riedl 2003, p. 89; Levit and Hoßfeld 2006). Plate is important in the context of the present paper, while he belonged to the most cited scientists in Rensch's major works. In the first edition of his *Neuere Probleme der Abstammungslehre* (Rensch 1947) Rensch cites Plate 23 times. Even Darwin with 19 references appears behind Plate in this central "synthetic" book of Rensch. In the third edition of this book (1972), we find 14 quotations of the major "architect" of the Synthesis Ernst Mayr, but Plate still is in the lead with 18 references.

Being, in principle, a form of neo-Lamarckism, Plate's old-Darwinism nevertheless cannot be fully reduced to any other theoretical school. The specificity of this theory lay in an attempt to combine the standard Darwinian factors of evolution (mutation, recombination, geographic isolation, and natural selection) with the neo-Lamarckian and orthogenetic mechanisms, and to define the exact role of all these mechanisms in the evolutionary process. Old-Darwinians legitimately insisted that they follow exactly the Darwin′s original ideas, which contained Lamarckian mechanisms and the idea of constraints as auxiliary hypotheses. Thus the idea of multiplicity of evolutionary mechanisms is characteristic for Plate and Rensch in his early works inherited this very concept.

According to Plate, old-Darwinism follows exactly the initial ideas of Darwin and Haeckel while at the same time adapting and processing all healthy and empirically verifiable scientific achievements. Plate tried to combine all fruitful theoretical approaches (Lamarckism, selectionism, and orthogenesis) with the most innovative fields of experimental biology such as genetics. The core of Plate's evolutionary theory can be condensed into two theses:

- 'Darwinism is a "stochastic theory" taking into account variations occurring by chance in the individuals of a certain species' (Plate 1913, p. 222).
- 'However the harmonic modification of various features is more easily conceivable from the Lamarckian standpoint' (Plate 1913, p. 224).

In Plate's later works (1932–1938), we find all the basic factors of evolution later adapted by the makers of the Synthetic Theory of Evolution (STE). Thus Plate claimed that random mutations and recombinations deliver the bulk of raw material for evolution. Natural selection and geographical isolation perform a major role in evolution (Plate 1933, p. 1045). Also what is now known as "population thinking" is of great importance for Plate, and he analyses the "laws of populations" with some mathematics (ibid., pp. 1047–1052). Yet Plate also allows other evolutionary mechanisms going beyond the STE. Thus he accepts both macro- and directed mutations, orthogenetic restrictions and the inheritance of acquired characters. Plate wrote a large monograph (more than 2,000 pages) in which he investigated how all these mechanisms can co-exist in evolution (Plate 1933).

In summary, where Rensch entered the German theoretical landscape he found the whole palette of Lamarckian teachings, well elaborated morphologically and genetically (according to the standards of those times). The Lamarckian movement in Germany was from the very beginning tightly united with orthogenesis and the idea of progressive evolution. Besides, in the light of the old-Darwinian synthesis the simple choice between "Lamarckism" and "selectionism" seemed to be a too primitive solution. Plate showed that the evolution is a complex process governed, with all probability, by several evolutionary mechanisms. The right question in this situation was not "which evolutionary mechanism is the true engine of evolution", but rather "what is the major mechanism of evolutionary progress and which mechanisms perform an auxiliary role". Rensch

[2] "Heredity researcher" is a synonym for "geneticist".

approached the major issues of evolutionary biology in his early works in precisely this way.

Lamarckism in Rensch's early work

Already in one of his earliest works, Rensch appealed to a key evolutionary issue by uniting studies of ontogeny and phylogeny. In a paper devoted to the causes of dwarfism and gigantism in domestic birds, Rensch investigated the embryonic development of various "races" of domestic fowl and came to the conclusions that the differences are due to different cell size and cell number, and that differentiation occurs in the course of embryogenesis. This fact (different cell size) brought the young author to the conclusion that inheritable racial [Rassen] differences should be seen as pre-stages of species (Rensch 1923).

Several years later, in the book *Das Prinzip geographischer Rassenkreise und das Problem der Artbildung* [The Principle of Geographic Ring Species and the Problem of Speciation]—written after his expedition to the Small Sunda-Islands (1927)—we find already a well-articulated evolutionary theory. The first sentence of this book reveals the author's true intensions. Following Richard Hertwig (1850–1937)—one of the major figures in the neo-Lamarckian movement in Germany—Rensch claimed that "the foundations of evolutionary theory lay in the analysis [kritik] of the species concept" and, first of all, in the problem of speciation [Artbildung] in the narrow sense of the word (Rensch 1929 p. 1). For Rensch, the most productive way to approach this problem included the description of the origin of races and the following portrayal of speciation taking place in ring species. The investigation of the lowest systematic categories is of special importance, Rensch emphasized, since it shows the initial steps in the origin of species. Under the lowest systematic categories Rensch understood, first of all, the notions of "geographic race" [geographische Rasse] and "geographic ring species" [geographischer Rassenkreis]. To give a description of these notions, Rensch contrast them to the "traditional concepts of species and subspecies" as formulated in Plate's early works (Plate 1913, 1914). Plate's species definition, popular in those times, was a sophisticated construction far away from the elegance of Ernst Mayr's later widely accepted definition of species, and it was formulated under the influence of "typological thinking" (later discredited by Mayr). Plate claimed that species under unchanging environmental conditions, can be identified through a unique complex of morphological features, considering that individuals deviating from this diagnosed type can still be interpreted as belonging to the same species if they are "intimately connected" with the basic type by intermediate forms; besides, all individuals, which are genetically linked to the basic pattern and successfully mating with it are seen as belonging to the same species. Natural (as contrasted to pathological) deviation from the basic type is defined as a subspecies [variety (Varietät)] (Fig. 3)

Rensch finds Plate's definition unsuitable, because of its insensitivity to the "lowest categories". Giving, first, a short historical survey of all possible definitions, beginning with Kant and ending with Juri Philiptschenko (1882–1930) and Otto Kleinschmidt (1870–1945), Rensch arrives at his own definitions of the "lowest categories":

1. Geographic race [geographische Rasse] is the lowest of the "lowest categories" and represents a complex of unlimitedly interbreeding and morphologically identical (apart from individual or ecological variability) individuals demonstrating heritable characteristic features; there are no other geographic races of the same ring species in the area of a race's spreading. Transitions from one geographic race to another (neighbor) race are very gradual [gleitend].
2. A ring species (*Rassenkreis*—in the direct translation: the "racial circle") is a complex of geographic races of common origin; the neighboring races have no fertility barriers. In Rensch's view, the ring species corresponds with some approximation to Kleinschmidt's *Formenkreis* and Plate's *Rassenkette*.
3. A species is a complex of unlimitedly interbreeding [untereinander unbegrenzt fruchtbaren] and morphologically identical (apart from individual or ecological variability) individuals with heritable characteristic features. The difference between species and

Fig. 3 Bernhard Rensch and his wife Ilse in Endeh (13 July 1927) during their Expedition to Lesser Sunda-Islands [preparation of the monitor lizard (*Varanus komodoensis Ouwens*)] (Gerhard Heberer's legacy, courtesy of Uwe Hoßfeld). This expedition stimulated Rensch not only to purely zoological insights, but also ultimately to philosophical, anthropological, and culturological considerations

geographic race consists in the dimension of morphological differences to the neighbor races/species; a species demonstrates more clear and sharp morphological borderlines. Therefore, a species does not consist of geographic races (Rensch 1929, pp. 11–15). Generally, the difference between species and race is defined through the notion of "sexual affinity". If we observe morphological divergence, however, by remaining sexual affinity to an initial form, we have to do with various races. The failure of the "sexual affinity" points out different species and the partial "sexual affinity" between various forms indicates a border case between species and race (ibid., p. 116).

Proceeding from his "principle of geographic ring species" Rensch discusses the mechanisms of evolution. He begins by describing a "dominating view" on the mechanism of evolution. The *dominating view* is for Rensch *strict selectionism* accompanied by *gradualism*. "The nowadays 'prevailing' view on the origin of species is founded on the well-known achievements of genetics. It is assumed that new heritable characters, i.e., new heritable varieties, occur only as a result of mutation. Every single mutation is assumed to be small—Schrittmutation—since one gained the experience that large mutational leaps [große Mutationssprünge] would destroy the physiological balance of an organism to the extent that such mutant characters cannot be inherited in the homozygotes. A geographic or ecological race consists of individuals or groups of individuals, which occasionally produce a number of such small genotypic differences (a mix of "biotypes"). If the environment changes, the pool [Bestand] of biotypes also changes as a result of natural selection […]. In this way the average characters of a race change and a new race appears. In case of crucial environmental changes, a new species appears due to isolation from the initial form (Rensch 1929, p. 17–18). It is easy to see that, if we replace in this definition "a geographic race" by "population", we deduce a quite modern selectionist explanation of evolutionary change. In a paper published 5 years later, Rensch summarized once again the views of his opponents from the selectionist camp (Rensch 1934) stressing the role performed by the mechanisms of isolation.[3] The geneticists assumes that "an animal form" produces from time to time new "random hereditary dispositions" (mutations). If the new individuals carry harmful mutations, natural selection eliminates them. A few positive or neutral mutations survive and increase their quantity in the course of time. Several steps of that kind lead to the occurrence of "forms" differing significantly from the initial "form" so that a new species occurs. The geographic or "physiological" isolation prevents interbreeding between the new species and the initial form.

The alternatives to this kind of selectionism, Rensch ascertained, include the concept of "direct inheritance" (direct environmental impact on an organism's heredity, a form of Geoffroyism) (1), orthogenesis or nomogenesis (the concept of directed evolution) (2), the concepts proving that new species occur due to polyploidy or cross-breeding (3), mutationism (de Vries, Goldschmidt) (4), and such marginal anti-scientific conceptions as Kleinschmidt's multiple creation (creationism). Rensch explained the heterogeneity of the theoretical landscape with various arguments. Thus neo-Lamarckism is not experimentally substantiated. Mutationism and selectionism (both coming from the camp of "geneticists", in Rensch's view: Rensch 1934) base their arguments on experiments with a few species (*Oenothera*, *Drosophila*). None of the theories is founded upon experiments with several different kinds of living beings. That is why all available concepts, Rensch claimed, are extremely heterogeneous and there is no ultimate solution to the evolutionary puzzle in the foreseeable future. Rensch saw the advantage of his own approach to the evolution in his consideration of the diversity of the living world, and in an attempt to describe a major and several auxiliary mechanisms of speciation without absolutizing one single evolutionary mechanism (Rensch 1929, pp. 19–20).

