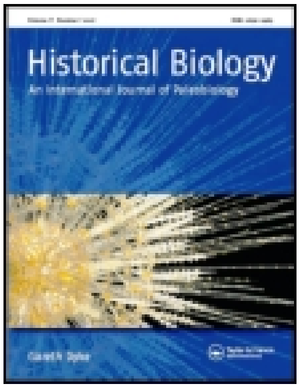


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Wolf-Ernst Reif was an outstanding German paleontologist, who, along with his empirical studies (biomechanics, functional and constructional morphology, etc.), paid significant attention to theoretical issues and the history of his discipline. Reif was a bridge-builder, skillfully synthesising history, theory and empirical studies within German-language paleontology. This paper briefly discusses sophisticated relationships between German paleontology and Darwinism based on the historical studies of Wolf-Ernst Reif. German paleontology did not fully embrace Darwinism until the 1970s. There are several reasons for this. First, alternative evolutionary theories (saltationism, neo-Lamarckism, orthogenesis) occupied a significant segment of the theoretical landscape in the German life sciences. Second, typological thinking persisted in German paleontology after the Second World War. Third, German paleontologists were relatively uninterested in discussing mechanisms of evolution, concentrating instead on reconstructing phylogenetic history.

**Keywords:** Darwinism; German paleontology; synthetic theory of evolution; Wolf-Ernst Reif



## Introduction: evolution and paleontology in Germany

Wolf-Ernst Reif was one of those rare scientists capable of performing cutting edge empirical research while simultaneously investigating the history and methodological foundations of his disciplines, paleontology and functional morphology. Wolf's deep understanding of both the older German-speaking paleontological research tradition and the new Darwinian approach made him an ideal bridge-builder in the situation which developed after the Second World War. From one side, German paleontology did not fully embrace Darwinism until the 1970s, so the establishment of a Darwinian framework within German phylogenetic studies was an urgent task. On the other side, German paleontological tradition was rich in its scope and empirical observations, so it was crucial to preserve its methodological and factual heritage. From the 1980s onward, he was one of the first Darwinians who emphasised the scientific importance of non-Darwinian paleontology. Rejecting the idealistic and vitalist biases of these non-Darwinian models, he nonetheless acknowledged them as early attempts to highlight macroevolutionary phenomena that had been eclipsed by the triumph of the evolutionary synthesis (Schoch, Hoßfeld, et al. 2010; Schoch, Junker, et al. 2010, p. 267). In doing so, Reif acted both as a historian and philosopher of science and as a scientist establishing foundations of his very own science. Thus, Reif was a bridge-builder in a double sense, both in his efforts to bring together German paleontology and Darwinism and in his commitment to historical methods as a necessary tool of theoretical research. The latter was a passion he shared with Stephen J. Gould that led both of them to undertake extensive research (albeit from very different points of view) along these lines.

The primary objective of this paper is to provide an overview of a theoretical climate in German life sciences which sheds some light on the sophisticated relationship between German paleontology and Darwinism. On the basis of Reif's historical investigations[1] and on our own recent studies, we formulate a hypothesis to explain a situation that was unique to the German lands.[2]

One might suppose that paleontologists would be drawn to Darwinism as mice are attracted to cheese. However, the history of evolutionary biology reveals a complicated story. Although Darwin himself appealed to paleontological data in support of his theory of evolution, major figures in the early history of German Darwinism (August Weismann, Ernst Haeckel, Ludwig Plate) were preoccupied with the search for specific mechanisms of evolution, appealing to the paleontological record only to substantiate already established views. Paleontology provided examples and arguments for Haeckel's version of Darwinism, but it did not amend his ready-made picture of evolution with a strong Lamarckian bias. Strict selectionism became rather a rarity among paleontologists. As Reif (1999, p. 180) put it (our translation): 'In German paleontology (as well as in international paleontology) attempts to interpret the fossil record in Darwinian terms ceased at the end of the nineteenth century'.

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For example, the German paleontologist Ernst Koken, who stood in the Haeckelian tradition, wrote at the beginning of the twentieth century that Darwin's 'theory of selection' had few advocates in paleontology. Rather, the majority of paleontologists attached more significance to neo-Lamarckian mechanisms (Koken 1902). Considering that orthogenesis (the concept of directed evolution) and idealistic morphology (based on typological methods) were also extremely influential in German paleontology, there was little space for the theory of natural selection to develop in this theoretical landscape.

