Major Research Traditions in Twentieth-Century Evolutionary Biology: The Relations of Germany's Darwinism with Them

Georgy S. Levit and Uwe Hoßfeld

Abstract Evolutionary theory has been likened to a "universal acid" (Daniel Dennett) that erodes its way into more and more areas of science. Yet, every single branch of biology has developed this context with its own specific characteristics, which, either through hindering or promoting, has affected the national scientific developments in evolutionary biology. We will argue that the Darwinian theories interacted with national research traditions such that the resulting conceptual body represented an amalgamation of a metatheoretical framework with the "purely empirical" theoretical beliefs such as the theory of natural selection. We will demonstrate this using the example of the German research tradition in evolutionary biology. We will analyse this German tradition comparing it to other major traditions in evolutionary biology such as the English- and Russian-speaking evolutionism. The problem of specific influences constituting the German, English-language (Great Britain and the USA), and Russian-language context of the first and the second Darwinian revolutions will be addressed. In addition, we will introduce a concept of "metaparadigm" reflecting the specificity of German evolutionary theory at the time of the first and the second Darwinian Revolutions.

Keywords National research traditions in evolutionary biology • German evolutionary biology • Metaparadigms • Johann Wolfgang von Goethe • Ernst Haeckel • Adolf Naef • Hans Böker • Bernhard Rensch

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1 Introduction

Evolutionary biology is a scientific discipline of a special kind (Junker and Hoßfeld 2009; Dennett 1995). Its appearance and development was and is closely related to literary insights, religious world views, philosophies, policies and national psychological peculiarities. All sciences are like that, but evolutionary biology is intertwined especially strongly with its social-cultural surroundings dependent on national intellectual traditions. To grasp such national peculiarities, we have introduced the notion of "metaparadigms" (Levit et al. 2014). Metaparadigms relate to a mental tradition detectable by language use rather than by politically determined national borders. For example, we speak about German-language or English-language evolutionary biology. Metaparadigms are not alike famous scientific "paradigms" of Thomas Kuhn (1922–1996) with their seclusion and revolutionary shifts from one steady state to another (Kuhn 2012). Metaparadigms are rather like "strange attractors" in the chaos theory: "A chaotic system has a strange attractor, around which the system oscillates forever without ever repeating itself or settling into a steady state of behaviour" (Boeing 2016). There are certainly some reservations about this comparison and the most important one being the duration of a system, which in the above definition "oscillates forever". While in the case of social-cultural system, an "attractor" appears at a certain time, where it flourishes and then gradually disappears. There are affinities between "metaparadigms" and the concept of "cultural attractor" as well (Buskell 2017), since a metaparadigm is a transformation pattern effecting scientific evolution. A metaparadigm crystallises due to internal and external influences. With regard to internal influences, we understand research traditions (broadly construed) are brought about by whatever epistemological beliefs that are essential for empirical sciences. External influences, however, may include social-political circumstances and national cultural peculiarities. Here, we concentrate on the "internal factors".

Simplified examples of metaparadigms are the Russian bias towards inclusive interpretations of living systems (organism plus its environment) (Levit 2007). Such a bias tended in Russia towards a cooperation model in the biosciences (Todes 1987), by contrast to an emphasis on competition model in the English-speaking world. In German lands, such a metaparadigm has crystallised around the monistic principle, which appeared in biology long before Darwin and persisted through the first and the second Darwinian revolutions. Monism was tightly coupled with typology, whereas the latter was the logical consequence of the first (in this very case). The objective of this chapter is to reconstruct this "strange attractor" of German evolutionary biology and to contrast it with English-speaking and Russian-speaking national traditions in evolutionary theory.

2 Goethe's Dangerous Idea

Both major figures of the first and the second Darwinian revolutions in Germany, Ernst Haeckel and Bernhard Rensch (1900–1990), regarded Johann Wolfgang von Goethe (1749–1832) as one of their most essential predecessors in biology. Citations from Goethe (epigraphs) introduce Haeckel's seminal Darwinian book *Generelle Morphologie* (General Morphology) (Haeckel 1866) as well as *Natürliche Schöpfungsgeschichte* (Natural History of Creation) (Haeckel 1868), a book written for the general reader. In this, Goethe is placed alongside Darwin and Lamarck as a forerunner of the theory of descent (Hoßfeld and Olsson 2003a). Yet, Goethe was not an evolutionist in a modern sense. What Goethe offered to the subsequent generations of bioscientists was a certain world view and methodology of biological—first, biomorphological—research. In the first half of the twentieth century, both Darwinian and non-Darwinian camps in evolutionary morphology and comparative anatomy appealed to Goethe as an authority and as a source of methodological inspiration. In their turn, debates between both camps shaped the agenda of the second Darwinian revolution in the German lands (Junker 2004; Levit and Meister 2006a, b) (Fig. 1).

In Germany, the very beginning of scientific morphology was closely connected to the name of Goethe (Kanaev 1970). This was one reason amongst others for the University of Jena to award Goethe an honorary MD in 1825. As a "low Church",

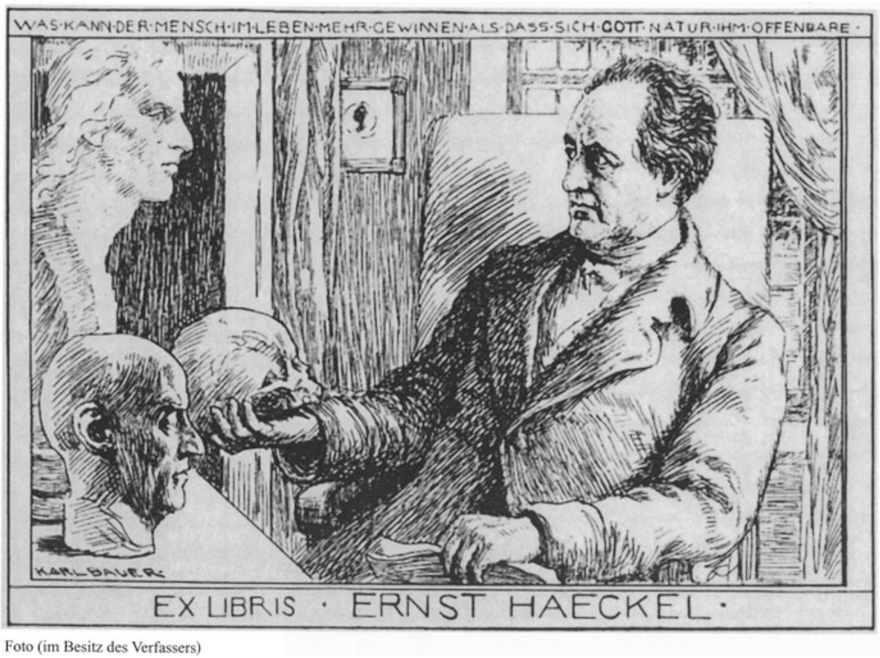

Fig. 1 A drawing with Goethe and Friedrich Schiller, Ex Libris Ernst Haeckel (private collection)