Throughout his entire 1929 book, Rensch enforces the thesis that "belonging to a certain geographic ring species is the norm, while the appearance of an isolated, geographically unvarying species is an exception" (ibid., p. 56). In other words, in his view, "species" and their origin is not the central issue of evolutionary theory, which should primarily explain the transformations of ring species. Following his broad research program, Rensch illustrates this thesis with a vast amount of empirical data including mammals, birds, insects, mollusks, and plants. Debating with selectionists, Rensch emphasizes that geographical variation is much more significant than individual variation. In cases of geographically remote races, geographical variation leads to a much more radical transformation of characters. For example, the individual variation of the bird *Sitta europaea caesia* (European nuthatch) results only in various tones of the light brown color of the abdomen. Geographical variation, by contrast, results in much more strong dissimilarity ranging from pure white to auburn (ibid., p. 81). The differences between various geographical races can be of the same magnitude as the differences between various species and, Rensch concludes, "there is no principal morphological difference between geographic race and species, i.e., we can interpret geographic races as a

[3] We here summarize Rensch's original German text close to his original terminology. For Rensch, genetics was a hotbed of selectionism and "the geneticists" means here "the selectionists".

variety of the advanced pre-stages of new species" (ibid., p. 85). The morphological characters of geographic races are heritable and in the extreme cases there is no difference between races and species also in this respect. Thus the voluminous ring species are ideal objects for evolutionary studies, because extremely different races transform like species and the study of transitions between them is a good model of evolutionary changes. According to Rensch, "normal", i.e., the most frequently observed kind of speciation includes five phases (ibid., pp. 116–117):

1. At the very beginning there is a homogeneous "form" (race), which occupies an ecologically more or less uniform area.
2. As a consequence of overpopulation, this initial form expands beyond the initial area and occupies ecologically heterogeneous landscapes. This causes the formation of new geographical races.
3. The progressive transformation of a new geographical race due to further environmental perturbations or due to "orthogenetic processes" lead to an increase of morphological differences and a decrease of "sexual affinity".
4. The new race becomes geographically isolated and morphologically clearly distinguishable, while "sexual affinity" to the initial form disappears or the physiology changes in such a way that the new form becomes reproductively isolated from the initial form.
5. In the course of time geological (environmental) causes or further expansion of the new form lead to the situation, when the new and old races (species) co-exist in parallel, but remain reproductively isolated (Fig 4).

Thus, rejecting the macro-mutationist (saltationist) model of evolution (Rensch 1929, p. 127) Rensch argued for a very slow, graduate transition from one race to another. To explain these phenomena, he analyzed several theoretically possible evolutionary mechanisms. The first possibility would be a gradual evolution due to minor random mutations, which then "sum up in one direction in an orthogenetic manner" (ibid., p. 124), i.e., in Plate's terms the directionality of evolution can be partly explained by "orthoselection" (the term was later imported by Rensch into his "synthetic works"). Under "orthogenesis" Rensch understands clearly detectable evolutionary trends. The concept of orthogenesis in its original "Eimerian" sense (defined by Rensch as "unknown internal evolutionary force") he considered to be neither disprovable nor acceptable (ibid., p. 129), and thus banned it from his explanatory model. Another possibility to explain evolution would be the concept of direct environmental impact on the organism's heredity, initially coined by Geoffroy and actively propagated in Germany by Nägeli.

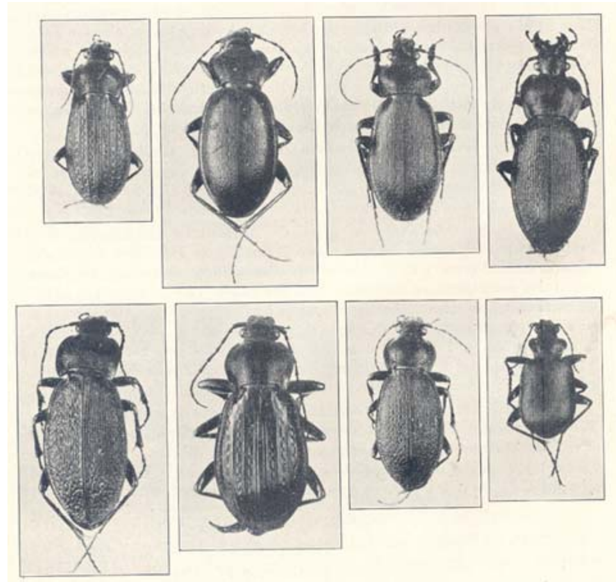


Fig. 4 Rensch's illustration of the difference between the Rassenkreis "ring species" and "species". Pictures 1–7 (from the *left*) demonstrate the races of *Carabus monilis.* Picture 8 shows a geographically unvarying species

In Rensch's view the gradual character of environmental (e.g., climatic) changes can be, in this case, an explanation for the gradual character of evolution.

Rensch argued against the "small random mutations + selection" scheme as the major evolutionary mechanism (Rensch 1933, pp. 48–49). The greatest difficulty with this model, he claimed, is its inability to explain the directionality of evolution, i.e., the evolution of characters in a certain direction, since the differences between races are partly invisible to natural selection. He also argued that selectionism is unable to explain the initial stages of speciation, because a subtle difference between neighboring races often "possess no selective value" (Rensch 1929, p. 125; Rensch 1933, 1934). For example, the titmice (Parus montanus) of Eastern Prussia are a bit greyer than the titmice in central German, but Rensch argues that this has no biological significance, and that this difference can be described only as an average value by examining large numbers of individuals. It is impossible to reduce the color differences between, for example, birds and mammals from eastern and western Europe to the protection function, because the potential predators exist in their own complex ecosystems (nourishment, natural enemies and so on) and therefore the interdependencies are not evident (Rensch 1933, p. 67). In as far as the characters have an evident selective value, the singular mutations and selection will homogenize a population (ibid., p. 49). Thus Rensch at that time anticipated Schmalhausen's concept of stabilizing selection (Levit et al. 2006), while at the same time neglecting the dynamic, creative form of natural selection so important to Schmalhausen. This view inspired another of Rensch's anti-selectionist arguments. If the "random mutations + natural selection" scheme is really the major mechanism of evolution, young races should be more heterogeneous then older ones, and this is not the case (Rensch 1934). Ultimately, Rensch concludes, the experiments by Victor Jollos (1887–1941) and Richard Goldschmidt (1878–1958) (see details on Jollos' experiments in: Levit and Olsson 2006; for Goldschmidt's work see, e.g., Dietrich 2000), which showed that "the environmentally induced mutations" do exist, and made the concept of natural selection redundant (although not improbable). Considering that there are also other kinds of direct impact on the "germ plasm" such as "somatogenic induction", Rensch saw no need for the natural selection hypothesis (Rensch 1934).

Along these lines Rensch concluded that the gradual transitions from one race to another can be at best explained by "direct environmental impact"[4] on race formation (Rensch 1929, p. 126). The gradual transformation of race characters is, according to Rensch, the major mechanism (he calls this "the normal case") directing evolution. For example, the direct climatic influence on body size would be the most probable explanation for "Bergmann's rule", "Allen's rule" (ibid., pp. 135, 145) and other similar regularities connecting variation in environmental conditions with morphological differences between organisms. Thus, for example, the length of a bird's wings (compared to its body size) transforms in such a way that races in warm regions have larger wings than races in cold zones. This scheme of the occurrence of heritable morphological changes was typical for "old-Darwinian" and neo-Lamarckian theorizing in those days. Rensch assumes that environmental influences lead to phenotypic varieties [Phaenovarietäten], which under the same environmental conditions and over a large number of generations produce new heritable features (ibid., p. 167) (Fig. 5)

Rensch thought that the Geoffroyian "normal mechanism" presupposing that the environment influences heredity was the major, but not the only factor of evolution (e.g., Rensch 1933, pp. 35, 72). He considered random mutations, geographic isolation as exemplified by the "island effect", the correlation principle (various parts of an organism correlate with each other), and "natural orthogenetic series", i.e., series evolving under natural environmental conditions (as contrasted to orthogenesis caused by internal factors also known as Eimer's orthogenesis) to be additional evolutionary mechanisms. Natural selection also played an important, but auxiliary role in evolution (Rensch 1936). Thus in the 1930s, Rensch was quite in accord with old-Darwinism in accepting that phylogenetic progress is due to multiple evolutionary mechanisms. The difference was however, that proper old-Darwinians claimed that natural selection is the major directing force in evolution, whereas orthogenesis and Lamarckian inheritance are auxiliary mechanisms. Rensch held the opposite opinion that "soft inheritance" is the "normal case", while orthogenesis and minor and major mutations play secondary roles.

Rensch developed his views in his later "pre-Synthetic" publications. In *Zoologische Systematik*, he discusses evolution above the species level from a Lamarckian–Geoffroyian standpoint (Rensch 1933, pp. 77–82), while at the same time giving more significance to natural selection (ibid., p. 80). Rensch here posed the question, which 15 years later constituted his major contribution to the Synthesis, namely, whether evolution above the species level can be explained by the same mechanisms that explain speciation. Rensch mentions Jurij Philiptschenko, who coined the term micro- and macroevolution and Leo S.

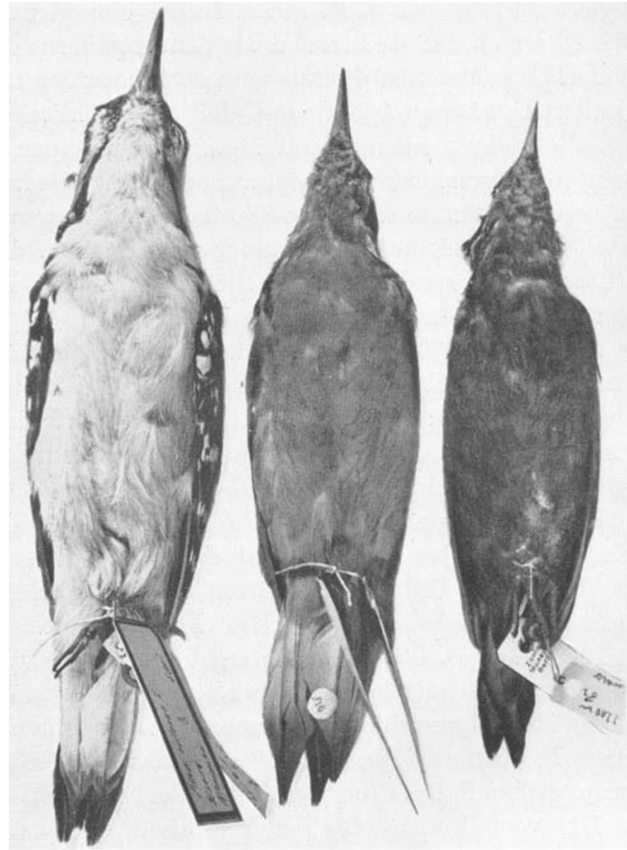


Fig. 5 Races of the woodpeckers *Dryobates villosus* examplifying Bergmann's and Gloger's rules (*villosus* from the Middle North America, *jardinii* from Mexico, *sanctorum* from Gonduras). Bergmann's rule asserts that the homeo-thermal animals increase in size in the colder regions if compared with the warmer areas

[4] German original: "direkte äußere Bewirkung".