Tension between neo-Lamarckian paleontologists and selectionist geneticists became more pronounced as experimental biologists began to formulate their evolutionary studies in relation to the rediscovered genetics. The joint meeting of the *Paläontologische Gesellschaft* and the *Deutsche Gesellschaft für Vererbungsforschung*, which took place in Tübingen in September 1929, highlighted the emerging conflict. The objective of the conference was to overcome contradictions between experimental and historical studies of evolution (Weidenreich 1930, p. 19). Unfortunately, the result of the meeting was just the opposite. As Otto H. Schindewolf reported, discrepancies between positions taken by the two camps (experimentalists and paleontologists) became 'so frustratingly evident' that, ultimately, no solution could be achieved (Schindewolf 1936, p. 1). Franz Weidenreich, Waldemar Weissermel and Edwin Hennig represented the neo-Lamarckians. Harry Federley, Walter Zimmermann and Max Hartmann rejected neo-Lamarckian explanations in favour of some sort of selectionism, although this does not mean that they were Darwinians in a contemporary sense (Hoßfeld 1998, p. 195; Junker 2004). Schindewolf himself advocated a sophisticated concept combining the elements of typology, saltationism and orthogenesis, a scheme that left little place for natural selection. Thus, as Federley (1929) claimed, paleontology and genetics at this time constituted two antipodes within the evolutionary sciences.

Finally, in September 1937, Othenio Abel, a leading paleontologist and advocate of both neo-Lamarckism and orthogenesis, convened one more conference of the *Paläontologische Gesellschaft*, in Göttingen, to discuss 'the current position of paleontology towards major issues of phylogenetic history (Stammesgeschichte)' (compare: *Paläontologische Zeitschrift*, Vol. 20, 1937). The Göttingen conference did not change the impasse. Reif (1999, p. 181) commented on this: 'There was very little knowledge of genetics and population biology in German[3] paleontology both before 1930 and for decades thereafter'.

The early 'synthetic theory of evolution' (STE), initiated by the publication in 1937 of Dobzhansky's seminal book, did little to alter the practice of integrating paleontology into pre-existing theoretical frameworks. While the STE concentrated mainly on unifying genetics and selectionism, one of its canonical co-architects was the paleontologist, George Gaylord Simpson. Yet, as Gould (1994) emphasised, the initial Synthesis denied any theoretical status to macroevolution and 'Simpson did not cash out his insight to paleontology's theoretical benefit because he followed the strict doctrine of the Modern Synthesis.'

In this respect, the situation in the German lands was not unique. The major issue is that there was not just the marginality of paleontology in relation to the Modern Synthesis. There was active resistance to the selectionist agenda due to the influence of scientific non-Darwinian evolutionism and idealistic morphology (typology), which were robust movements in paleontology as it was practised in the German-speaking countries, even quite long after the Second World War. This intellectual framework contributed to the persistence of non-Darwinian thinking in paleontology:

> 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 lawful [eigengesetzlicher], holistic process. They were unable to change the paradigm. (Reif 1999, p. 182)

Consequently, Reif claimed, the Synthesis played little part in German paleontology until the 1970s. In the German-speaking lands, Reif himself contributed greatly to the historical and theoretical reunification of paleontology and Darwinian evolutionary biology. In a series of papers, he (Reif 1983, 1986, 1999; Reif et al. 2000) reconstructed the relationship between paleontology and Darwinism in the German-speaking countries. Already, early in his scientific career in the 1980s, Reif disclosed his intent, admitting that, at that time,

> evolution was still less important in paleontology than in biology. Paleontology had many other practical and theoretical tasks than to provide a model for macroevolution or to consider whether selection theory could be a unifying concept for macro- and microevolution. Hence, a conspicuous scientific revolution, a paradigm shift from internalism to Darwinism (synthetic theory), has never taken place . . . . (Reif 1983, p. 199).

The internalist tendencies can explain the disregard for discussion of evolutionary mechanisms in paleontology, but they cannot give a reason for the persistence of alternative (to strict selectionism) evolutionary theories. Below we offer an explanation for this situation, reconstructing some episodes in the history of German evolutionary biology.

## Darwin, Darwinism and the STE

As a historian of science, Reif was preoccupied with amending the historical accounts of evolutionary biology that had been presented by the architects of STE, especially by Ernst Mayr.

Reif (2001) saw Darwinism as a dynamic and complex theoretical system, consisting of many necessary, equally important, interconnected postulates and numerous auxiliary hypotheses. The difficulty in defining Darwinism is connected with the fact that the theory of natural selection achieved its logical consistency and conceptual maturity decades after Darwin's death. Hence, an appeal to Darwin's own writings is not necessarily the best argument in favour of the Darwinian character of a concept in question. This situation differs from that of theories in physics (which are paradigmatic for philosophers of science) where a quotation, say, from Einstein's theory of relativity would constitute an immediate and strong argument in favour of the 'Einsteinism' of a theory in question. In contrast, contemporary Darwinian schools compete for the prerogative of retrospectively classifying concepts as either 'Darwinian' or 'non-Darwinian'. S.J. Gould's attempts to establish the 'Darwinian' nature of his views are prime examples of this practice (Gould 2002). Competing schools view the history of Darwinism from their own embattled vantage points. This prerogative was initially legitimised by logical consistency with the STE, but subsequent generations of historians of science have significantly refined the initial picture. Reif developed a classification of the history of Darwinism which we introduce below with some clarifications and revisions (Reif 2000, 2001; Reif et al. 2000):