his morphology and comparative anatomy were comparative studies of various organic structures. These studies had also an applied aspect. For example, Goethe championed the establishment of a veterinary school in Jena and frequented, on a daily basis, this school from 1816 until his death (Levit et al. 2016). Remarkably, Goethe tried to involve the veterinary school in fundamental anatomical studies as well, because comparative anatomy was always a priority for him as a science constitutive of his world view. The origin of comparative plant biology can be traced to Goethe as well: Goethe's plant archetype "provided the conceptual basis for much that followed historically" (Niklas and Kutschera 2016) (Fig. 2).

In fact, Goethe looked for differences and similarities between organisms and their parts to arrive at a general doctrine of form, in order to grasp the *idea* of a certain structure by means of empirical studies and scholarly intuition. His methodology was opposed to the mainstream Newtonianism, and arose from the holism of Kant and Spinoza, as well as from Spinoza's hylozoism, especially considering that Spinoza "had dared to fuse hylozoism [. . .] with monist metaphysics" (Bulman and Ingram 2016: 260). In Ernst Mayr's words, "it was a rebellion against the reductionism and mechanization of Newtonianism" (Mayr 1982: 387). The influence of Kant and his critical stance towards Newtonianism can be traced in

Fig. 2 Goethe's discovery: *Intermaxillary Bone*

Goethe's attitude towards teleology. His objections to teleology are summarised in "*Versuch einer allgemeinen Vergleichungslehre*" (an attempt of a general comparative doctrine 1794) (Goethe 2006: 50–55): "In language similar to his later criticisms of a Newtonian doctrine he finds fault with teleology as a traditional concept of the world"[...] (Tantillo 2002: 96–97). Goethe's "living being" did not come about in accord with external purposefulness and its *Gestalt* is not determined by a "conscious primary force" (*eine absichtliche Urkraft*) (Goethe 2006: 51).

Goethe's universe is an interdependent whole, where organic and inorganic are tightly interlocked. This concept is less metaphysical than a contemporary biologist could expect. Goethe's fish exist in the water and this means the water gets its form and functions within a certain environment. The idea that humans are nature's final purpose is alien to Goethe as well (Tantillo 2002: 99), since the picture he offered was a dynamic one. For example, in describing plants Goethe attempted to reconstruct the ultimate conformation (*Gestalt*) of nature hidden behind the observable. This was the ultimate goal of his structuralist method (Richards 2002: 440, 490). His morphology as a "high Church" had as its subject a moving, emergent and disappearing Gestalt: "The doctrine of Metamorphosis is the clue to all signs of Nature [Zeichen der Natur]" (cited and translated from Jahn 1998: 279). For Goethe, morphology was a fundamental enquiry into the most essential features of life and ultimately of the universe. The "high Church" methodological principles guided empirical research and principles of the "low Church".

Goethe's structuralism followed his concept of the morphological archetype (Williams and Ebach 2008: 29–30), which connected both "high Church" and "low Church" principles. The archetype is, for him, an ideal structure (*Bauplan*) of an organism partly expressed in the basic elements of real organismic organisation: "Thence appears a proposition about an anatomical type, a general entity, which covers (as far as possible) the structures (*Gestalten*) of all animals and allows to specify each animal in a certain system (*Ordnung*)" (Goethe 1795). The search for a vertebrate archetype resulted, for example, in the discovery of the *intermaxillary bone* in man (Goethe [1786] 1988: 111–116). Goethe's intention was to compare various vertebrate "osteological" structures to search for the general vertebrate archetype: "Goethe tried to reach a clear idea of the vertebrate archetype not only from wide induction but also from a study of function. A bone which is not only present in most vertebrates but also obviously serves a very important function is likely—for both these reasons—to belong to the archetype" (Wells 1967). The "archetype" (*Der Typus*) was, for Goethe, a "main thread" running through the labyrinth of Gestalts, a general scheme to be found because of empirical generalisations. In the works of the 1790s, devoted to the structure of animals, Goethe put forward the idea of the archetype as a pattern to be used in comparative morphology, but most importantly he saw the archetype as "a dynamic force actually resident in nature" (Richards 2002: 440), as a potentiality: "... an anatomical archetype will be suggested here, a general picture containing the forms of all animals as potential, one of which will guide us to an orderly description of each animal. [...] The mere idea of an archetype in general implies that no particular animal can be used as our point of comparison; the particular can never serve as a measure for the whole" (Goethe [1794–1795] 1988: 118).

As an epistemological aspect of his morphology, Goethe advocated a cognitive method, which he described in a short essay, *Judgment through intuitive perception* (Goethe 1988: 31–32). There, Goethe undertook a short critical analysis of Kant's thesis that human cognition is restrained by the "discursive judgement" (logical, analytical thought) as opposed to intuitive "viewing of a whole to the parts". In other words, Goethe claimed that "intuitive perception of a whole is a valid scientific method" (Heitler 1998: 65). In *A Study based on Spinoza*, Goethe abandoned empiricism and emphasised that a living thing must be measured by its own gauge. Its essence is spiritual and cannot be found through the senses (Goethe 1988). Goethe's morphological studies certainly contained more than the aspects described above, but they are crucial for our purposes. All these parts are interconnected. Thus, the search for an archetype presupposes the use of intuitive perception, and the presence of the divine in nature was an immanent part of experience. At the same time, Goethe's comparative morphology wasn't only a "Faustian" project aimed at the cognition of the final causes of the Universe, but also an applied science. Goethe himself saw this site as a place for conducting research of both practical and theoretical relevance (Levit et al. 2014).