Berg, the father of the nomogenesis theory,[5] as advocates of the autonomous character of macroevolution. It is remarkable, that already in this early publication Rensch argued that "from the viewpoint of taxonomy there is no difference in principle between higher and lower categories" (Rensch 1933, p. 78). There are also no sharp boundaries between race, species, and ring species, subgenus [Untergattung], and genus, Rensch continued. These "totally continuous transitions from one category to another" show that there is no discrepancy between evolution of higher and lower categories. At the same time Rensch argues in favor of progressive evolution [Höherentwicklung] and here appeals to Plate's notion of "perfection" [Vervollkommnung] (ibid., p. 80). Rensch, just like Plate, abandoned Eimer's orthogenesis as "an immanent evolutionary force" [immanenter Entfaltungstrieb] and claimed that natural selection gives no preference to the more complex forms, and that this is why both highly developed animals and protozoans can co-exist in the modern world. The latter does not mean that evolution has no direction, because every species has only a few potential evolutionary directions, for biomechanical and other reasons. This is an explanation of the "orthogenetic series", which can be exemplified by the laws of Cope and Dépérét[6] and explained in causal terms. Thus the increase of animal size in the phylogenetic series, Rensch argues, can be explained by the adaptability of adaptive plasticity of the small forms. That is why phylogenetic series often begin with small forms and end with the larger ones. "The existence of directed evolution", Rensch continues, "does not enforce the hypothesis of immanent evolutionary force". Along these lines Rensch comes to his general claim that "there are no reasons for assuming that higher systematic categories represent a special kind of evolution [anders geartete Entwicklung]. We can consider the entire evolutionary process rather as a single process, so that speciation and race formation constitutes in fact the crucial point of the entire complex of [evolutionary] problems" (ibid., pp. 81–82).

Thus, already in the early 1930s Rensch developed a multifaceted concept, which later constituted the core of his evolutionary theory in the "Synthetic" period. This concept included the idea of reducibility of macro- to microevolution, and the claim that gradual continuous changes represent the major route of evolution. Concerning evolutionary mechanisms underlying evolutionary changes, Rensch was quite in accord with Plate's old-Darwinism in that he saw evolution as a result of several factors such as Geoffroyan effects, orthogenesis, and natural selection. The most important difference between Rensch and other champions of old-Darwinians, Lamarckis, and orthogenesis was his rejection of the autonomy of macroevolutionary processes. Plate, for example, postulated special molecular mechanism to explain macroevolutionary trends.

Besides, it is worthy to remark here that the majority of the "biological rules" (such as "Bergmann's rule"), which played a crucial role in Rensch's later theorizing, became included in his theoretical system already in this early period.

From Haeckel to Eternity:[7] Rensch's selectionist turn and his works on macroevolution

Toward the end of the 1930s, Rensch tends to give more significance to natural selection. As Junker (2004, p. 177) ascertained, Rensch's very last explicit Lamarckian publication was written in 1934. Yet, Rensch himself emphasized that his turn to the strict selectionism took several years. As early as 1936, Rensch claimed, he began interpreting the major biological rules in selectionist terms and in 1938 was already definitely a selectionist.[8] At the same time he stressed that he never excluded selectionism completely and even in 1925 explained the cuckoo's mimicry in a Darwinian way.

His article *Typen der Artbildung* published in 1939, but submitted 1 year earlier, is of a bridging character, which makes it interesting to analyze (Rensch 1939). The way this voluminous paper is divided into chapters is in itself remarkable. After a very short introduction Rensch devotes one chapter (II) to "random speciation" [richtungslose Artbildung]. This is followed by a detailed analysis of "directed speciation" [gerichtete Artbildung] with and without natural selection (chapters III and IV). Two chapters are devoted to the "integral transformations of races and species" [ganzheitliche Formumwandlungen bei Rassen- und Artbildung] and the "evolution of higher taxa". In both chapters a separate section is devoted to orthogenesis, while the second—"macroevolutionary"—chapter discusses a whole range of topics connected with the problem of directed evolution such as the irreversibility of evolution, the Cope-Dépérét-rule and evolutionary progress. Thus, orthogenesis is arguably a central issue in this early Darwinian work by Rensch.

[5] See details in Levit and Hoßfeld 2005. Rensch borrowed Berg's term "nomogenesis" and converted it into "bionomogenesis" in his *Biophilosophy* (Rensch 1971).

[6] See details on orthogenesis theory in Levit and Olsson 2006.

[7] This is a paraphrase of the title of Mario di Gregorio's book "Ernst Haeckel: From here to Eternity" (di Gregorio 2005).

[8] Preußischer Kulturbesitz Staatsbibliothek zu Berlin, Handschriftenabteilung, Nachlass B. Rensch Nr. 126, Kt. 2 (Korrespondenz), Rensch an Koehler, 25.3.1948.

Another remarkable feature of this work, which appears quite striking after reading Rensch′s pre-Darwinian papers, is his the radical change of position toward genetics. If in the early 1930s he used the word "geneticist" in a derogatory way, he now appeals to genetics as a criterion for judging if a piece of work is scientific. It is also noteworthy that the paper incorporates all the basic empirical generalizations made or gathered by the author during his pre-Darwinian time (such as Bergmann's or Cope's "rule"), which again directly or indirectly connected with the problem of directed and progressive evolution, into his new explanatory paradigm.

Basically, Rensch maintains that "undirected mutation and natural selection may be regarded as sufficient premises for evolution" (Rensch 1939, p. 219). At the same time he claims that there are non-selectionist "types" of evolution. The latter can be due to biased (directed) mutations. Directed mutations can explain the cases, in which no connection between morphological alterations and environmental factors directing natural selection is detectable, but there are nevertheless clearly distinguishable orthogenetic series expressing themselves in the parallel evolution of closely related genera. In other words, these "biased mutations" replace Rensch's earlier Geoffroyan explanations of the parallel evolution of features presumably neutral with respect to natural selection. Rensch provides no ultimate explanation for this phenomenon, but coins the new term "mutation potencies" [Mutationspotenzen] (ibid., p. 191). He writes that a possible explanation could be that the races developing in parallel carry certain constraining factors as a cryptic pattern [eine kryptomere Musterung vorliegt]. In other words, evolutionary constraints that cannot be explained in terms of adaptation and natural selection. To separate the cases in which orthogenesis is due to natural selection, Rensch employs the term orthoselection. Orthoselection, i.e., directed selection, is the mechanism underlying, e.g., the Cope-Dépéret-rule: "Orthogenetic series arise mostly through continual selection of the larger individual variants and the resulting changes of proportions due to the heterogenic growth of single organs, or through orthoselection (e.g., the ancestral series of *Equus*)" (ibid., p. 219).[9] He adds that orthoselection explains the most obvious cases of orthogenesis (ibid., p. 214). Accordingly, Rensch also tries to reconcile Karl Beurlen's (1901–1985) claim, that there are clearly definable periods of explosive appearance of new taxa in the paleontological record, with Darwinian gradualism. Beurlen's idea of "the phylogenetic explosion" was part of his sophisticated concept of orthogenetic cycles (Levit & Olsson 2006). Rensch recognizes the reality of "phylogenetic explosions", but insists that they can be explained in selectionist terms by acknowledging the considerable role that "circumstances of selection" (such as geographic isolation) play in "the explosive appearance of new forms and their subsequent decay" (Rensch 1939, p. 215). In addition, Rensch argues that natural selection operates on the entire individuals (organisms as wholes) directing the coordinated reconstruction [Umkonstruktion] of an organism's morphology. Although Rensch was in this respect under the influence of theoreticians such as Nikolai Timofeev-Ressovsky, D'Arcy Thompson, Alexei Sewertzoff (1866–1936) and many others, he paid special attention to Böker's concept of "reconstructions", while at the same time trying to "Darwinize" Böker's notion. It is remarkable that at the same time, in the same theoretical field, Ivan I. Schmalhausen (1884–1963) presented his holistic approach to natural selection in his book *The Organism as a Whole in Ontogeny and Phylogeny* (Schmalhausen 1938), although Schmalhausen's concept appears to be much more elaborated and detailed than Rensch's at this time.

Rensch concludes that the most intensely debated evolutionary issues, such as orthogenesis, "phylogenetic explosions", and evolutionary progress [Höherentwicklung], can be explicated from the standpoint of Darwinian selectionism. In other words there is no need for theories other than the gradualism of Darwinian natural selection for the explanation of both micro- and macroevolutionary processes.

The Second World War put Rensch into relative scientific isolation. In October 1944 Rensch became full professor of zoology at the German Charles University in Prague, which was occupied by the German army at the time. The Zoology Department was quite small. Both teaching and research consisted of these major components: evolutionary theory, biogeography, and ecology. Rensch lectured on *The Comparative Zoology of Invertebrates* and gave methodological seminars. Unfortunately, we do not know much about the contents of his methodological seminars, but the fact that he gave them shows that at the time of writing his major contribution to evolutionary biology, the book *Neuere Probleme der Abstammungslehre* (Rensch 1947), which was written in Prague, Rensch was from the very beginning thinking about general methodological issues. (Fig. 6).

The war made the achievements of Rensch's Russian and Anglo-Saxon colleagues almost unavailable to him. In this situation, Rensch improved his macroevolutionary theory and made it into the cornerstone of his theoretical system, thus deserving to be called a "co-architect" of the Evolutionary Synthesis (Rensch 1947). Later on, Rensch counted Huxley, Mayr, Simpson, Schmalhausen, Dobzhansky, and Stebbins as the co-founders of "what later became known as neo-Darwinism" (Rensch 1988, p. 24).

[9] The quoted passage is originally in English.