(a) *Classical Darwinism*. This is Darwin's own theory, which pushed forward the very idea of organic evolution and common descent and introduced the principle of natural selection in a broad theoretical context. This encompassed a multiplicity of evolutionary mechanisms including inheritance of acquired characters, direct environmental influence on organisms' heredity, sexual selection and some mutationism (Darwin's famous 'sports'; Darwin 1872). In addition, this initial version of Darwinism incorporated the germs of a concept of evolutionary constraints, which later gave rise to a theory of orthogenesis (Reif 1983; Levit and Olsson 2006). Historians of science disagree about the role of various evolutionary mechanisms in Darwin's explanatory paradigm. For example, Winther (2000) claims that 'Darwin was caught in the logical bind', because any emphasis on the importance of non-selectionist mechanisms of adaptation necessarily decreased the importance of his major discovery: the role of natural selection. In contrast, Ernst Mayr saw no conflict among various evolutionary mechanisms within Darwin's own theoretical system: 'For Darwin inheritance of acquired characters and a direct effect of the environment were compatible with natural selection' (Mayr 1997). Yet, all agree that 'Darwin himself was a pluralist who granted pride of place to natural selection, but also advocated an important role for Lamarckian and other nonselectionist factors' (Gould 1982). The eclectic nature of Darwin's pluralism (he never succeeded in determining the exact role of selectionist and non-selectionist factors) led to the split of classical Darwinism into two rival selectionist movements – old- and neo-Darwinism – determined by the position adopted towards the pluralism of evolutionary mechanisms included in Darwin's heritage.

(b) *Neo-Darwinism versus old-Darwinism*. At the end of the nineteenth century, the Canadian-born English psychologist George John Romanes (1848–1894) recognised the crucial importance of the question 'whether natural selection has been the sole, or but the main cause of organic evolution' (Romanes 1895, p. 1). Answering this question, Romanes opposed Darwin (admitting that natural selection had been assisted by 'subordinate principles') to Alfred Russel Wallace, who along with August Weismann maintained that natural selection should be regarded as the only cause of evolution. To denote 'the pure theory of natural selection to the exclusion of any supplementary theory', Romanes (1895, p. 12) coined the term neo-Darwinism. In the category of 'supplementary theories', Romanes included 'Lamarckian factors' (use inheritance) and the theory of sexual selection. Darwinism, in any form, was to be distinguished from a neo-Lamarckism that assigned higher importance to Lamarckian factors than to natural selection. The original Darwinian line of thinking preserved the priority of natural selection, but combined it with Lamarkian factors, moderate orthogenesis and some mutationism. This 'old-Darwinian' school was initially represented by the 'German Darwin', Ernst Haeckel and later by his successor at the University of Jena, Ludwig Plate.

(c) *The STE* or *the Modern Synthesis* originated in the early 1930s, after a period of 'eclipse' of Darwinism (Bowler 1983) and the associated dominance of alternative (non-Darwinian) theories of evolution. According to Mayr (1999), the Synthesis was completed in 1947, when the period of the so-called 'post-synthesis' began. The STE proposed a logically coherent and empirically well-substantiated theoretical system that incorporated several branches of biology, such as classical genetics, population genetics, systematics, evolutionary morphology, developmental biology and paleontology. Within the STE, 'non-selectionist factors of evolution, especially

> isolation, chance events, and population size are emphasized. Selection is regarded as important, but only as one of several evolutionary factors' (Reif et al. 2000). With all these factors taken into account, the STE succeeded in proposing a convincing theory of macroevolution (Rensch 1947). It advocated a multiplicity of evolutionary mechanisms: in this sense, it opposed the single-factor explanatory paradigm of neo-Darwinism. But, the pluralism of STE was essentially unlike that of Darwin's own theory: the STE proposed an explicit system of 'factors of evolution', constituting a logically coherent and empirically fruitful research programme, whereas Darwin's eclectic pluralism remained speculative and often self-contradictory (Winther 2000). The STE made the hypothetical emergence of a neo-neo-Darwinism (a new single-factor theory) impossible. Presently, the observed 'expansion' or 'extension' of the STE is unfolding along lines that incorporate new evolutionary mechanisms into the existing theoretical framework.

Reif insisted in his historiography on the international character of the Synthesis in all its phases. The Evolutionary Synthesis itself (1930s and 1940s – according to many authors 1937 to 1950) took place simultaneously in all evolutionarily significant cultural regions, primarily in the Anglo-American world, German-speaking countries and the USSR (Junker and Engels 1999; Brömer et al. 2000; Levit et al. 2006; Olsson et al. 2010; Schmalhausen 2010).

Nonetheless, after the Second World War, the synthetic theory was much more prevalent in Anglo-American countries than it was in Germany, France and the Soviet Union. This theoretical rift that can be explained by the persistent influence of alternative (non-Darwinian) evolutionary theories, for ideological reasons in the USSR and the GDR and on other accounts elsewhere outside the English-speaking realm. Below, we outline these alternative theories (Figure 1) and we propose a hypothesis to explain their persistence in German lands.