To summarise, Goethe proposed three methodological principles, which became pivotal for the subsequent German-language evolutionary biology:

1. The first principle was a typological thinking, which Ernst Mayr unfairly equated with essentialism (Winsor 2006; Levit and Meister 2006b). The cornerstone of the typological method was the concept of type as an abstract pattern representing a certain class of phenomena and embodying the norm of this class. The primary objective of pure typology was to create classification systems for living organisms based on structurally explicable (morphological) characters without references to phylogenetic history or causal explanations. At the same time, the typological method, as it is, was quite compatible with the idea of evolution. In other words, a conflict between typological thinking and evolutionary idea was neither a direct nor an inevitable logical consequence of typology.
2. The second major methodological belief Goethe coined was the monistic principle. Goethe never used the term, and he was not a monist in a Haeckelian sense, but within German science history ultimately, it was not Spinoza but Goethe who established a unified view of nature, claiming the unity of nature and God (Kleeberg 2005: 246). The hylozoistic bias of German monism can be traced back to Goethe as well.
3. The third principle championed by Goethe, and highlighted here, was holism, which appeared in both poetic (Goethe 1950: 157) and scientific writings (Meyer-Abich 1949). Goethe's holism was especially inspirational for non-Darwinian biological thought between the second half of the nineteenth and the first half of the twentieth century. As Bernhard Rensch noted: "At the time this idea of wholeness and the allied conception of 'Gestalt' have misled

scholars into inadequate and occasionally almost mystical utterance. Many have sought support from Goethe's words: [...] *No time and no power dismembers Moulded Form which Life develops*" (Rensch 1972: 42).

These principles determined the paths of German evolutionary biology by offering a logically coherent "metaparadigmatic" construction. Yet, the way these principles were applied within Darwinian and non-Darwinian traditions were different.

3 Riot in Goethe's Garden: First Darwinian and Non-Darwinian Revolutions in Germany

It is not our intention here to fully reconstruct the history of Darwinian and non-Darwinian revolutions in Germany and elsewhere (compare: Bowler 1988, 2017). We are going to mention a few crucial figures of the late nineteenth and early twentieth centuries with the objective of demonstrating the crucial influence of Goethean principles on both Darwinian and non-Darwinian camps (which were, at that time, difficult to distinguish).

Haeckel was certainly the most prominent champion of early Darwinism in Germany (Hoßfeld 2016a, pp. 146–180). Quite soon, after the publication of Darwin's seminal *On the Origin of Species* (Darwin 1859), Haeckel began with the serious research along these Darwinian lines. It is now 150 years ago that Haeckel published his first major scientific work, *Generelle Morphologie der Organismen*, in 1866 (Haeckel 1866; Hoßfeld 2016b). Here, he, for the first time, started to formulate his Biogenetic law, which he later developed further in a monograph on calcareous sponges (Haeckel 1872). Neither *General Morphology* nor the calcareous sponges monograph were ever translated into other languages and reached a limited audience even in the German-speaking lands (Olsson et al. 2017). The popularisation of Haeckel's ideas followed in 1868 when a collection of lectures that he had held at Jena University (where he was the first professor of zoology) were published as *Natural History of Creation* (Haeckel 1868). This popular science book became a bestseller and was also translated into many different languages (Hoßfeld 2010, 2016a) (Fig. 3).

The *Generelle Morphologie der Organismen* consists of a first volume called "The General Anatomy of Organisms" and a second volume called "General Developmental History". The subtitle is *General principles of the organic form-science, founded mechanically through the theory of descent as reformed by Charles Darwin*. The first volume was dedicated to Haeckel's teacher, the anatomist Carl Gegenbaur (1826–1903), and the second volume to the "founders of the theory of descent", Darwin, Goethe and Lamarck. This book is the key to Haeckel's later work, its goal being to apply Darwin's theory to biology in general but especially to morphology. Haeckel presents here his first ideas on the relationship between ontogeny and phylogeny and introduces a system of the existing groups of

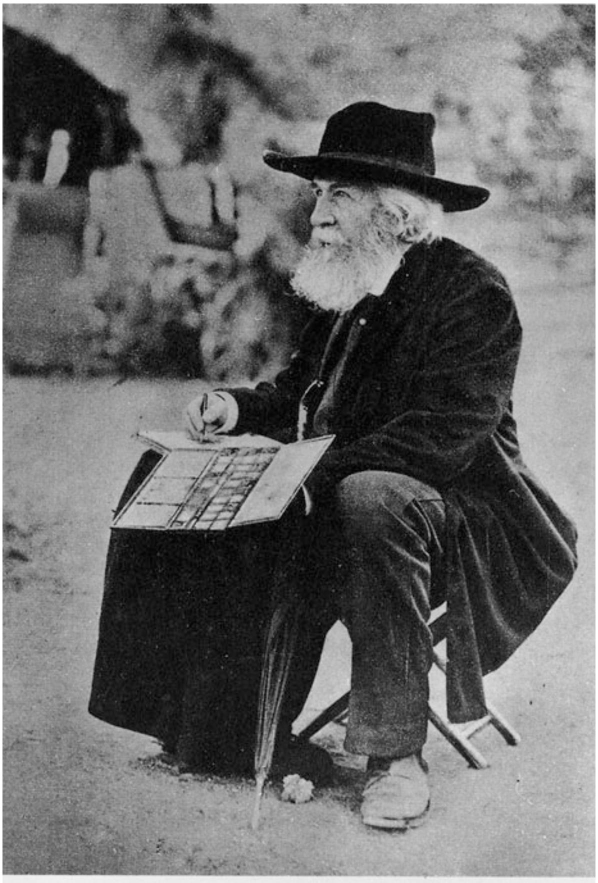

Fig. 3 Ernst Haeckel sitting on the beach of Rapallo and painting, winter 1903/1904 (Archive of the Ernst Haeckel House, Jena)

organisms based on genealogy rather than the old typological or idealistic concepts (Hoßfeld et al. 2016).

Another important aspect of the book is Haeckel's attempt to establish a promorphology—a general theory of basic forms—in the first volume. The second volume can be viewed as the first attempt to establish evolutionary morphology and evolutionary embryology as new fields of research. In the seventh "book" (one chapter within the second volume), Haeckel also formulates his ideas for a biological anthropology based on Darwin's theory of evolution. In Haeckel's view, evolution is a universal phenomenon affecting everything from inorganic matter to man. He believed in the unity of body and soul and the unity of spirit and matter. This monism guided Haeckel's work from the *Generelle Morphologie* to his last book on *Crystal souls* (Haeckel 1917).