The work of these “co-architects”, however, was taken into account by Rensch only in the second edition of his *Abstammungslehre* (Rensch 1954) and in the English version of this book (Rensch 1960). The first edition (Rensch 1947) contains only five references to Mayr and only to his “pre-Synthetical”, empirical papers (Mayr 1932), and no references at all to such towering figures of the international “synthetic” movement as Schmalhausen, Stebbins, and Simpson. Huxley’s *Evolution, the Modern Synthesis* (which Rensch mistakenly, but symptomatically quotes as “*the new synthesis*”) as well as Stebbins’, and Mayr’s “synthetic works” became available to Rensch when his book was already in press, and Rensch simply expresses his regrets for not knowing these works earlier (Rensch 1947, p. 374)

The rough copy of the contents of the book (Fig. 7) found in *the Archives of the Academy of Sciences in Prague* shows that Rensch conceived his work from the very beginning as a deep theoretical investigation with explicit methodological reflections. It is not a coincidence that in the first edition of the book, the German philosopher Theodor Ziehen (1862–1950), Rensch’s main philosophical inspiration, is mentioned more often than Darwin. Ziehen was Rensch’s philosophical teacher, a friend of his scientific supervisor Valentin Haecker (1864–1927)[10] and was in intensive personal communication with Rensch.[11] As we know from Rensch’s diaries the intensive reading of Ziehen’s epistemological works immediately paved the way for writing the *Abstammungslehre* [Evolution above the Species Level].[12] Thus on 9 January 1944, Rensch made a note that he was working every evening with Ziehen’s text, while comparing Ziehen’s book (presumably: Ziehen, 1898) with the Bible concerning the “spiritual support” (geistiger Halt) it gives. Seven months later Rensch starts writing his major work on evolution. Thus the decisive step

Fig. 6 The building Rensch worked in during his stay in Prague

in Rensch’s selectionist turn was accompanied by the intensive epistemological considerations. His “philosophy” was not an auxiliary addition to his “biology”, but served as a basis for the scientific inquiry.

From the purely scientific side, Rensch’s objective was to involve as broad empirical data as possible in order to come to terms with one of the major difficulties in the discussion with neo-Lamarckians and early Darwinians, namely, experimenting with only a few model organisms.

The *Abstammungslehre* is full of citations of Rensch’s German-language theoretical opponents and supporters such as Othenio Abel, Beurlen, Cope, Plate, Schindewolf, Sewertzoff, Timofeev-Ressovsky and Philiptschenko. Considering the lack of information on the latest developments in both Russian- and English-language theoretical biology, one can conclude that he moved predominantly in the German-language theoretical field.[13] His concepts of macroevolution and evolutionary progress were completed in parallel to comparable concepts in other national traditions in evolutionary biology, and have their roots predominantly in the German-language scientific and philosophical traditions.

Below we describe very briefly the theoretical field in which Rensch moved, concentrating on the views he was opposed to, because his own views of the “synthetic” period are more than well-known. In principle, Rensch argues along the lines already outlined in the *Typen der Artbildung*, however with a clear emphasis on macroevolution. Even a superficial look at the structure of *Abstammungslehre* (Rensch 1947) shows that the book is

[10] We thank Rudolf Hagemann for pointing out this fact.

[11] Just at the time of Rensch’s evident selectionist turn (1936–38) we find traces of his intensive communication with Ziehen concerning the questions of epistemology and cognitive psychology. For example, Ziehen’s letter to Rensch, 19.11.1936 (Preußischer Kulturbesitz Staatsbibliothek zu Berlin, Handschriftenabteilung, Nachlass B. Rensch Nr. 126, Kt. 3): „*In absehbarer Zeit hoffe ich Ihnen wieder eine [......?] Arbeit schicken zu können. Wenn Sie die Untersuchung über das Zeichen fortsetzen, rate ich eingehende Berücksichtigung der vorzüglichen Hallenses Dr.-Diss. Von Herbert Graewe, Über d. Entwicklung des Zeichens, die auch separat im Verlag von Herman Schroedel, Halle 1932 erschienen ist… Derselbe Autor gibt im Archiv f. d. ges. Psychol. 1936, Bd. 96 eine sehr vollständig. Histor. Überblick über die Psych. D. kindl. Zeichens, c. 120 Seiten.*“

[12] Ibid., Nachlass B. Rensch Nr. 126, Kt. 27 – Tagebücher: “*9. Januar 1944 - Seit Jahresbeginn arbeite ich wieder jeden Abend an Ziehens Erkenntnistheorie (Vorstellungen: In der ältesten Auflage). Der geistige Halt. So wie anderen die Bibel.*”[…]“*19 August 1944—Ich beginne das erste Kapitel meines geplanten Buches über transspezifische Evolution.*”

[13] Some of the authors often cited by Rensch (Sewertzoff, Timofeev-Ressovsky, Philiptschenko) were Russians. However they were publishing in German or residing in Germany and thus influential in the German-speaking world.

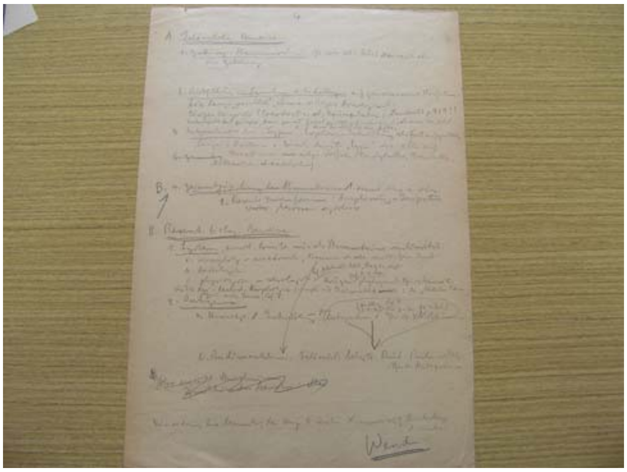


Fig. 7 Draft of the Rensch's major work *Evolution above the Species Level* (from the Archives of the Academy of Sciences in Prague)

about orthogenesis and cyclic processes in evolution. This is not by chance, because the most prominent evolutionary biologists and paleontologists of his time believed in directed evolution. Already in "Introduction" Rensch mentions Henry F. Osborn and Beurlen as his theoretical opponents. Both were important figures among the English- and German-speaking advocates of orthogenesis, respectively. Among the supporters of his own position Rensch mentions, for example, Timofeev-Ressovsky, Hans Bauer (1904–1988), Hans Stubbe (1902–1989), Theodosius Dobzhansky (1900–1975), Walter Zimmermann, and the today much less known Edward M. East (1879–1938). As an expert on systematics, Rensch retains the terminology he used before his selectionist turn, and continues to use the notions of races and ring species. He imports all the empirical generalizations such as Bermann's, Allen's, and Gloger's rules mentioned in his earlier work, and repeats his argument that geographically gradual variation can take place with only minor influences of natural selection, and partly uses examples from his "pre-Darwinian" work (Rensch 1947, pp. 30–40). However, all "types" of speciation differing from the orthodox scheme (random gradual mutation + selection) are either eliminated from the discussion or explained in Darwinian terms. Thus, the "mutation potencies" disappear from the field of plausible hypotheses. Instead Rensch explains non-selective race formation in terms of "successive alterations of characters without any selection due to loss of alleles", i.e., in terms of Darwinian population genetics. In the majority of cases, however, evolution is reduced to geographic, sexual-physiological, or ecological isolation accompanied by random mutations and natural selection. The same is true for macroevolutionary trends. In addition to the already mentioned Osborn and Beurlen, Rensch also attacks Carl von Nägeli, Edwin Hennig, Edgar Dacqué, Rudolf Wedekind, Otto Schindewolf, Leo S. Berg, and other orthogeneticists.

A very brief excursion into the meaning of orthogenesis is needed to understand what Rensch was struggling against. The term "orthogenesis" was coined in 1893 in Germany by Haeckel's student Wilhelm Haacke, who introduced this concept based on the ideas of von Nägeli (1884) and Eimer (1888). Later, in his turn, Eimer (1897) adapted Haacke's term and made it widespread. Thereafter the concept of orthogenesis was developed by an international network of scientists, who in the majority of cases were reflecting upon the work of their predecessors and also influenced each other. Orthogenesis was especially strong and persistent in the German-speaking world. This is related to the generally strong opposition to the Modern Synthesis in Germany even after WWII. Ernst Mayr reported from the "Phylogenetic Symposium" in Hamburg (1956),[14] where he presented the basic principles of the STE and where "all those attending (with exception of the geneticist de Lattin) argued against the Synthesis". Orthogenesis was part of this broad opposition.

Considering its history, orthogenesis can be defined in general terms as a concept of interior or exterior constraints, restricting variation in such a way that evolution will be canalized in a certain, theoretically explicable, and therefore predictable direction. In a more narrow sense, advocated by Haeckel himself and several other theoreticians (for example, Eimer, Osborn, Beurlen, and Schindewolf), orthogenesis means that fundamental organismic structures exist, which predispose living beings to vary only in certain directions. In the majority of theories, orthogenesis is opposed to the idea of evolution as an immediate and permanent adaptation of organisms to their environments, although there is no logical necessity for orthogenetic evolution to be non-adaptive, as was shown by Leo Berg for directed and adaptive mass mutations. Rather, orthogenesis implies that there are trends in development and evolution, which can be seen as non-adaptive considering the immediate needs of the organisms. Some orthogeneticists (Beurlen, Schindewolf) advocated a concept of cyclic evolution. A minority of directed evolutionists (Dacqué and Beurlen after 1937) argued in favor of mystical forces directing evolution.

Rensch argued against all forms of orthogenesis. In the *Abstammungslehre* he put an emphasis on empirical

[14] The "Phylogenetic Symposium" (1956-) was founded as an annual event by Curt Kosswig (1903–1982), Wolf Herre (1909–1997), and Adolf Remane (1898–1976) (Kraus and Hoßfeld 1998).

evidence proving that there are no reasons for taking orthogenesis as a general evolutionary trend seriously. In other words, Rensch maintains that there is nothing to explain here, since "all biologically possible evolutionary directions" have been realized in the course of evolution (Rensch 1947, pp. 56–65). At the same time, he accepts the existence of minor orthogenetic series, but attributes these phenomena to Plate's orthoselection. Concerning "phylogenetic explosions" and cyclic evolution Rensch, in principle, repeats his arguments from 1939, although he brings much more empirical evidence to support his case. The same is true for Böker's concept of "Umkonstruktion", which Rensch elaborates in much more detail, but keeps the old lines of argumentation.