## Alternative theories of evolution and the history of paleontology

The heyday of the alternative evolutionary theory was the period between the rediscovery of genetics (circa 1900) and the establishment of the STE, which came to dominate the theoretical landscape of the Anglo-American world by the late 1940s. In the USSR, and in East Germany after the Second World War, basic principles of the STE were advocated by such influential figures as Schmalhausen Timoféeff-Ressovsky or Hans Stubbe, but their arguments were overshadowed by those of politically influential Lysenkoists (Hoßfeld and Olsson 2002). In West

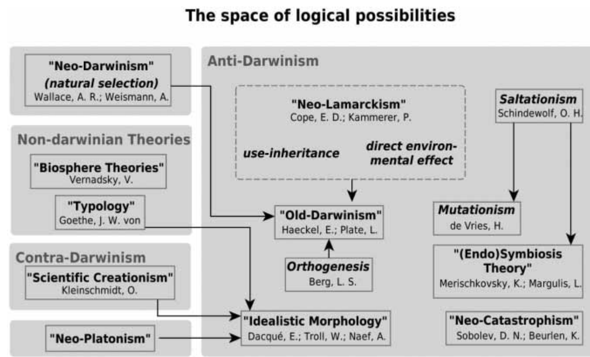


Figure 1. The whole panoply of alternative evolutionary theories imaginable in the first half of the twentieth century. Some of these persisted into the 1950s and 1960s. Neo-Lamarckism, saltationism, typology and orthogenesis played major roles in the discussion of evolutionary mechanisms and were very influential in paleontology. Names in the boxes are prominent proponents of a corresponding theory.

Germany, alternative evolutionary theories persisted, not because of stubborn ideology (as in the East), but primarily because of theoretical inertia within evolutionary biology itself. Apart from the slow reaction time of the discipline, paleontologists were preoccupied with their, no doubt important, empirical studies:

> Paleontologists were right to concentrate on solid, empirical problems of earth science, because whenever a trend spilled over from biology to paleontology it was not a challenge for a rational research project, but was a vague idea like neo-Lamarckism (organisms directing their own evolution by their instincts), the materialism-vitalism dispute or the Nazi idea that evolutionary theory was *undeutsch* and *westlerisch* (Zimmermann, 1948). (Reif 1983, p. 199)

It should be noted that these evolutionary mechanisms were not always mutually exclusive, and only a minority of anti-Darwinians completely rejected natural selection. The issue turned on the relative importance of various mechanisms. For example, the majority of twentieth century Lamarckians combined one or both neo-Lamarckian mechanisms (use inheritance and direct effect of the environment) with natural selection and orthogenesis. Influential advocates of neo-Lamarckism include the Austrian paleontologist, Othenio Abel (1875–1946); the German experimental biologist, Paul Kammerer (1880–1928); the American paleontologist, Edward D. Cope (1840–1897); the pioneer of experimental physiology in Sweden, Nils Holmgren (1877–1897)[4]; as well as the German anatomist and zoologist, Hans Böker (1886–1939). Future co-architects of the Synthesis, Bernhard Rensch and Ernst Mayr, also began their careers as neo-Lamarckians, before 1937.

Carl von Nägeli (1817–1891) proposed a theoretical system characteristic of those that combined several anti-selectionist mechanisms. He argued for a 'direct environmental effect'[5] (*Theorie der direkten Bewirkung*) on the organism's heredity (von Nägeli 1884), combined with a strong version of orthogenesis. Von Nägeli influenced the later versions of this theory of directed evolution, which became influential in German (and not only German) paleontology.

Natural selection played a significant role in many largely neo-Lamarckian theories. Describing the neo-Lamarckian school of the USA, Romanes claimed:

> Without denying to natural selection a more or less important part in the process of organic evolution, members of this school believe that much greater importance ought to be assigned to the inherited effects of use and disuse than was assigned to these agencies by Darwin. (Romanes 1895, p. 14)

This is certainly also true for German-speaking neo-Lamarckism. Even such a prominent neo-Lamarckian as Paul Kammerer 'supported Haeckel's old-school (as opposed to "neo-") Darwinism' (Gliboff 2006). Richard von Wettstein (1863–1931), an influential Austrian neo-Lamarckian botanist and evolutionist, summarised this position in his brochure 'Neo-Lamarckismus und seine Beziehungen zum Darwinismus', claiming that 'it is absolutely impossible to explain all evolutionary processes [Formenbildung] in the same way; Lamarckian and Darwinian views do not exclude each other, but should rather co-exist' (von Wettstein 1903, p. 8).