Monism and evolutionary theory were for Haeckel parts of the same research program labelled the "monistic doctrine of evolution" (*monistischen Entwicklungslehre*). At the core of the monistic world view was the idea that "all sciences exploring humans and their soul activities [and especially so-called humanities] ... as well as special fields of zoology can be interpreted as natural sciences" (our translation from Haeckel 1904: 48). The strong connection between the concepts of evolution and monism can be seen on an example of Haeckel's work *Monism and the Link between Religion and Science. The Creed of a Natural Scientist* (Haeckel 1892). In this printed lecture, Haeckel confessed that "our monistic idea of God" is compatible with natural sciences and recognises "the spirit of God on all things"; God cannot be seen as a "personalised being" anymore, i.e. "an individual with a constrained spatial and temporal extension" (Haeckel 1892). Furthermore, Haeckel claimed that "*the Truth, the Good, and the Beautiful* are the three noble divinities before which we kneel" (our translation, original italics, Haeckel 1892: 35–36). There will be new altars built in the twentieth century, Haeckel argued, to celebrate the "trinity of monism" (Nöthlich et al. 2006; Weber and Hoßfeld 2006) (Fig. 4).

The affinity of Haeckel's monistic world view to Goethe's conceptual heritage is easy to see: "Firstly, it was Goethe whose *Naturphilosophie* served as an interpretive pattern within which Haeckel moves; it is not an accident that his *General Morphology* and each of its chapters are introduced with quotes from Goethe" (our translation from Kleeberg 2005: 114). There were typological elements in Haeckel's doctrine as well. In the second half of the nineteenth century, the

Fig. 4 Entry of the Phyletic Museum in Jena (1910) with a handwritten note by Haeckel. One can see a Goethe citation on a ceiling ledger (1908): "Wer Wissenschaft und Kunst besitzt, hat auch Religion, wer jene beiden nicht besitzt, der habe Religion" (Who science has and art he has religion too, who neither of them owns religion is his due) [Archiv des Ernst-Haeckel-Hauses, Jena]

theoretical landscape of morphology and evolutionary theory was dominated by the Jena school, i.e. by Haeckel and his senior friend Carl Gegenbaur (1826–1903). They succeeded in moving the centre of gravity in morphological research to comparative phylogenetic studies (Hoßfeld and Olsson 2003b). At the same time, their concepts appear contradictory from the modern viewpoint. Gegenbaur failed in making the methodology of evolutionary morphology either consistently evolutionary (historical) or consistently Darwinian. Although the results of his research were presented in phylogenetic terminology, the way he posed the problems was significantly typological (Starck 1965; Coleman 1976). Haeckel's Darwinism was accompanied by a strong typological bias as well (Levit and Meister 2006b; Hoßfeld 2010). Thus, Haeckel as well as Gegenbaur along with their direct successors failed in creating a consistent evolutionary morphology. "Typological thinking" survived in their concepts. As Di Gregorio suggested for Haeckel: "The old wolf had survived in sheep's clothing" (Di Gregorio 1995). Haeckel's famous embryos can serve as an example. As Hopwood explained: "Haeckel's synthesis recalls Goethe's much more ambitious intuition of the 'original plant' from accumulated observations, and Haeckel, who with a bit more talent might have become an artist, was as strongly committed to aesthetic judgment in science" (Hopwood 2006).

Haeckel's "oecologie" can be interpreted as a by-product of the revolution in biology he began in 1866 with his *General Morphology* (Kutschera 2016). "Oecologie" was for him a branch of physiology replacing the tasks and subject matter of a discipline formerly known as "economy of nature". Insofar, Haeckel successfully re-introduced the research programme of *Naturgeschichte* into his post-Darwinian monist project. The holistic attitude of Alexander von Humboldt (1769–1859) certainly influenced Haeckel: "Haeckel similarly emphasized a unique form of holism, describing the unity of nature in his philosophy of monism" (Grim and Tucker 2014: 65). To this end, Haeckel created his pro-Darwinian theoretical system along the lines of Goethe's methodological principles.

Yet, German non-Darwinians saw themselves as Goethe's disciples as well. Sometimes they were even more explicit in advertising their affinity with his ideas. At the core of non-Darwinian currents in Germany was an alternative vision of morphology. An outstanding German morphologist, Dietrich Starck (1908–2001), argued that after the death of Gegenbaur, in 1903, comparative anatomy in Germany began to fade (Starck 1977; Hoßfeld and Junker 1998, 1999). In addition, Ghiselin pointed out that morphology took no real part in the Evolutionary Synthesis and existed in "another world" in relation to the rest of biology (Ghiselin 1982: 181). Yet, the "failure" of morphology was a "failure" only from the retrospective standpoint of the Evolutionary Synthesis, which asseverated the triumph of Darwinian (historical) method (Ghiselin 1969). In contrast, from the structuralist viewpoint it was a time of rebirth and the (re)emergence of a "true" idealistic methodology, which at that time seemed to represent an effective alternative to the self-contradictory evolutionary morphologies (Rieppel 2011, 2012, 2016; Rieppel et al. 2013). In the German-speaking world, idealistic morphology had a great influence during the whole first half of the twentieth century and to a certain extent even after the Second World War. This differed substantially from the situation in Anglo-American morphology (Reif 1983). All idealistic morphologists proceeded from the same initial idea that the organism is a structural phenomenon and the purpose of comparative morphological studies must be an exact mental reconstruction of the fundamentals, the typical elements of this structure.

The first comparative-morphological theories were clearly based on the typological-teleological methodology and this made possible not only morphological but also physiological studies as well. In the early twentieth century, the theoretical landscape experienced such a serious influence of typologists, especially in morphology and paleontological studies, that one can talk about the Renaissance of the idealistic morphology in the German biological sciences (Levit and Meister 2006b). Almost simultaneously several biologists declared themselves to be adherents of typology. However, as distinct from the early typology, this new movement, which became known as "idealistic morphology", consciously opposed typological method to the method of evolutionary morphology. Correspondingly, they stood in opposition to Darwinism. This movement was represented by Edgar Dacqué (1878–1945), Wilhelm Troll (1897–1978), Wilhelm Lubosch (1875–1938), Adolf Naef (1883–1949), Otto H. Schindewolf (1896–1971), Adolf Remane (1898–1976) and many others (Rieppel 2011, 2012, 2016; Rieppel et al. 2013; Williams and Ebach 2008). At the same time, idealistic morphology hardly represented a kind of methodological monolith opposed to the Darwinian evolutionary morphology (Starck 1980). All of them followed the basic principles of typology but interpreted the results of typological classification differently (Levit et al. 2008a; Levit and Meister 2006b). There are also examples of non-Darwinian, but not primarily typological theories, explicitly referring to Goethe as their inspiration. One such theory was a neo-Lamarckian holism of the German anatomist and zoologist Hans Böker (1886–1939) (Fig. 5).