Discussing evolution of body plans and the problem of evolutionary progress, Rensch repeatedly discusses the orthogenetic ideas of Schindewolf, Beurlen, Dacqué, Plate, etc. Rensch admits only strictly empirically observable phenomena and invents selectionist explanations for all of them. In the majority of cases Rensch imports the phenomenology from the anti-Darwinian or neutralist concepts. For example, when debating the developmental mechanisms underlying phylogenetic changes, Rensch uses Sewetzoff's classification into anaboly, middle stage deviation and archallaxis (see Levit et al. 2004 for a review). However, Sewertzoff himself tended to interprete the ontogeny–phylogeny relationship in selectionist terms in these cases, but initially presented his concept as neutral in relation to any hypothesis of evolutionary mechanisms. Rensch, as well as Sewertzoff's immediate pupil Schmalhausen, incorporated this scheme into Darwinian evolutionary theory, but the logic of Sewertzoff's concepts does not necessarily imply selectionist mechanisms. A new theoretical dimension appearing in the book is epistemology, which Rensch adapts for the needs of evolutionary biology. We discuss these matters in detail in the next chapter.

In conclusion, in the *Abstammungslehre* Rensch repeated his arguments in favor of Darwinian selectionism already presented in *Typen der Artbildung*, although elaborated in much more detail, and with a much broader empirical basis. Really novel is the line of argumentation developed as a contribution to epistemology, philosophy of science, and metaphysics and written under the influence of Spinoza (1632–1677) and especially Th. Ziehen. We argue, and this is one of the major theses of this paper, that Rensch's philosophy became an asylum for the concept of orthogenesis that Rensch banned from his evolutionary theory. Unable to explain the directionality of evolution in terms of empirically based science, he "pre-programmed" the occurrence of human-level intelligence by a sophisticated philosophy combined with a seemingly naturalistic evolutionary biology.

A meta-methodological framework for Rensch's evolutionary theory

In this chapter we reconstruct Rensch's attempts of creating a scientifically founded worldview, philosophy and general methodology. We apply the term "meta-methodology" for designating this work.[15] The term "meta-methodology", as contrasted to the term "philosophy", emphasizes that we are dealing here with the ultimate methodological foundations of his theoretical system instead of simply "a philosophy" of "a scientist". Rensch's meta-methodological reflections are of a universal character and include elements of scientific methodology, epistemology, philosophy of science and a general world view. At the same time, all these "philosophical" elements are intimately connected with the applied part of Rensch's theoretical system. It is therefore insufficient to simply talk about the "philosophy" of a "scientist". Rensch developed the "theoretical" part of his system as a framework and foundation for his applied scientific methodology. Both parts developed tightly interconnected and interdependent.

In one of his latest works, the book *Probleme genereller Determiniertheit allen Geschehens* (The Problems of the general Determinacy of all Events) Rensch presented his *pantheistic* metaphysics as a holistic and scientifically based world view. This work is far from being an eccentricity of a retired scientist, but rather sums up methodological reflections that began, according to Rensch himself, in 1939 (Rensch 1988, p. 11). We summarize his meta-methodology as it is represented in this culminating book, taking the earlier works such as his "Biophilosophy" (1971, originally published in German in 1968) into account.

Rensch constructs his meta-methodology proceeding from the general epistemological assumption that "the only entirely reliable foundation for a philosophical world view is the indisputable reality [Wirklichkeit] of the phenomena [Tatsachen] of consciousness", which normally appear as a "stream of consciousness" and this is what should be analyzed from an evolutionary viewpoint (ibid., p. 11).The very human ability to analyze is an inherited feature acquired in the course of evolution, Rensch claims. The most essential trait of our ability to "draw conclusions" can be explained by the adaptedness of the human mental

[15] One of the definitions of meta-methodology: "It is useful to distinguish three separate domains of inquiry. The first domain is of theories, hypotheses, and conjectures, T, ~ T2, T3,…,T*n*. Second is the domain of methodologies which evaluate these theories (among other things), and we shall label these, M, M1, M2,…, M*n*. Finally, we shall distinguish the domain of meta-methodologies which have the important function of evaluating methodologies (among other things), and we shall label these, S1, S2' S3,…, Sn. In brief, theories are about the world, methodologies are about theories, and meta-methodologies are about methodologies"(Sarkar 1980).

apparatus to the regularities of the external world. This adaptedness to the lawfulness of the "extra-mental" reality is the premise of the correlation between the mental and extra-mental worlds.

Already on the first pages of this book Rensch makes a crucial point, when commenting on the difference between his concept and "evolutionary epistemology". Responding to the criticism by the evolutionary epistemologist Gerhard Vollmer, who claimed that Rensch's panpsychistic identism is redundant if one considers Konrad Lorenz' (1903–1989) concept of "fulguration", Rensch argued against all attempts to multiply reality, as was done by Lorenz or Karl Popper (1902–1994), with his idea of triple worlds. For Rensch, as we will see below, there is only one single reality having, however, two fundamentally different aspectas: the mental and the material.

The basis of Rensch's philosophy includes the negation of acausal processes, i.e., in his view both the inorganic and the organic worlds are causally determined (Rensch 1988, pp. 15–16). Thus natural selection is the major factor determining organismic evolution. Biological progress and perfection can be fully explained in terms of Darwinian selectionism. Referring to Plate's concept of orthoselection, Rensch emphasizes that it is sufficient for explaining orthogenetic series. Insofar as evolution is "a process determined in all its stages by the fundamental law-like principles, which control both the structures' development and their functions" (ibid., pp. 23–24). For Rensch material, biological evolution is a determined and gradual process, although it involves stochastic events such as random mutations.

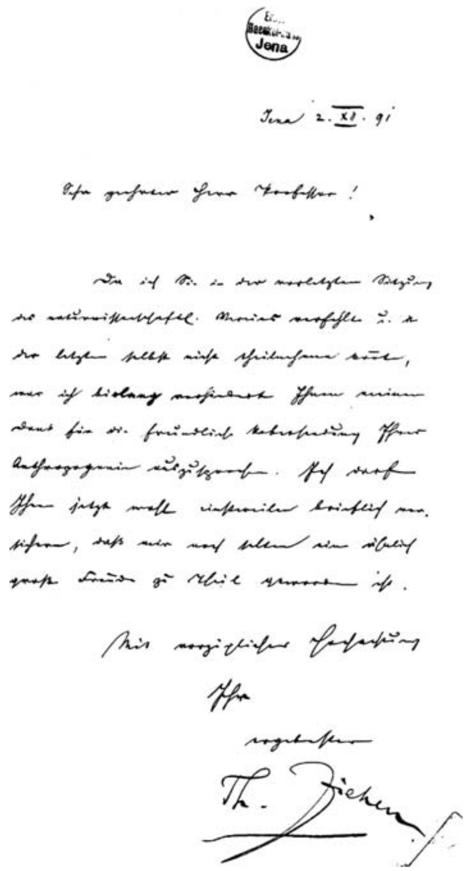
The evolution of the nervous system and intellectual abilities is directed by natural selection as well, due to the adaptive advantages of more differentiated and specialized cells as compared to homogenous cell conglomerates. Accordingly, even the formation of the highest intellectual abilities is a directed and gradual process: "The humans—i.e., the five species of the genus *Homo* (the extinct *H. habilis*, *H. erectus*, *H. modjokertensis*, *H. neandertalensis*, and the existing *H. sapiens*) including various types and intermediate forms—differ in all anatomic and physiological aspects, but only gradually from the semi-erect primates (like gorillas, chimpanzees, and orangutans)" (ibid., p. 30). Going down the phylogenetic tree to lower vertebrates, one can experimentally show that they possess primitive forms of mental abilities [Vorstellungen], for example, generalizations. Even mollusks, Rensch argued, have primitive taste-like sensations.

The evolution of human cultures proceeds mostly on the level of biological non-heritable characters, Rensch continues, and it is important to distinguish between psychic and neurophysiological phenomena. Rensch defines Popper's concept of the relation between psychic and neurophysiologic levels as a *dualism*. Popper assumed that there are two principally different essences [Seinswesen]: the psychic phenomena, on the one hand, and the neurophysiological on the other. These two different kinds of processes are interconnected, that is why Rensch labels this concept interactionism as well. Rensch formulates his own position by contrasting it with Popper's dualism and interactionism. If purely psychic phenomena, as for example volition, could influence muscle contractions, Rensch argues, it would violate the law of energy conservation making the purely biochemical explanation of muscle contractions impossible (ibid., p. 34).

Another possibility would be to assume that mental [geistige] processes run in parallel to events in a material world. This position Rensch labels *psychological parallelism*. Yet, psychological parallelism cannot explain why the physiologically identical brain processes can cause various mental effects. To come to terms with these difficulties, Rensch examines the epistemological foundations of the major categories involved in the discussion. First of all, he analyses the concepts of "matter" and "material processes".

For each human being, Rensch argues, the only indisputable objects are his own psychic phenomena resulting from the immediate experiences: perceptions, imaginations, feelings, and thoughts. Only an analysis of these experiences makes it possible to develop concepts of extramental reality, which appears to be a visible and testable formation [Gestalt]. Thanks to physics we know that matter consists of atoms, elementary particles, and waves. Finally, matter appears to be "the ultimate something", which will perhaps in the future be described only in terms of interactions of various forces, causal chains, and fundamental constants. Rensch appeals to the reductive realism of the German philosopher and psychologist Theodor Ziehen, one of the most cited authors in Rensch's works, who posed the question of the suitability of "matter" as a scientific term. Ziehen is known as an author of psycho-physiological epistemology (e.g., Ziehen 1898) based on the philosophy of monism widely spread in Germany, first of all, due to the "German Darwin" Ernst Haeckel (Fig. 8). Rensch shares the philosophy of Ziehen and labels it a "monistic principle" (Rensch 1971, p. 29). As any kind of philosophical monism, the "monistic principle" constitutes an ultimate, ontologically definable reality, which cannot be multiplied or decomposed into further elements, representing the very foundation of the Universe and providing it with the elements of an individualized whole. In other words, monism implies elements of holism. Rensch was looking for this type of universal principle.

Rensch argued that the reduction of the basic mental features (sensations and imaginations) to their foundations will inevitably lead to the concept of "the ultimate


Jena

Th. Ziehen

Fig. 8 Theodor Ziehen was in personal communication both with Haeckel and Rensch. Here Ziehen's letter to Haeckel (from the EHH Archives): "Jena, 2.12.[18]91. Sehr geehrter Herr Professor! Da ich Sie in der vorletzten Sitzung des naturwissenschaftlichen Vereins verfehlte und an der letzten selbst nicht teilnehmen konnte, war ich bislang verhindert Ihnen meinen Dank für die freundliche Übersendung ihrer Anthropogenie auszusprechen […]. Mit vorzüglicher Hochachtung. Ihr ergebenster Th. Ziehen"

something" and why not call this "something" matter (Rensch 1988, p. 35). It is therefore possible to advance a monistic view. A possible candidate could be a kind of spiritualism,[16] for example the idealism of George Berkeley (1685–1783), Rensch maintains. But the natural scientists would evidently have difficulties with accepting Berkeley's idealism. Alternatively one can appeal to Benedict de Spinoza's concept of substance (1677), in order to avoid dualism. Spinoza postulated the basic and self-explanatory substance available for experience due to its attributes (*substantia cogitans* and *substansia extensa*). Along with Schelling and Hegel, who represented a similar position "to a certain extent" Rensch also listed a couple of dozens of modern philosophers and scientists (e.g., Mario Bunge, Arthur S. Eddington, Ernst Haeckel, and Bertrand Russel), who, in his view, developed the same or a similar methodology.