Due to Haeckel's influence, old-school Darwinism was especially powerful in Germany. The figurehead of the movement in the twentieth century was Ludwig H. Plate (1862–1937) (Levit and Hoßfeld 2006). It must be emphasised that Plate (like Haeckel) was seen by many influential contemporaries as *the* Darwinian. For example, the prominent Russian biologist, geographer and anti-Darwinist, Leo S. Berg (1876–1950) saw Plate as his main scientific opponent (Berg 1926). The American paleontologist, Henry F. Osborn (1857–1935), who sought a compromise among selectionist, orthogenetic and neo-Lamarckian methodologies, likewise honoured Plate as a 'prominent selectionist' (Osborn 1926). Erik Nordenskiöld (1926, p. 572) claimed that Plate's *Selektionsprinzip* (1913) contained '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'. The American evolutionary biologist, Vernon Kellog (1909) estimated Plate's importance along the same lines, but emphasised the discrepancies between neo- and old-Darwinian views:

> Plate is an able friend and defender of selection, but his point of view is not that of Poulton. The Englishman holds rigidly to the neo-Darwinian anti-Lamarckism; the German takes the real standpoint of Darwin, he calls on the inheritance of acquired characters to aid selection in its evolutionary task.

Old-Darwinians combined standard Darwinian causal factors (mutations, recombination, geographic isolation, natural selection) with neo-Lamarckian and orthogenetic mechanisms, seeking to determine the exact role of each mechanism in the evolutionary process. They insisted that their approach followed exactly in the footsteps of Darwin. In addition to Darwin, Haeckel and himself, Plate counted Richard Semon (1859–1919), Wilhelm Roux (1850–1924), Richard Hertwig, Fritz von Wettstein (1895–1945), Berthold Hatschek (1854–1941), Jan Paulus Lotsy (1867–1941), Franz Weidenreich (1873–1948) and Bernhard Rensch among the old-Darwinians. From the viewpoint of the Modern Synthesis, there is no rational basis on which to distinguish old-Darwinism and neo-Lamarckism as two essentially different schools of thought. Their theoretical divide appears, to a contemporary observer, to be fuzzy and quantitative one, not qualitative, depending on the emphasis placed on several evolutionary variables that could be involved. Neo-Lamarckian mechanisms played a significant role in both theoretical movements.

The concept of orthogenesis was the third major component of both Darwinian and alternative evolutionary theories at the beginning of the twentieth century. Orthogenesis played an essential role in German paleontology, even after the Second World War. The term 'orthogenesis' was coined by Wilhelm Haacke (1855–1912), who defined the concept (Haacke 1893) on the basis of the work of von Nägeli (1884) and Theodor Eimer (1888, 1897). It assumes that variation is constrained, as opposed to the presumption that natural selection acts on copious, even inexhaustible variation. Haacke wielded this concept primarily against the neo-Darwinism of August Weismann. Darwin, himself, was not so categorical in denying any form of constraint, as the following quotation demonstrates:

> The foregoing discussion naturally leads to the question, what is the limit to the possible amount of variation in any part or quality, and, consequently, is there any limit to what selection can effect? Will a racehorse ever be reared fleeter than Eclipse? Can our prize-cattle and sheep be still further improved? Will a gooseberry ever weigh more than that produced by 'London' in 1852? Will the beet-root in France yield a greater percentage of sugar? Will future varieties of wheat and other grain produce heavier crops than our present varieties? These questions cannot be positively answered; but it is certain that we ought to be cautious in answering them by a negative. (Darwin 1883, p. 228)

Orthogenesis answered this question 'by a negative', assuming that constraints restrict variation in ways such that evolutionary change is canalised to modify form in theoretically determined and therefore predictable directions.

Orthogenetic evolution proceeds, Haacke (1893, p. 32) claimed, 'only in a certain direction within each phylogenetic line; orthogenesis is a universal phenomenon'. We emphasise that he distinguished orthogenesis from 'epimorphism', which claimed that evolution proceeds in the direction of increased perfection (i.e. from the idea of evolutionary *progress*).

In the first half of the twentieth century, the idea of directed evolution became especially popular. It was incorporated into more than 20 theories (Levit and Olsson 2006). Some of these theories included finalistic ideas (Mayr 1982, p. 959) and some involved elements of vitalism. But, the common denominator for all of them was the idea that constraints (morphological, molecular, etc.) direct phylogeny in ways such that the mechanism of natural selection becomes superfluous, either as a cause for the whole of an organism's evolution or during certain periods of its phylogenetic history. The majority of advocates of directed evolution proceeded from the assumption that organisms are predisposed to vary in certain directions, and that this bias determines major transitions in evolution. They were convinced that these directional shifts can be observed empirically in the paleontological record and that they are clearly definable (Figure 2). Accordingly, it was assumed that evolutionary events follow certain clearly recognisable patterns and restrictions, and that evolution can proceed at times or even predominantly in non-adaptive directions. In other words, orthogenesis was strongly coupled to the idea of non-adaptive trends in evolution.