In 1924, Böker wrote a paper entitled *Begründung einer biologischen Morphologie* (Justification of Biological Anatomy), where he declared his Lamarckian research programme by stating that species "vary before our very eyes by means of inheritance of acquired features" (Böker 1924: 20). Böker, like many biologists of his time, believed he could create a new "evolutionary synthesis". He was aware of the mutationist and selectionist research programmes but maintained that they were unable to deliver the whole truth (Böker 1937: iv; Hoßfeld 2002) (Fig. 6).

Böker was opposed to the search for "separate features" and proposed the holistic research programme combining idealistic morphology, genetics, evolutionary morphology (Lamarckian version), functional explanations, ecology and even ethology (Hoßfeld 2002). He called his doctrine "comparative biological anatomy" and proceeded from the assumption that the organism is a kind of "construction" that consists of parts while being confronted with its environment. In our context, it is important to note that Böker saw himself as part of a tradition greatly influenced by Goethe (Böker 1932). Furthermore, later representatives of German holism such as Adolf Meyer-Abich (1893–1971) fully realised the role of Goethe for the growth of holistic methodology (Meyer-Abich 1949, 1970). In summary, all idealistic

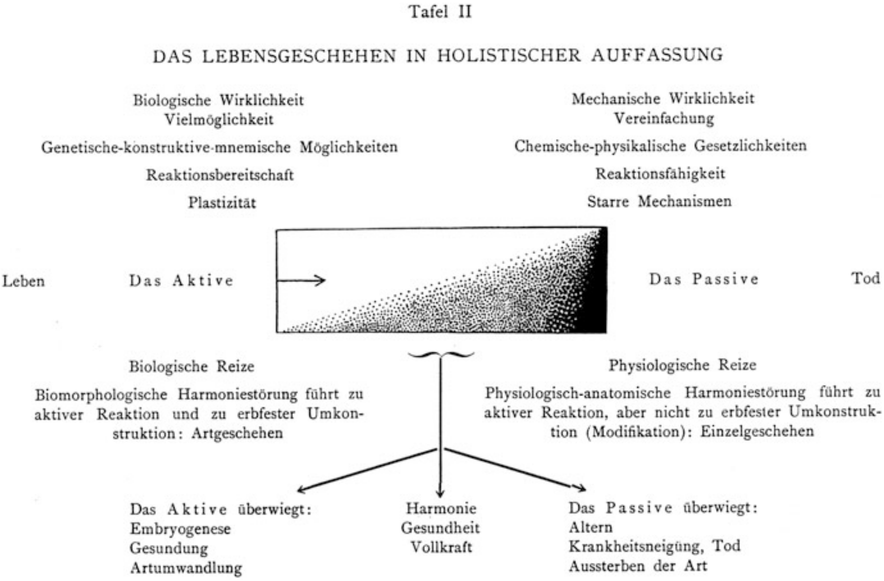

Fig. 5 The scheme by Hans Böker representing the life processes from the holistic viewpoint (from: Böker, H.: Form und Funktion im Lichte der vergleichenden biologischen Anatomie. Folia Biotheoretica 1, Ser. B: 27–41, hier S. 38, Tafel II). According to Böker, a new scientific discipline "comparative biological anatomy" would breathe a new life into the entire anatomy and, ultimately, into biology by bringing into account not only phylogenetic research (genesis) but life appearances along with environmental conditions

Fig. 6 Portrait of Bernhard Rensch (1954) given as a gift to Gerhard Heberer in 1960 (private archive of U.H.)

morphologists explicitly referred to Goethe's principles as the source of their inspiration. Holists, like Böker, saw themselves as Goethe's disciples as well. Considering the influence of Haeckel's version of Darwinism in German lands, one can say that both Darwinian and non-Darwinian pre-Synthetic evolutionary currents were under strong influence of Goethean ideas.

4 Second Darwinian Revolution in German Lands and Its Specificity

The growth of the Evolutionary Synthesis in Germany is a complex topic. Thomas Junker in his seminal tome *The Second Darwinian Revolution* (2004) names thirty biologists who directly influenced the growth of the Modern Synthesis in Germany. Here, we pick up on two names characteristic for both the "evolution" of evolutionary theory and our specific objectives. Ludwig Plate (1852–1937) was one of the most influential pre-Synthetic (but post-Haeckelian) Darwinians (Levit and Hoßfeld 2006), whereas Bernhard Rensch was the major "architect" of the Modern Synthesis in German lands (Reif et al. 2000; Junker and Hoßfeld 2009). The choice of Plate is not an accident. Plate was not only Haeckel's immediate successor in Jena but also the greatest influence on the early Bernhard Rensch (1900–1990). For example, in the first edition of Rensch's most crucial "synthetic" book, *Neuere Probleme der Abstammungslehre* (Evolution above the Species Level) of 1947, Rensch cited his fellow "synthetic Darwinian" Ernst Mayr only five times in contrast to 23 references to Plate. Even Darwin, with 19 references, appears behind Plate in this central "synthetic" book by Rensch. In the late third edition, Rensch (1972) increases Mayr's citations to 14, but Plate is still in the lead with 18 references. Plate's example shows as well how difficult it was at that time to distinguish "proper Darwinians" from "non-Darwinians" (Delisle 2017).

Both Plate's empirical and theoretical works had an enormous impact during his lifetime and are still cited in the morphological literature (e.g. Reynolds 2002). He was translated into Russian early on (Plate 1928). Plate campaigned for a revival of the "original Darwinism" (so-called old-Darwinism) combining selectionism with neo-Lamarckian ideas and was seen by many contemporaries worldwide as a proper advocate of Darwinism (Levit and Hoßfeld 2006; Hoßfeld and Levit 2011). An American evolutionary biologist like Vernon Kellogg (1867–1937) claimed in *The American Naturalist* that Plate "takes the real standpoint of Darwin" (Kellogg 1909). A prominent Russian biologist, geographer and anti-Darwinist Leo S. Berg (1876–1950) saw Plate as his main scientific opponent (Berg 1926). The American palaeontologist Henry F. Osborn (1857–1935), who sought a compromise between selectionist and neo-Lamarckian methodologies, likewise honoured Plate with the title "prominent selectionist" (Osborn 1926). Another of Plate's contemporaries, the Swedish anti-Darwinian historian of science Erik Nordenskiöld (1872–1933) claimed that Plate's *Selektionsprinzip* (1913) contains "all that can be adduced in modern times in defence of the old Darwinism. And as its champion Plate has done a great service, thanks to his wealth of knowledge, his strong convictions, and his honesty" (Nordenskiöld 1928: 572).