Along these lines Rensch created his concept of *psychophysical identism* (Rensch 1988, p. 36). Already in the first edition of his major "synthetic" publication, the *Abstammungslehre* (written in the Prague period as shown above) Rensch, in his own words, "presented this world view for the first time", although at that time Rensch employed the awkward term *hylopsychism*. In fact, commenting on the "psychic" bias of his epistemology, Rensch stated: "We would like to point out here once more that this world view is an idealistic one, since what is primarily given to us is the "psychic"; there is definitely no opposition between subject and object, matter and soul; even the abstract reductionist world [Reduktwelt] of natural scientists should not be searched for outside of the 'conscious' [Bewußten]" (Rensch 1947, p. 372). Here Rensch reformulates what Ziehen labels as the basic idealistic principle [idealistische Grundprinzip] suggesting that "what is given is only a psychic, in the habitual language use; the so-called material things are not given, but ought to be revealed"[17] (Ziehen 1922, p. 2).

In the *Biophilosophie* (Rensch 1968; English: 1971) Rensch converted Ziehen's "idealistic principle" into the identistic foundation of his philosophy of biology, and coined the term "panpsychistic-identical or polynomistic world view". Rensch formulated two basic "facts" constituting the basis of panpsychistic identism: "(1) The only reality of which we can be absolutely certain relates to experienced phenomena, which include sensations, mental images, feelings, and volitional processes as a whole. (2) Man does not consist of two separate components—matter and mind, or body and soul, but represents an indivisible psychophysical unity" (Rensch 1971, p. 299).

In the paper published in 1969 in the German philosophical journal *Philosophia Naturalis* and reprinted in the third edition of the *Abstammungslehre* as a supplement to the basic text (Rensch 1972, pp. 400–418), Rensch summarized his views and distinguished "five roots of the panpsychic identism". Taking for granted that several epistemological approaches are possible, Rensch—and this is a crucial point—claims that his version of identism is at best compatible with the picture drawn by modern natural science.

The first source of panpsychism, according to Rensch, is the concept of psycho-phylogeny, which claims that all psychic abilities developed gradually in the course of phylogenesis. What is the source of anything new in the Universe? *Nil de nihilo fit*, Rensch answers, and thus

[16] Rensch means (subjective) idealism in more ordinary terms.

[17] Complete quote in German: "Gegeben ist uns nur Psychisches im Sinne des gewöhnlichen Sprachgebrauchs, die sogenannten materiellen Dinge sind nicht gegeben, sondern werden erschlossen".

everything develops from preexisting entities. This is also true for psychic phenomena. Even protists react on impulses in a way similar to that of organisms with a nervous system. But if we admit that the psychic abilities developed during the entire course of phylogeny as a continuous process, why should we ascribe "the Psychic" only to the first stages of biological evolution without looking for its roots in the geological and astronomic prehistory of evolution? Rensch claims that we can go this way down to the level of proto-phenomena preceding any kind of material evolution (abiotic and biological) and underlying the phenomenological nature of the material world: "the proto-phenomena precede even the inanimate pre-stages of phenomena, and respectively matter is of a proto-phenomenal nature" (Rensch 1972, p. 406). In other words, the protopsychic properties are immanent to matter. *Nihil est in intellectu, quod non fuerit in sensu* can therefore be substantiated also phylogenetically, Rensch concludes.

Human embryology—and this is the second root of "panpsychistic identism"—proves that individual development follows the same course as phylogeny and the embryo becomes more complex and "conscious" in the course of ontogeny. And this is not by chance, since both phylogeny and ontogeny reflect the process of matter becoming ever more compley in its organization, per definition obeying certain directing laws.

But what is matter? Rensch approaches this question from both epistemological and physical viewpoints. From the viewpoint of physics matter appears to be a kind of "lawfully determined energy complex" (Rensch 1971, p. 263). Epistemologically matter appears to be "a spatial–temporal structure [Gefüge] of something, which can be described following further physical analysis" (Rensch 1988, p. 410). Yet neither time nor space are absolute categories and depend on our sensations acquired in the course of evolution. "It is an issue of greatest epistemological significance", Rensch explains, "that absolute space is not primarily phenomenologically given, but that the idea of it can only be constructed from the spatial properties of sensations belonging to different modalities"[18] (Rensch 1971, p. 259). The philosophical or scientific concept of matter is also the result of abstraction. If we are going to grasp the essence of matter based on the phenomena given to us (i.e., the phenomena we perceive), we should consider that the intensities of our perceptions do not necessarily correspond to the physical characteristics of an impulse (for example, the electromagnetic waves above 725 μm are invisible). Therefore, Rensch continues, the creation of an adequate conception of matter implies the process of philosophical reduction. Reduction means here that in thinking about a physical object "we abstract from the properties of one's perceptions and emotional reactions [Gefühlstöne], and consider the assignability [Übertragbarkeit] of intensities and, to an extent, of the spatial and temporal properties of our perceptions as well" (Rensch 1972, p. 410). Reduction relates to only certain properties of consciousness, and does not involve the entire mind. Therefore "these 'reducts' are in fact protopsychical spatio-temporal complexes, devoid of qualities" (Rensch 1971, p. 263), which however still do possess some kind of consciousness [Bewußtheit] and point out the existence of an "ultimate something". This "ultimate something" corresponds to the concept of proto-phenomenology. Rensch's epistemological approach does not provide the ultimate evidence for the proto-phenomenal nature of matter, as he himself stressed, but it is a kind of epistemology and ontology compatible with natural science.

The fifth root of pansychistic identism [along with (1) psychophylogeny, (2) psychoontogeny, (3) epistemological reduction, and (4) physical analysis)] is the conception of the psychophysical substrate. The human body consists, Rensch begins his argument, of two different kinds of substance. The first kind of substance enables the existence of the mind (nerve cells); the second constitutes the rest of the body. Does the first kind of substance—the psychophysical substrate—consist of special molecules? As far we can tell, Rensch answers, the molecules of the psychophysical substrate are of the same nature as the other molecules. The gangliosides and cerebrosides of the brain can also be found in, e.g., spleen, liver, and erythrocytes. The studies of embryogenesis with the help of radioactive marking of nucleic acids and proteins prove that brain neurons metabolize and gain new substances from nutrition. Consequently, Rensch concludes that there is only one kind of matter: "Yet when we attribute the proto-phenomenal nature to all atoms and molecules, we will get a possibility to reduce the phenomena of consciousness down to the law-governed integration of systemic components and processes" (Rensch 1972, p. 413). Along these lines Rensch comes to the conclusion that there is no principal difference between material and psychic [Geistige] phenomena. Any causal physiological explanation would at the same time be an explanation of psychic processes, and vice versa. In other words, psychic and physiological events should be interpreted as in a certain sense identical processes. That is why Rensch labels his philosophical direction identism.

According to Rensch the five sets of arguments described above support the concept of "panpsychistic and realistic identism" and are at the same time completely compatible with the natural-scientific methodology and

[18] Rensch maintains that the spatial properties will be experienced in various forms such as visual, tactile, vestibular, kinesthetic, and auditory space (= various modalities).

epistemology substantiating natural science. Identism unites naïve scientific realism (materialism) with the critical idealism of the majority of European philosophers (Rensch 1972, p. 417).

From the viewpoint of biology, the key issue is how and to what extent identism substantiates evolutionary theory. In other words the question is how and to what extent the concept of a pre-phenomenal nature of matter relates to the problem of directionality in evolution. In his attempt to answer this question Rensch, first of all, underscored that there are no special "forces" [Triebe] in evolution and no divine plan for it. He rejected any kind of teleology in relation to organic evolution. Evolution is under the exclusive control by natural selection. The selective pressure favors an increase of the number of cells in organisms and leads to a more efficient "division of labor" between them, thereby causing centralization [Zentrierung] and intensification of basic functions at same time as it produces new structures and systems. The increasing number of neurons and the appearance of a centralized nervous system is the most important of these processes, which enabled the appearance of new reflexes, taxisms and instincts. The development of these new abilities made the organisms more independent of their environments. This kind of organismic autonomy is the major characteristic of evolutionary progress (Rensch 1988, p. 24).

The resulting picture of the evolutionary process suggests that "the entire organismic evolution should be understood as an inevitable [zwangsläufig] continuous process without any gaps" (ibid., p. 25). The same is true for past and future human evolution. Rensch's claim about the absence of "gaps" in evolution is of central importance for him.

In the voluminous book *Das universale Weltbild* [The Universal Worldview] originally published in 1977 (Rensch 1977; the 2nd ed. 1991) we find Rensch's most detailed and inclusive account of his philosophy of evolution. Like Ernst Mayr, Rensch maintained that the laws of evolution differ in principle from the laws of physics, because biological laws can have exceptions. Thus he prefers to talk about the law-like character [Regelhaftigkeit] of evolution. Rensch lists about a 100 basic law-like regularities in evolution, although even these 100 rules do not exhaust the record. Below we extract some characteristic examples essential for understanding Rensch's position in relation to progress and determinacy in evolution.

The most universal evolutionary regularities in Rensch's list correspond to the standard set of rules of the Modern Synthesis, claiming that all plants and animals undergo random mutations, while sexually propagating organisms obey the laws of Mendel and all organisms produce an excess of offspring. Natural selection controls all developmental stages of all organisms, but acts also on and above the species level, therefore ultimately controlling ontogeny and phylogeny. The new and advantageous structures appear and evolve due to natural selection. In the case of weakly specialized forms ("law of the unspecialized forms") it leads to evolutionary progress (Höherentwicklung, Rensch 1991, p. 102). The steady and long-term selection under certain environmental conditions causes orthogenetic series (orthoselection). Thus all major evolutionary events and transitions can be explained exclusively by means of natural selection. The concept of the pre-phenomenal nature of matter plays no direct role in Rensch's evolutionary explanations. Furthermore, even cultural evolution, Rensch asserts, is directed by natural selection, the only difference being that genetically nonheritable features play the major role. The most important part in the history of civilization is assigned to science, which is driven by selection processes as well. The evolution of human cultures has been determined, first of all, "by the growing scientific knowledge[19] bringing about new technologies and social institutions", whereas scientific knowledge itself makes progress due to the positive selection of concepts (Rensch 1988, p. 116).