Various evolutionary biologists developed the concepts of orthogenesis with their own unique terminologies. For example, Osborn had *aristogenesis*; the Austrian zoologist, Hans Przibram (1874–1944) defined *apogenesis*; Othenio Abel, a founder of *Paläobiologie*, introduced *Trägheitsgesetz* (the law of inertia) (Rieppel 2012b); the Italian zoologist, Daniele de Rosa (1857–1950) conceived *ologenesi* (hologenesis) and the Russian biologist and geographer Lew (Leo) Berg employed the term *nomogenesis*. This last term is a good example of an orthogenetic concept that combines the idea of direct environmental impact on heredity (Geoffroyism) with 'saltationism' (Levit and Hoßfeld 2005).

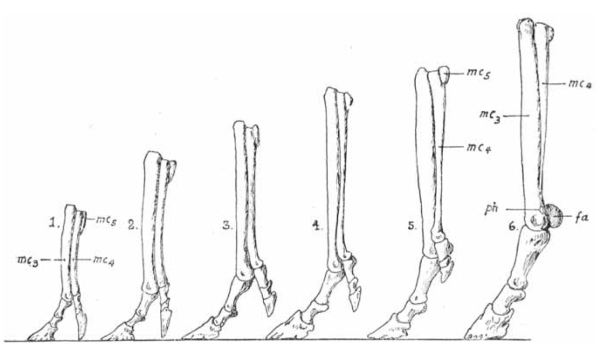


Figure 2. Othenio Abel's illustration of directionality in evolution (Abel 1928, p. 35).

Saltationism is the fourth major anti-Darwinian pattern of evolutionary change. It remains influential even today (e.g. Theißen 2006; Kutschera and Niklas 2008). Advocates of saltationism deny the neo-Darwinian idea of gradually increasing divergence of form or other characteristics as the only viable means of evolutionary change. Classical saltationists did not completely dismiss gradual change as an outcome of natural selection. However, they claimed that entirely new 'body plans' can come into being as a result of sudden, discontinuous change, arising by means of macromutations or a series of macromutations and resulting in *saltations*. These are said to be responsible for the rapid appearance of new species or even higher taxa, including classes and orders of organisms, while minor variations are responsible for fine-scale adaptations at or below the species level. Hence, species-level saltationism (mutationism) claims that new species can appear in a single step, whereas large-scale saltationism makes the far grander claim that a new body plan can appear in the space of a few generations by way of sudden ontogenetic change.

Almost all the early geneticists were mutationists. The British scholar, William Bateson (1861–1926), who introduced the term 'genetics', was an advocate of evolution by means of discontinuous 'sports'. Perhaps, the best-known large-scale saltationist was Otto Heinrich Schindewolf (1896–1971), the most influential paleontologist in post-war Germany (Reif 1993). He championed a complex theory that embraced saltationism, orthogenesis and typology.[6] Schindewolf's Weltanschaung was a product of the whole history of alternative theories in Germany. In his opinion, the Darwinians had driven paleontology and morphology onto the unsteady ground of transient hypotheses: 'The old morphology[7] was unbiased and free of hypotheses, i.e. it conducted comparative form studies with the greatest possible objectivity. It was the phylogenetic turn which introduced strongly subjective elements into morphology' (Schindewolf 1962, p. 60). From his viewpoint, it was necessary to bring evolutionary theory back to the solid ground of empirical data. This meant, above all, morphology. To accomplish this, Schindewolf created his theory of 'typostrophy', the central element of which was the concept of *typogenesis*. This involved the sudden, undirected, explosive appearance of a new type (i.e. a totally new body plan, potentially able to give rise to a new order or even a class) by means of rapid, random alterations in the early stages of ontogeny. These were said to lead to changes in the adult stages in succeeding generations. Schindewolf called this process *proterogenesis* (Schindewolf 1936, pp. 26, 101). Generally, saltationists explained sudden change in the fossil record as the outcome of a series of mutations that led to rapid modification of phenotypes. Natural selection (in the

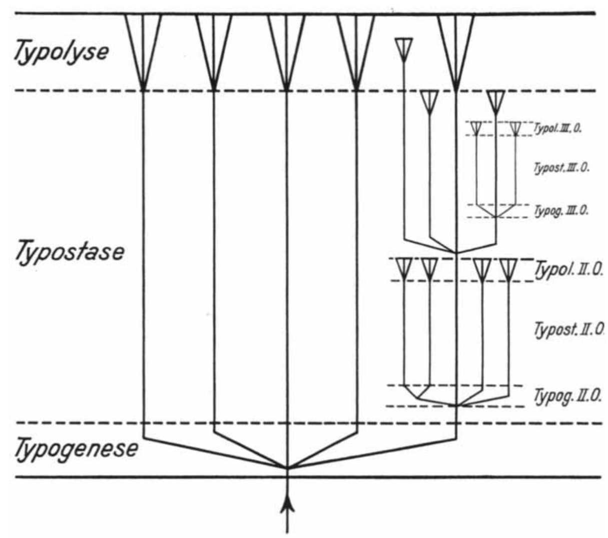


Figure 3. Schindewolf's view of the evolutionary process, schematically divided into three phyletic phases: typogenesis, typostasis and typolysis. In the phase of typogenesis, the *Bauplan* (body plan) of a new clade appears. This immediately splits up into subtypes which conservative throughout the whole phase of typostasis. In the ultimate short phase of typolysis, the subtypes lose their core identity and undergo degenerative subdivisions (from: Schindewolf 1964, p. 89).

form of orthoselection), in Schindewolf's theory, operates as a 'fine tuning' mechanism, adjusting organisms more precisely to their environments (Figure 3).