Even from our contemporary view, "old-Darwinism" in its fully established and explicit form cannot be reduced to any other theoretical school. The specificity of this theory lay in combining the "standard" Darwinian factors of evolution (mutation, recombination, geographic isolation, natural selection) with the neo-Lamarckian and orthogenetic mechanisms in order to define the exact role of all these mechanisms in evolutionary process proceeding from the whole complex of biosciences including genetics. Old-Darwinians legitimately insisted that they follow the initial ideas of Darwin, who assumed some roles for Lamarckian mechanisms as well as for the auxiliary hypothesis of constraints. The very idea of combining various evolutionary mechanisms was widespread at that time within various cultural contexts (see Loison and Herring 2017).

In addition to Darwin, Haeckel and himself, Plate counted Richard Semon (1859–1919), Wilhelm Roux (1850–1924), Richard von Hertwig (1850–1937), Fritz v. Wettstein (1895–1945), Berthold Hatschek (1854–1941), Jan Paulus Lotsy (1867–1941), Franz Weidenreich (1873–1948) and the future "co-architect" of the Evolutionary Synthesis, Bernhard Rensch, amongst the old-Darwinians. According to Plate, old-Darwinism exactly followed the initial ideas of Darwin while at the same time adapting and processing all healthy and empirically verifiable scientific achievements. Plate aimed to combine all fruitful theoretical approaches (Lamarckism, selectionism, orthogenesis) with the most innovative field of experimental biology. The core of Plate's evolutionary theory can be grasped into two theses:

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

In Plate's later works (Plate 1932–1938), we find all the basic factors of evolution later adapted by the Evolutionary Synthesis. Thus, Plate claimed that random mutations and recombination deliver the bulk of raw material for evolution. Natural selection and geographical isolation perform a major role in evolution (Plate 1933: 1045). Also, what is now known as "population thinking" is of great importance for Plate as he analyses the "laws of populations" with some mathematics (Plate 1933: 1047–1052). Yet, Plate also admitted other evolutionary mechanisms going beyond the basic tenets of the Synthetic Theory of Evolution. Plate accepted both macro- and directed mutations, orthogenesis and the inheritance of acquired characters. As to Plate's general "philosophical" standpoint, he "distanced himself from what he saw as the atheism and antireligious politics of monism, but not necessarily from the scientific agenda", Gliboff argues. Plate "continued to consider himself a monist, but emphasized a unity of nature that could include aspects of the divine and need not entirely exclude his Christian and Germanic identity" (Gliboff 2012).

The same strategy of combining up-to-date evolutionary biology with the monist methodology was applied by Bernhard Rensch. Towards 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) (Levit et al. 2008b; Delisle 2008). He contributed to the "Darwinisation" of biological systematics through the criticism of various anti-Darwinian movements in the German lands, but more importantly he promoted a Darwinian macro-evolution in accord with the principles of gradualism (Reif et al. 2000; Junker and Hoßfeld 2009). In the course of time, Rensch's version of the STE developed into an all-embracing metaphysical conception based on a kind of Spinozism situated within the same tradition as Goethe's hylozoism and Haeckel' monism.

Most astonishing in Rensch's case is the continuity in topics, methodology and empirical generalisations, despite the shift in his views from the "old-Darwinian Synthesis" to the "Modern Synthesis" (Delisle 2008). This continuity in Rensch's theoretical system can be explained, in part at least, by the guiding role of general methodological principles, which underlay his entire system, explicitly or implicitly. For example, Rensch's "philosophy" became an asylum for the concept of orthogenesis which Rensch (as well as other champions of the STE) 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 monist philosophy combined with a supposedly naturalistic evolutionary biology. At the core of Rensch's "philosophy" is the idea that the only indisputable objects for a researcher are his or her 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 extra-mental reality, which appears to be visible and testable phenomena [Gestalt]. Thanks to physics, Rensch continues, 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 (1862–1950), 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 psychophysiological epistemology (e.g. Ziehen 1898), a philosophical current akin to Haeckel's monism. Rensch did not just share the philosophy of Ziehen; he showed it was absolutely crucial for his whole theoretical system. Rensch labelled Ziehen's epistemology a "monistic principle" (Rensch 1971: 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, thus representing the very foundation of the Universe and providing it with the elements of an individualised whole. In other words, monism implies elements of holism. Rensch was looking for this type of universal principle (Levit et al. 2008b).

Along these lines, Rensch created his concept of *psychophysical identism* (Rensch 1988: 36). Already in the first edition of his major "synthetic" publication, the *Abstammungslehre* (Rensch 1947), written during the Second World War, Rensch "presented this world view for the first time", although at that time Rensch employed the awkward term *hylopsychism*. Again, psychological identity was not for Rensch a "philosophy" supplementing his biology; rather, it is the core of his world view and his scientific methodology. Rensch championed an all-embracing evolutionism and selectionism. Natural selection was for him the major source of lawfulness in evolution and it was "possible to characterize evolutionary regularities [*Regelhaftigkeiten*] as laws [*Gesetzlichkeiten*]" (Rensch 1991: 107). Considering that natural selection continuously selects the better variants, evolution appears to be channelled into tight pathways, i.e. inevitably proceeds in certain directions. Here, we can observe a long echo of Ludwig Plate's concept of "orthoselection". Although elementary evolutionary events appear to be random, evolution towards human intelligence and evolution of intelligence itself takes place along invisible rails.

Rensch's view on the inevitability of evolution towards human-level intelligence is in sharp contrast to most other leading Synthetic and "post-Synthetic" 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: 133). Rensch, on the contrary, insisted that the origin of humans from ape-like ancestors "was presumably a lawfully determined [*gesetzmäßig bedingter*] process" (Rensch 1991: 225). He did not reduce his concept of "lawfulness" to vulgar determinism and instead coined 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. These overlap and interact, bringing about seemingly stochastic events, which, in fact, can be explicated in terms of lawful processes. In other words, for him randomness does not play the central role in organic and cultural evolution, such that life would certainly occur on other planets with comparable chemical-physical conditions and evolve in a comparable way to evolution here on Earth (Rensch 1991: 108).