The same is true for the evolution of religion, Rensch claims. Religion as a kind of explanation for external world events and the intelligent thinkers (humans) excluded the "improbable" explanations in favor of more consistent and "probable" ones: "In fact, the selection of various ways of thinking [Denkmöglichkeiten] took place", Rensch concludes (1988, p. 61). The evolution of religious beliefs is a process determined psychically and physiologically, and proceeding in a way analogous to biological evolution. Again, the religious beliefs are not heritable in genetic terms and biological heredity is replaced here by the transmission of an intellectual heritage. The law-like progress[20] of religious beliefs manifests itself in the adaptation of beliefs to the general growth of knowledge, and in an increase of spirituality [Vergeistigung] in religious systems. For example, Rensch argues that the majority of polytheistic religions have evolved toward monotheism. The great religious systems, once created, began splitting into sub-systems, sects and so on showing also in this respect a parallelism to organic evolution (ibid., p. 116).

So, Rensch represents an all-embracing evolutionism and selectionism. Natural selection is the major source of lawfulness in evolution and although it differs from the lawfulness of physics, "it is nevertheless, nevertheless, possible to characterize evolutionary regularities

[19] Rensch's italics.

[20] Rensch here uses the same term „Höherenentwicklung", that was central for discussions about evolutionary progress in the German lands in the first half of the twentieth century.

[Regelhaftigkeiten] as laws [Gesetzlichkeiten]" (Rensch 1991, p. 107). Considering that natural selection continuously selects the better variants, evolution appears to be canalized into tight pathways, i.e., inevitably proceeds in certain directions. Thus, although elementary evolutionary events appear to be random, evolution toward human intelligence and evolution of intelligence itself takes place along invisible rails.

Rensch's view on the inevitability of evolution toward human-level intelligence is in sharp contrast to most other leading Synthetic and "post-Synthetic"[21] evolutionists (T. Dobzhansky, G. Simpson, F. Ayala, E. Mayr, J. Monod, and many others), which tend to claim that "there is no indication in the geological record that the evolution of intelligence is at all inevitable"(Barrow and Tipler 1986, p. 133). Rensch, on the contrary, insists that the origin of humans from ape-like ancestors "was presumably a lawfully determined [gesetzmäßig bedingter] process" (Rensch 1991, p. 225). He does not reduce his concept of "lawfulness" to vulgar determinism and coins the notion of "polynomic determination". Polynomic determination implies that the whole range of biological, physical, chemical, social, and other natural laws control the entire process of evolution, intercrossing and interacting and bringing about seemingly stochastic events, which, in fact, can be explicated in terms of lawful processes. In other words there is little chance in organic and cultural evolution, and life would certainly occur on other planets with comparable chemical–physical conditions and evolve in a comparable way to evolution here on Earth (ibid., p. 108).

Methodological remarks

Even a superficial look at Rensch's philosophy reveals its astonishing rootedness in the German, in particular the Haeckelian, tradition. These two evolutionists share four basic characteristics: (1) The attempt to make biology the foundation for a universal world view, and to lay philosophical foundations for scientific inquiry. (2) Specifically, both thinkers proclaimed monism as a reasonable scientific meta-methodology and basis for a new *Weltanschauung*. (3) An all-embracing, but organism-centered evolutionism (4) Anthropocentrism. Indeed, according to Rensch himself, Haeckel's teaching was unambiguously a kind of panpsychic identism (Rensch 1991, p. 230).

Rensch succeeded in developing the Haeckelian approach much more consistent and compatible with modern science than Haeckel himself had managed. The cornerstone of Rensch's revolution of Haeckelianism was the emphasis on gradualism at all levels and in all spheres of inorganic, organic, and social evolution, without exceptions. From this viewpoint Rensch's selectionist turn was not a parting from Haeckelian old-Darwinism, but a step toward Haeckelianism, an attempt to develop and complete the monistic philosophy as a foundation of a new science and cultural self-reflection of humanity.

Rensch's selectionist turn was also not a radical parting from his earlier ideas. In addition to the loyalty to empirical generalizations present in the foundations of his pre-Darwinian works (like various "biological rules"), Rensch consequently developed several constitutive ideas. The phenomenology of orthogenesis and the idea of evolutionary progress [Höhrenentwicklung] are important in this respect as well as Plate's concept of orthoselection. The concept of evolutionary progress states that evolution is a vectored process and this vector points in only one direction: complication, differentiation, and centralization accompanied by the *Vergeistigung* (spiritualization) of matter in either a direct or a metaphorical sense. The idea of evolutionary progress dominated the German biological landscape beginning with Goethe (Breidbach 2006) (we ignore the problem of the applicability of the term "evolution" to Goethe's views) and became important in the first half of the twentieth century in the works of Haeckel, Plate, Böker, and especially for Haeckel's "scientific grandson"[22] Victor Franz (1883–1950). It is remarkable that Böker and Franz also consequently and significantly exaggerated the capacities of their science, trying to make their theories into a kind of universal *Weltanschauung,* which should provide an all-embracing explanatory pattern for social, biological and even mystical phenomena (Levit & Meister 2006b). All these authors belonged to Rensch's favorite sources of references.

Furthermore, Rensch imported the idea of progressive adaptation to changing environments into his selectionist theory, suggesting that higher organisms are better adapted to potential environmental perturbations, i.e., that they are more autonomous in relation to their environments. In Rensch's philosophical works all these concepts received an anthropocentric dimension relating them closely to the religious and world-view related questions. Rensch was in accord with the Haeckelian tradition in biology, but his method of converting biology into a world view and back was much more sophisticated than that of earlier monists. Rensch was not a direct successor of Haeckel and champion of his views. He rather belongs to the tradition associated with Haeckel's name, because he was arguably the most characteristic representative of this tradition. The immediate source for Rensch's philosophical inspiration was Th. Ziehen's Spinozism. Ziehen, in his turn, developed a monistic philosophy deeply rooted in German *Naturphilosophie*. Rensch's appeal to this tradition was not unusual for German biology of first half of the twentieth

[21] "Post-Synthesis" is, according to Ernst Mayr, a period after 1947.

[22] This metaphor was coined by Hoßfeld and Olsson (2003).

century, as we have shown elsewhere (Levit and Meister 2006b). Unusual was the attempt to combine naturphilosophical monism and neo-Spinozism with the Modern Synthesis as a most radical and empirically based form of Darwinian selectionism. We use the term neo-Spinozism here because the Spinozism that Rensch subscribed to differs significantly from the Spinoza original concept (as, actually, all –isms differ from the original concepts). Spinoza, for example, "insisted that any cause operating in nature considered as a system of thought is identical with a cause operating in nature considered as a physical system. This entails that, for every change in a human mind, which can be explained in psychological terms, there must be a replica in the body which is a change to be explained in the terms of physical laws" (Hampshire 1996). By contrast, in Rensch's Spinozism there is no strong dependency between mental and physical events and the mental world possesses a certain kind of autonomy, namely, the different psychic events can have the same replica at the physiological level. Rensch needs this autonomy for opposing free will to the deterministic world of physical processes, because free will is a source of random variation at the cultural-social level analogous to mutations in biological evolution. Spinoza, by contrast, supported that "in the mind there is no absolute, or free will, but the mind is determined to will this or that by a cause which is also determined by another, and this again by another, and so to infinity" (Spinoza 1996 II/129; p. 62). Nevertheless the idea of Substance and its attributes, central for Spinoza, can be clearly detected also in Rensch's works. So Rensch shared a Spinozism of a special kind, deeply rooted in the German romantic tradition and monistic movement. So how was it possible to combine such a philosophy with synthetic Darwinism?

Arguably the most intimate concept in Rensch's monism, which he acquired from the German naturphilosophical tradition and shared with Haeckel,[23] was anthropocentrism. Anthropocentrism means here that the entire evolution of the Universe is seen as if it would inevitably lead to the emergence of a human-like intelligence. In Haeckel's system it was guaranteed by the animated character of matter ("cell-souls", "crystal-souls") along with natural selection and neo-Lamarckian evolutionary mechanisms at the biological level of evolution. Paradoxically, the idea of immediate adaptation to environmental conditions was hardly compatible with the rest of the theoretical system. Immediate adaptation would damage the built-in evolutionary "program" that channel phylogenesis into certain directions. Because of this, the majority of influential orthogeneticists evolved from an initial neo-Lamarckism to mutationism and saltationism (Levit and Olsson 2006). Random selectionist variation protects the "interior of things" [to use Teilhard de Chardin's (1881–1955) vocabulary] from direct adaptation and, even more importantly, Geoffroyian manipualtions of the environment of hereditary mechanisms. Thus, neo-Lamarckian evolutionary mechanisms are not compatible with the anthropocentric program in evolution. Random variation, by contrast, is the cause-of-itself and connected with the environment by means of mediating natural selection. Natural selection, in this case, accumulates the most complete[24] of competing "programs", which gives the organisms more and more autonomy. The latter, as we remember, is important for Rensch's characterization of evolutionary progress. In addition, Darwinian selectionism is associated with very gradual evolutionary changes, which allow very fine "tuning" to the environmental conditions and, what is extremely important in this situation, excludes even a potential possibility of any kind of saltations. Everything develops and evolves gradually without jumps and revolutions, because nothing is new in principle. Everything is rooted in the pre-existing conditions.

Accepting random variation means, however, that evolution loses its orthogenetic characteristics and becomes a stochastic process. In order to preserve the anthropocentricity of the tradition Rensch belonged to, he removed orthogenesis from the world of phenomena into the pre-phenomenal nature of things. It is not just by chance that he compared his version of identism with the concept of *natura naturans* by the scholastic thinker Averroes. As Rensch puts it: "the evolving forms are substantiated already in the essence of the 'matter' and the lawfulness of the world" (Rensch 1991, p. 528).[25] In the following passage Rensch comments that "everything material, everything trans-subjective is something proto-psychic" (Id.). Only with the occurrence of *Homo Sapiens*, he claims, does this "ultimate something" become integrated to such an extent that nature can become aware of itself and of its own regularities.[26] In other words, the "proto-

[23] Haeckel is important here as the most characteristic and representative protagonist of the monistic and naturphilosophical tradition in Darwinian evolutionary biology.

[24] Complete from "completion", one of the possible translation of the term "Vervollkommnung".