Schindewolf was influenced by 'typological thinking' developed in the context of the so-called *idealistic morphology*, which experienced a powerful revival in Germany in the first half of the twentieth century (e.g. Rieppel 2011, 2012a). The cornerstone of idealistic morphology was the concept of the 'type' as an abstract, ideal form, representing a certain class of biological phenomena and embodying the norm of this class. The objective of pure typology was to create systems of classification for living and extinct organisms that are based on structurally explicit characters, without reference to phylogenetic history or causal explanation. Typology, as a non-phylogenetic foundation of idealistic morphology, was conceptually neutral with respect to evolutionary mechanisms. Yet, only a few idealistic morphologists practised pure typology. Idealistic-morphological theories employed typological methodology, accompanied by other elements, such as Lamarckism, saltationism, creationism, mutationism, orthogenesis and natural selection combined by each author to constitute a unique theoretical structure. Reif (1997) explained Schindewolf's typology as follows: 'Schindewolf showed that there was neither coincidence (nor an inner contradiction) but a logical link between his typology, his phylogenetic methods and his theory of mechanisms of evolution.'

The German paleontologist, Edgar Dacqué was another characteristic proponent of idealistic morphology (Levit and Meister 2006). His works were among the most popular publications in natural history of his time (Zimmermann 1953). Dacqué had a significant influence on other idealistic morphologists and on contemporary debates over evolutionary issues (Rensch 1947). His book *Vergleichende biologische Formenkunde der fossilen niederen Tiere* (Dacqué 1921) is regarded as one of the most important 'contributions to study of the comparative anatomy of extinct animals...' (Reif 1986). A contemporary of Dacqué, the botanist Werner Zündorf (1911–1943), who was a Darwinian of sorts, labelled his theory as the 'supreme manifestation' of idealistic morphology (Zündorf 1940, p. 16).

Dacqué (1923) was active in popularising evolutionary theory. In 1911, he published a paper in a compendium entitled 'Die Abstammungslehre' (The Theory of Descent), intended to make the idea of evolution intelligible to non-specialists. Other prominent anti-Darwinian theorists, including Richard Goldschmidt (1878–1958), Othenio Abel (1875–1946) and Paul Kammerer (1880–1928), participated in this project. Dacqué's ideas strongly influenced later advocates of typology, including Adolf Remane (1898–1976) (e.g. Remane 1956), Oskar Kuhn (1908–1990) (Kuhn 1981) and Otto Schindewolf.

Dacqué left a significant scientific-empirical heritage of important contributions to paleontology (Dacqué 1915, 1921, 1935). Altogether, he published more than 100 scientific works, fully half of which were of a theoretical nature. He first criticised Darwinian selectionism in his early theoretical publications (e.g. Dacqué 1904). This work was purely typological in its approach to classification, without the transcendental metaphysics he would later introduce. In Dacqué (1911), he still pleaded for the use of 'strictly exact methods' and the avoidance of 'speculations'. Dacqué understood all theories looking for causal explanations of coherence between organic forms as 'speculations'. In later years, he changed his mind, concluding that both competing methodologies are ultimately rooted in metaphysics.

In one of his mature works, Dacqué (1935) devoted a long chapter to the methodological issues of morphological research. He claimed that two main methodologies are applicable in this field. Following another influential idealistic morphologist, Adolf Naef (see Reif 1998), Dacqué distinguished 'systematic' from 'dynamic' views of organisms. Both can serve as foundations for morphology. The primary objective of systematic morphology is 'to present the whole living world as a stepladder of variously organised forms or types, whose modifications appear as more or less similar or "akin" to subtypes and genera, respectively' (Dacqué 1935, p. 1). The important premise of this procedure (hence the reason why Dacqué put the word 'akin' in quotation marks) is that a systematising morphologist is not concerned with the real biological relationships of forms he describes. In contrast, 'dynamic' morphology concentrates on real descent and on causality. Consequently, there are two basic methodologies: the idealistic-morphological methodology and that based on evolutionary morphology (*deszendenztheoretische Morphologie*). The purpose of pure idealistic morphology is to reduce 'various concrete natural organic forms' to an *ideal* series of types.