The combination of anthropocentric progressionism and pantheism championed by Rensch along with selectionism was certainly in sharp contrast to what other influential selectionists thought. Rensch's major trick was to make 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. As 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. To make his concept compatible with the natural-scientific world view, Rensch concealed this obviously teleological concept into the concept of universal selectionism because selectionism was already 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 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 typology very close to Mayr's notion of selectionism: there is an "interior of things" (to use the expression of Teilhard de Chardin), the hidden side of evolution getting explicit on its last evolutionary stages. Finally, as a proponent of a "cosmic view of evolution" (Delisle 2009), Rensch championed a kind of holism as well. Overall, Rensch developed his theoretical principles along the methodological principles developed by Goethe and Haeckel, although on a qualitatively different theoretical level.

5 Comparative Remarks and Conclusions

Leading German evolutionists were persistent in applying the three basic principles introduced by Goethe—Monism, Typology and Holism—to their theoretical systems. These principles were not unknown in Russia and English-speaking countries (see Esposito 2017) but did not play such a prominent role as they played in the German lands. It was a set of interconnected methodological principles that survived over centuries despite of political revolutions and paradigmatic shifts in science. German-, Russian- and English-speaking traditions were literally "infected" by holistic thinking, but the roots, theoretical context and, correspondingly, methodological consequences of holism were different in different language realms. For example, Russian holism was initially tightly coupled with both the Darwinian and non-Darwinian traditions but ultimately allied with the mainstream Darwinism. The roots of Russian holism are in the environmental thinking, in approaching organisms as parts of ecosystems. One can detect this bias beginning with early Darwinians and ending with mature representatives of the Modern Synthesis such as Schmalhausen and Timofeeff-Ressovsky (Levit et al. 2006; Levit and Hoßfeld 2009). Russian holism is an outcome of empirical studies, which demonstrated close connection between organisms and their environments. An "environmentalist holism" was characteristic for both Darwinian and non-Darwinian doctrines. Leo Berg's "Nomogenesis" accompanied by the theory of landscape zones may serve as an example. In its extreme manifestation, Russian holistic tradition brought about the biosphere theory. Note that there is only one biosphere on Earth and, maybe, in the whole universe and so in describing the biosphere and its evolution, one is not in the search for a certain "type" (Levit and Hoßfeld 2005). German evolutionary holism (Haeckel, Meyer-Abich, Böker, etc.) takes its roots in typological thinking developed by Goethe. The objective of the German-language tradition was to describe essential morphological features of a certain class of phenomena, i.e. a type (archetype). This explains why German holism in German lands allied with non-Darwinian theories and ultimately developed into a self-sustaining theoretical current in biology.

The second German bias in evolutionary biology, monism, was well known in both Russia and English-speaking countries but found a few followers.

Characterising Haeckel's "Monistic Creed", his contemporary, a zoologist of Stanford University, David Starr Jordan (1851–1931) wrote in *Science*:

> I have myself not the slightest objection to 'Monism' as philosophy. As a dogma it is certainly more attractive than many others which have been brought like lightning from the clouds, as a stimulus to creeping humanity. My objection lies against the use of the divining rod in connection with the microscope. These instruments do not yield homologous results (Jordan 1895).

Jordan's publication was a response to the book review published in *Science* by William Keith Brooks (1848–1908) of Johns Hopkins University under the title *The Tyranny of the Monistic Creed*. The latter claimed that "the monistic confession of faith has led to the discounting of the possibilities of future discovery, and that it has thus obstructed progress" (Brooks 1895). Jordan and Brooks expressed the critical position of many American natural scientists towards monism. Monism had even less currency in Britain:

> Here the term was used by philosophers and psychologists in the sense of mind and matter being two sides of the same coin. But this usage does not seem to have been taken up outside certain academic circles, and many associated debates over religious issues took place without the actual term 'monism' being used (Bowler 2012).

Certainly, monism had some influence within US American and British philosophy. A German–American champion of panpsychism, Paul Carus (1852–1919), the founding editor (from 1888 till 1919) of the journal *The Monist*, generated discussions around monism in the English-speaking world. Yet, Carus cannot serve as an example of a direct influence of monism of the Haeckelian kind on mainstream biological doctrines. As Peter Bowler summarised it:

> Haeckel's naturalistic monism was certainly discussed in Britain and America, especially following the translation of his *Riddle of the Universe* in 1900. But one gets the distinct impression that even some of those who discussed it sympathetically wanted to divorce their version of monism from Haeckel's strident naturalism (Bowler 2012).

The concept of monism, Bowler concludes, is not a very useful category for analysing British intellectual life around 1900 (Bowler 2012). Monist currents in Russian evolutionary biology were arguably even less visible. Igor Polyanski (Polyanski 2012) maintains that monism was central for politically relevant philosophical debates in Russia and that Vladimir I. Lenin (1870–1924) devoted his famous *Materialism and Empiriocriticism* (Lenin 1909) predominantly to the criticism of the Russian *empiriomonism* of Alexander Bogdanov (1873–1928). Bogdanov, in turn, was presumably quite familiar with Haeckel's major works; there is no direct evidence that he read Haeckel, but the indirect evidence is compelling (Adams 1989). Yet, the influence of empiriomonism is overestimated. In his *Materialism and Empiriocriticism*, Lenin names Bogdanov explicitly: "I personally know so far of only one empirio-monist in literature—a certain A. Bogdanov".[1] Lenin's criticism of Bogdanov was a reflection on an internal

[1] https://www.marxists.org/archive/lenin/works/1908/mec/four5.htm

discussion of a quite marginal political current (the RSDRP). On further inspection, in the recently published comparative history of evolutionary theory by Edouard I Kolchinsky, there are no references to Bogdanov at all (Kolchinsky 2014).

Despite terminological influences, Bogdanov's empiriomonism is crucially different from Haeckelian monism, since it represented an amalgam of theoretical elements borrowed from Spencer, Haeckel, Ostwald and especially Marx (Krementsov 2011). At the core of Boganov's epistemology is Marxist materialism: "To Bogdanov, the school of Empiriocriticism was not a rejection of materialism but rather its revival. Materialism, he maintained, had lost its original meaning, the concept of matter having shed its sensuous nature and having turned into a vague abstraction" (Bolls 1981).