[25] The original quotation in full length: "Das entspricht bis zum gewissen Grade der in der christlichen Scholastik gelegentlich vertretenen, wohl schon von Averroës (=Ibn Raschid) vorbereiteten Vorstellung einer 'natura naturans', die besagt, *daß die sich entwickelnden Formen bereits im Wesen der 'Materie'und der Weltgesetzlichkeit begründet sind*" (Rensch's italics).

[26] The original quotation in its full length: "Das fast unbegreifliche an der Stammesgeschichte des Psychischen ist die Tatsache, daß sie mit der Entwicklung der Hirnfunktionen und 'Ich-Komplexe'des Homo Sapiens zu einer Integrationsstufe der protopsychischen 'Materie', des 'letzten Etwas', geführt hat, die es ermöglicht, *daß Natur sich selbst und die Zusammenhänge und Gesetzlichkeiten der übrigen Natur zu erkennen vermag*" (Rensch's italics) (Rensch 1991, p. 258).

psychic" becomes entirely "psychic" by instrumentalizing humans for the purpose of the self-disclosure and self-cognition of the Universe. Our contention is that this is a hidden form of orthogenesis, because although phylogeny is biologically directionless, it appears to be determined on the much deeper level of the "ultimate something". Rensch's polynomic determination turns out to be a very sophisticated form of determinism.

How does Rensch's world view compare to the more conventional philosophies of the Evolutionary Synthesis? Before we answer this question on the general position of Rensch's philosophy in the "synthetic context", some remarks are needed on the most prominent and influential "synthetic" philosophy, which was developed by Ernst Mayr and became a kind of "official" philosophy of the Synthesis. We will not even try to sketch his entire sophisticated metaphysics and epistemology, but concentrate on only one, but central aspect of Mayr's philosophy—his anti-essentialism.

For Mayr, essentialism (= typology in his vocabulary) is a cardinal sin in evolutionary biology, while so-called "population thinking" is a way to escape the typological temptation. Mayr's views on typology underwent a significant evolution and were fully formed by 1959 (Chung 2003). Since that time he interpreted the "population versus typological thinking" controversy as a key issue in the entire history of Western philosophy and science. He declared that typological thinking is based on essentialist philosophy (he often defined essentialism as ideology, Mayr 1997, p. 428), which can be traced back to Pythagorean geometry. Plato's philosophy made essentialism more explicit by postulating that "the world consisted of a limited number of classes of entities and that only the type (essence) of each of these classes of objects had reality, all the seeming variations of these types being immaterial and irrelevant. These Platonian types (or eide) were considered to be constant and timeless, and were sharply delimited against other such types" (Mayr 2001). Correspondingly, the basic objective of essentialists was to discover this hidden nature of things. Essentialists dominated the intellectual landscape during the medieval and into the modern era. Nearly all philosophers up to Darwin's time, Mayr argues, were essentialists and "all of Darwin's teachers and friends were, more or less, essentialists" (Mayr 1991, p. 41).

Mayr argued that essentialism had direct and harmful consequences for biology, because species were considered to be clearly discontinuous "natural kinds" with constant characteristics (species fixism). It was Darwin, Mayr claimed, who radically improved the situation by perceiving the uniqueness of every individual in every sexually reproducing species. This view became a cornerstone of a new mode of thinking—population thinking—and laid the foundation for the theory of natural selection. Population thinking postulates that biological reality consists of uniquely different entities, while the statistical mean value is an abstraction (Mayr 1982, pp. 46–47).

Population thinking was developed by Darwin and flourished when population genetics emerged in the first third of the twentieth century. Darwinian gradualism along with population genetics cleared the way for creating an evolutionary theory; a revised theory of natural selection. However, even this revised form of Darwinism had been established, a number of scientists refused to accept population thinking, and remained by the archaic teaching of essentialism.

As we have shown elsewhere (Levit and Meister 2006a), Mayr's understanding of essentialism was based, first of all, on nineteenth century essentialism, while essentialism in the twentieth century, which was especially strong in the German lands, was not so tightly connected with Platonism and species fixism. The search for the "hidden nature of things", was a main preoccupation, and was believed to be influential in terms of real biological evolution. In this sense, Rensch proposed an essentialist theoretical system, however, with a minimized and only indirect influence of the "hidden nature of things" on the course of evolution. Until the last days of his scientific and philosophical creativity Rensch was trying to reconcile the concept of stochastic evolution with the idea of determinacy of all processes on all levels from proto-matter up to social-cultural events.

Rensch's combination of anthropocentric progressionism and pantheism with a selectionist world view is certainly in sharp contrast to what other influential selectionists thought. Rensch's major trick was to make the most unimaginable anthropomorphic feature—consciousness—into the imaginary object of pre-organic determined evolution and natural selection. However, the postulation of the pre-phenomenal nature of matter had as a corollary that every particle of perceivable reality became supplied with a tiny particle of intelligence. Because intelligence is now an essential attribute of the Universe, the evolution of the Universe implies a pre-programmed movement in the direction of human-like intelligence. This strongly reminds us of P. Teilhard de Chardin ideas. He saw the Universe as a "closed quantum", where nothing can appear what did not already exist. Teilhard de Chardin also saw biological evolution as a continuation of pre-biological evolution, but Rensch would never go as far as Chardin and create a theology of evolution. To make his concept compatible with the natural-scientific world view Rensch conceals this obviously teleological concept into the concept of universal selectionism, because selectionism is widely accepted to be a respectable "teleology-free" concept. In other words, Rensch's anthropocentric determinism is dressed up as universal selectionism. Yet, what he actually did was to fragment teleology and place it into the interior of things, thus making it subject to natural selection. It is sophisticated and camouflaged, but still a kind of essentialism.

Conclusions

At the time of Rensch's selectionist turn, the strictly empirical arguments in favor of Darwinian selectionism were approximately as convincing as the arguments of the anti-Darwinists, especially saltationists, orthogeneticists (Goldschmidt, Schindewolf) and old-Darwinians like Plate. The arguments of saltationists and orthogeneticists were particularly strong and remained influential in the German lands until the late 1950s (Levit et al. 2008). Rensch balanced the various arguments in favor and against strict selectionism, beginning with firm empirical evidence and ending with general ontological and epistemological claims. Initially a convinced anti-Darwinian, Rensch changed his mind to the end of 1930s and began to advocate the "selectionism + gradualism" model, which he integrated into his theory of systematics and geographical isolation. The latter theory remained unchanged in its foundations throughout his entire life as a theorist, and was adopted into his selectionist evolutionary theory. The idea of reducibility of macro- to microevolution followed Rensch's insights into biological systematics and was developed long before his selectionist turn. The latter brought about the expansion of selectionism and evolutionism and making it into the universal explanatory model covering the entire range of observable phenomena, beginning with the inorganic word and ending with social-cultural events.

Several factors played important roles in his selectionist turn. We need to consider that Rensch, in the first half of the 1930s, was not just sympathetic to neo-Lamarckism and orthogenesis, as were many of his contemporaries. Beginning with his first (1929) book Rensch entered science as a strong theoretician developing his own all-embracing concept of evolution. His criticism of Darwinian selectionism is one of the strongest and most thorough in the first-third of the twentieth century. His Geoffroyism was a well-founded and theoretically coherent concept. Taking these circumstances into account, Rensch's sudden selectionist turn seems to be a puzzle, which cannot be solved by appealing to simple explanations. With all probability the whole complex of factors moved him toward strict selectionism. Certainly, as an empirical scientist he was sensitive to new discoveries in biology, and the triumph of experimental population genetics was a significant stimulus to distancing himself from neo-Lamarckism and orthogenesis. For example, the failure to prove Jollos' experiments on directed mutations, which played a significant role in Rensch's theoretical construction, contributed significantly to his rethinking of the evolutionary model. His own *Drosophila* experiments, which he made in the laboratory of one of the Germany's most brilliant geneticists and molecular biologists, the Russian born biologist Nikolai Timofeeff-Ressovsky, played a significant role in Rensch's selectionist turn. Timofeev-Ressovsky was an immediate pupil of the pioneer of population genetics Sergej Chetverikov (1880–1959) and an important figure in the interdisciplinary and international group of scientists that studied the structure of genes. Intense discussions between Timofeeff-Ressovsky and Rensch (Rensch 1979, p. 76) were certainly an important factor in Rensch's re-labeling as a selectionist.

We believe that the general philosophical background of his theorizing, his general meta-methodological views, also played an important role in Rensch's theoretical development. As becomes clear in his latest works, Rensch argued in favor of the gradual development of the entire world. For him there were no qualitative barriers even between inert and living matter, animals and humans. The evolution of the universe was gradual in all its aspects. Our contention is that that the very idea of gradualness was central for Rensch throughout his life as a theoretician. The Synthetic model of biological evolution allowed Rensch to apply the idea of gradualness, thereby reducing the diversity of evolutionary mechanisms to gradual stochastic microevolutionary events. At the same time he tried to rescue the anthropocentrism that he had acquired from the German naturphilosophical tradition by appealing to another major German philosophical current—monism.

The same concept of gradualness, but applied to the problem of the origin of human intellectual abilities, lead to the concept of panpsychism propagating the idea of gradual development of the psychic side of the universe beginning with the pre-phenomenal stage of matter. Being a Darwinian ("Synthetic") at the purely empirical-descriptive level, Rensch became a controversial philosopher, whose claims went far beyond the conventional "biophilosphies", such as the paradigmatic philosophy of the Synthesis articulated and propagated by Ernst Mayr.

In addition, our analysis of Rensch's theoretical work can be seen as a case study of the problem of the heterogeneity of the Modern Synthesis. The scale of this heterogeneity is, in fact, so significant that the picture of the Synthesis as a unified movement needs to be deconstructed. The idea that the Synthesis is an interdependent body of beliefs covering not only all major branches of empirical biology, but also the general questions of methodology, history, and philosophy of science, collapses in front of such hardly compatible world views as Rensch's and Mayr's. It is also important to remark that all parts of their theoretical constructions were equally important for their arguments in favor of Darwinism for both Mayr and

Rensch. Rensch's holistic theoretical system is in almost direct opposition to Mayr's philosophy, coinciding with it only on the purely phenomenological level and in empirically testable explanations. Indeed, beyond the elementary level of accepting mutation, recombination, geographical isolation, and natural selection as the most important factors of evolution, there is little that unites them considering deep philosophical differences between their systems. This makes the picture of the Synthesis as an amalgamation of closely interrelated theoretical systems very questionable. If it was possible to describe the key "Darwinian" mechanisms of macroevolution from both anti-essentialist and quite essentialist points of view (as a meta-methodology), then either any philosophy is redundant to sound evolutionism or there is a need for much more substantial methodological investigations into the history of modern evolutionary theory.

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