To sum up, this discussion has explored various logical possibilities that are available to interpret both evolutionary change and the paleontological record in terms of systematics. In their original incarnations, many of these options are logically incompatible with strict selectionism, but their history is one of combinations and mergers. Almost every alternative evolutionary theory has incorporated at least a part of the Darwinian theoretical heritage. In the history of evolutionary biology, we are rarely confronted with single-factor theories, but rather with complex theoretical systems involving a multitude of evolutionary mechanisms, like that of Darwin himself. In the German-speaking countries, alternative evolutionary theories and typology remained influential even into the 1950s and 1960s, especially in paleontology due to the lasting influence of Schindewolf.

The lingering influence of alternative evolutionary theories slowed the acceptance of Darwinism by German paleontologists, but there was a significant lack of interest in studying mechanisms of evolution throughout the German life sciences. As Reif (1983, pp. 198–199) argued (with some exaggeration):

> Evolution was never an important subject in German biology in the first five or six decades of this century. This is the reason why there were so few German evolutionary biologists of international reputation. It is very difficult to explain this trend. There is no indication that it had anything to do with religion, in a country where the influences of Catholics and Protestants approximately balance each other. Biologists usually had no problems accepting the theory of descent, but they hesitated to go along with Darwin's selection theory, which they regarded as too mechanistic and materialistic. The tradition of a misrepresented, misunderstood Romanticism led them to search for organismic laws rather than physicalistic, mechanistic laws. An explanatory model (selection) for the theory of descent that did not account for all aspects and complexities of life could not be satisfying.

Traces of the romantic worldview can be found in the German natural sciences in the first and even the second halves of the twentieth century. German idealistic morphology was a major 'stronghold' of Romanticism. Evolutionary (historical) methodology played a subsidiary role in the late-nineteenth and early-twentieth century biology of the German-speaking world. It co-existed, more often than not as a junior partner, with the idealistic methodological tradition. The idealist tradition, in its turn, caused German paleontologists to exhibit a strong preference for deterministic explanations of patterns of evolutionary change, rather than being prepared to cede a large role to chance.[8]

## Conclusions

Central tenets of Darwinism gradually insinuated themselves into German paleontology only in the latter half of the twentieth century. There are several reasons why this was so.

Part of the problem was derived from the persisting influence of idealistic morphology, even after the end of the Second World War. Ernst Mayr presented the basic principles of the Evolutionary Synthesis at the 'Phylogenetic Symposium' of 1956, held in Hamburg.[9] Later, he reported that 'all those attending (with exception of the geneticist de Lattin) argued against the Synthesis'. Addressing the question 'Why then was there so much opposition in Germany?' Mayr (1999) advanced several reasons. First among these was the role of the typological or idealistic-morphological tradition, which was much stronger in Germany than elsewhere. The second factor was the 'preoccupation of German zoology with phylogeny', which was connected to the fact that 'the students of phylogeny almost without exception adhered to the idealistic-morphological philosophy'. The third reason cited by Mayr was a general ignorance about modern genetics among German biologists. This was likewise related to the continued adherence of German morphologists and paleontologists to 'typological saltationism' (Mayr 1999). In other words, all the factors listed by Mayr are ultimately rooted in one and the same theoretical movement: that which privileged idealistic morphology. There were many idealistic morphologists and champions of the typological method among the influential paleontologists of the time, notably including Edgar Dacqué, Karl Beurlen and O.H. Schindewolf.

Another important factor was the general influence of non-Darwinian theories that characterised supposed evolutionary mechanisms. Neo-Lamarckism, saltationism (including mutationism) and orthogenesis, in various combinations, dominated the German theoretical landscape in the first third of the twentieth century, and they remained influential into the post-war period. This combination of typological methods, along with the alternative evolutionary theories, created an especially strong theoretical amalgam of immunity to selectionism. These factors, along with the preoccupation with phylogenetic and more minor technical issues, together created substantial resistance to the penetration of Darwinism into German paleontology. Wolf-Ernst Reif's pioneering synthetic (in all senses) approach significantly contributed to the process of its Darwinisation.

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## Notes

1. One of us (Hoßfeld) was Reif's co-author.
2. We do not claim that Germany was the only country in which paleontology and Darwinism were in a sophisticated relationship. We claim, however, that it is possible to explain the specific situation in Germany.
3. The adjective 'German' is employed here to refer to any work done in the German language or by citizens of nations where use of this language predominates.
4. Swedish biologists were under German influence to a significant extent. The resistance to Darwinism in Sweden was remarkably strong and persistent (for more details, see Olsson 2005).
5. This approach is known as *Geoffroyism* (after E. Geoffroy Saint-Hilaire, 1772–1844).
6. Typology is an empirically based methodology that asserts the primacy of structure over function. It sees organisms as structural phenomena to be ordered in logical schemes in accord with their morphological features.
7. 'Old' in the sense of pre-Darwinian.
8. We are thankful to Roger D.K. Thomas for this phrasing.
9. The 'Phylogenetic Symposium' (1956 to until today) was founded as an annual event by Curt Kosswig (1903–1982), Wolf Herre (1909–1997) and Adolf Remane (Kraus and Hoßfeld 1998).

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