Including some Haeckel into a theoretical framework was not something extraordinary. After all, Haeckel's major works were translated into Russian and Haeckelian monism was well known and relatively widespread: "By the 1890s, many Russian naturalists had adopted Haeckelian monism as a basic philosophy of their investigations" (Krementsov 2011: 35). The problem, however, is that a large number of these "many naturalists" were marginalised for evolutionary biology or had a status of exotic "visionaries". The panpsychistic monism of the rocket scientist Konstantin Tsiolkovski (1857–1935) can serve as an example. Being a school teacher in a provincial town, he had a few possibilities to influence the Russian intellectual landscape. Besides, a closer look at Tsiolkovski's theoretical heritage shows that his monism, although certainly influenced by Haeckel, differs from it in crucial points. For example, an antireligious motivation of Haeckelian naturalism is plainly incompatible with Tsiolkovsky's deism (Lytkin 2012).

Leading evolutionists such as Alexander Kowalevsky (1840–1901), Elie Metschnikoff (1845–1916) or Kliment Timiryazev (1843–1920) were critical not only of Haeckel's monism but also of Haeckel's speculative theories in general. Haeckel, by contrast, appreciated Kowalevsky's work very much. In his *Anthropogenie*, Haeckel wrote: "The most significant germ histories in the recent time were those of Kowalevsky" (Haeckel 1874: 49). It is astonishing in this respect that both Kowalevsky and Metschnikoff were either indifferent or even hostile to Haeckel and his theories. There was no letter exchange between Kowalevsky and Haeckel as there was between Darwin and Haeckel. The Archive of the Ernst Haeckel House in Jena holds not a single letter to Haeckel, neither from Kowalevsky nor from Metschnikoff, although there are more than 100 letters from other Russian correspondents in the Archive (Hoßfeld and Breidbach 2005). This is even more curious considering that Kowalevsky's younger brother, Vladimir, undertook his doctoral work under Haeckel's supervision (Uschmann 1956) and that Haeckel's Gastraea theory was to a significant extent based on Kowalevsky's data. In the 185 letters from Kowalevsky to Metchnikov, we find only seven short mentions of Haeckel (Gaisinovich 1974).

To summarise, Haeckel's monism, as well as other versions of German monism (such as Ostwald's), was well known in the pre-revolutionary Russia, but its relatively marginal place in Russian evolutionary biology cannot be compared to its centrality in Germany. As to the third Goethean principle (typology), it is well

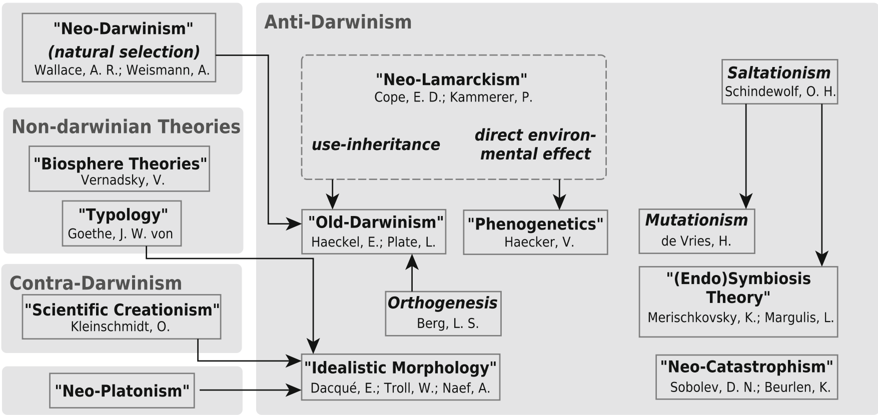

Fig. 7 Scheme: The first decades of the twentieth century became the heyday of alternative evolutionary theories (non- and anti-Darwinian), as they flourished simultaneously in various countries and achieved clarity and conceptual maturity

known that typology under different names (e.g. idealistic morphology) was widespread in German lands before the First World War and even after the Second World War. While English-speaking countries experienced the rapid expansion of the Evolutionary Synthesis, the growth of evolutionary theory in Soviet Union and, partly, in East Germany was distorted by the political repressions associated with the infamous name of Trofim D. Lysenko (1898–1976) and his partisans (Roll-Hansen 2005; Hoßfeld and Olsson 2002) (Fig. 7).

Yet, there was a strong scientific opposition to the Evolutionary Synthesis also in West Germany, which enjoyed all the democratic liberties of the post-war period. Basic principles of the Modern Synthesis became well known in Germany, simultaneously with Great Britain and the USA (Reif et al. 2000). Nevertheless, when Ernst Mayr reported on the "Phylogenetic Symposium" in Hamburg (1956), where he presented the basic principles of the Evolutionary Synthesis, he noted that "all those attending (with the exception of the geneticist de Lattin) argued against the Synthesis" (Mayr 1999). Answering the question "Why then was there so much opposition in Germany?", Mayr gave several reasons. The first reason was the typological or idealistic-morphological tradition, which was in Germany much stronger than in English- or Russian-speaking scientific traditions. The second reason was the "preoccupation of German zoology with phylogeny", which was again connected with the fact that "the students of phylogeny almost without exception adhered to the idealistic morphological philosophy". The third reason was, according to Mayr, the general ignorance of modern genetics by the German biologists, which was again related to the adherence of German morphologists and palaeontologists to the "typological saltationism" (Mayr 1999). In other words, all reasons for the anti-Synthetic resistance in Germany listed by Mayr are ultimately rooted in one and the same theoretical movement: idealistic morphology, which he equates with typology and essentialism.

Alone Mayr's astonishment at the situation in Germany shows that German influence of typological methods in German evolutionary biology was unusually strong. Indeed, already in Darwin's time, typology was not a burning point in British biology: "Because ideal morphology had made so little headway in Great Britain in Darwin's day, Darwin was able to ignore this alternative" (Hull 2010: 135). Idealistic morphology remained barely influential in Great Britain and the USA during both Darwinian revolutions, while it was strikingly prominent in Germany:

> The evolutionary discussions between the German speaking paleontology and biology were interrupted after 1943 [...]. Typological thinking persisted in applied paleontology as well as in systematics and stratigraphy. Therefore there was no reason to study the issue of population genetics. [...] Even after 1945 the German speaking paleontologists continued to exist within a paradigm interpreting evolution as a self-legislating [*eigengesetzlicher*], holistic process. They were unable to change the paradigm (Reif 1999, our translation).

It is not an accident that a prominent historian of German biosciences, Wolf-Ernst Reif (1945–2009), mentioned "typology" and "holism" in one breath. The rigidity of the "paradigm" Reif described was due to the interrelated set of methodological principles highlighted by Goethe, which included typology, holism and monism. In order to emphasise its temporal durability and theoretical complexity, we label this phenomenon a "metaparadigm" (Levit and Hoßfeld 2013).

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