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The differing fortunes of Ernst Haeckel's biogenetic law: from the Nazi *Führerprinzip* to the evolutionary synthesis

Georgy S. Levit^{1*} and Uwe Hossfeld¹

Abstract

Background Ernst Haeckel's biogenetic law was critically revised by several post-Haeckelian morphologists. Among the most significant between the two world wars were the German zoologist Victor Franz and the Russian morphologist Alexei Sewertzoff. Both were committed Darwinians who developed analogous theoretical systems consisting of two interconnected components: a revised version of the biogenetic law and a theory of evolutionary directions. The two biologists knew each other personally, and their developmental theories shared substantial common ground. Nevertheless, the trajectories of their ideas diverged sharply. Sewertzoff founded a powerful school of evolutionary morphology, and his student Ivan Schmal-hausen integrated Sewertzoff's concepts into the Soviet formulation of the Evolutionary Synthesis and subsequently into the broader international Darwinian movement. Franz, by contrast, attempted to employ his theory to provide a biological justification for Hitler's dictatorship; after World War II, his theoretical contributions were largely forgotten and remained of interest only to historians of science.

Results Despite the apparent similarity of their theories, a crucial difference distinguishes them. Sewertzoff's theory was highly elaborated, grounded in an extensive body of empirical research, and articulated with maximal scientific precision. Franz, by contrast, remained speculative in both his conception of development and his understanding of evolution. Although he claimed to follow the intellectual lineage of Haeckel and Goethe in his vision of evolutionary progress, his actual argumentation remained decidedly speculative. The speculative nature of his theoretical system made it unusually easy to adapt to ideological purposes during the Nazi regime.

Conclusions Franz approached the problem of ontogeny and phylogeny in a manner similar to Sewertzoff; however, he remained at an abstract level and did not engage with the empirical detail thoroughly elaborated by Sewertzoff. As Schmal-hausen had already pointed out, Franz's theory of evolutionary directions was one-sided, taking into account only a single aspect: centralization accompanied by differentiation. Franz pushed this principle even further, extending it to the sphere of social evolution in an attempt to justify Hitler's absolute dictatorship. The speculative nature of Franz' hypothesis made it vulnerable for ideological distortions.

Keywords Alexei Sewertzoff, Victor Franz, Ivan Schmalhausen, Ontogeny, Phylogeny, Biogenetic law

*Correspondence:

Georgy S. Levit
georg.levit@uni-jena.de

¹Biology Education Research Group, Friedrich Schiller University Jena, Am Steiger 3, 07743 Jena, Germany



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Introduction

Soon after the publication of Darwin's principal works [4, 5], Ernst Haeckel formulated his well-known biogenetic law, succinctly expressed in the dictum that ontogeny recapitulates phylogeny [25, 31, 43]. Proceeding from his principal aim of demonstrating the very reality of biological evolution, Haeckel constructed a theoretical parallel between the developmental sequence of the individual organism and the hierarchical series of animal forms revealed by comparative anatomy and systematics [24, 39]. For the same reason, Haeckel employed the term *Entwicklung* ("development") to designate both ontogenesis and the historical evolution of lineages. To these two parallels he added a third, based on paleontological evidence, the progressive "development" of forms through geological time [32, 42]. He emphasized this threefold genealogical parallelism of phyletic (paleontological), biontic (individual), and systematic development [24, II: 371ff]. The causal explanation of this triad he termed "the fundamental law of organic development," or, in short, the biogenetic law [43]. Haeckel was not the originator of the threefold parallelism. The scheme was formulated in a pre-evolutionary context and most fully elaborated by Louis Agassiz; Haeckel's contribution lay in reinterpreting it within a Darwinian framework [3].

Haeckel himself was aware of the difficulties inherent in the biogenetic law [57, 58], since a "complete and faithful recapitulation" is never observed in nature. But his "old-school" Darwinism retained pronounced neo-Lamarckian elements that penetrated even his interpretation of natural selection [35, 36]. Haeckel tried to pursue a selectionist research program, but in fact went deeper into the neo-Lamarckian paradigm. This conceptual dualism undermined his project to construct a strictly Darwinian morphology, rendering his recapitulation theory, in essence, "a Lamarckian rather than a Darwinian concept" [2].

A new generation of uncompromising selectionists, among whom German zoologist Victor Franz and Russian morphologist Alexei Sewertzoff (alternative spelling: Severtsov) were prominent, was expected to accomplish the task of rendering both development and evolution explicit selectionist in character. A related but theoretically distinct revision of the biogenetic law was proposed by the Swiss-born zoologist Adolf Naef, who worked along partially similar lines yet adhered to an idealist morphological theoretical framework fundamentally opposed to Darwinism [39]. Although Naef, Sewertzoff, and Franz developed their revisions of the biogenetic law in parallel and with mutual awareness, Naef will not be considered further here, since our analysis concentrates on explicitly Darwinians.

Already Haeckel's contemporaries were quick to criticize his schematic interpretations of development. It is

well known that he based his biogenetic law largely on the empirical investigations of the Russian embryologist Alexander Kowalevsky. Haeckel himself emphasized that "the most important germ histories of recent times are those by Kowalevsky" [26, p. 49]. Kowalevsky and his friend Ilya (Elias) Metchnikov, later Nobel Laureate in 1908, had provided detailed descriptions of the ontogeny of numerous invertebrates and lower chordates, revealing fundamental homologies in early embryonic stages [39, 41]. Together they formulated a universal theory of germ layers, asserting the homology across all Metazoa. Yet both remained sharply critical of Haeckel's oversimplified recapitulationism, objecting to its inherently speculative character.

The Kowalevsky–Metchnikov concept of the evolutionary malleability of all stages of embryonic development, with particular emphasis on the evolutionary significance of early ontogenetic phases, was further elaborated in the works of the founder of the Russian-Soviet school of evolutionary morphology, Sewertzoff [37]. Sewertzoff exerted his principal influence in the Russian- and German-speaking scientific communities, and his theoretical system represented perhaps the most comprehensive and radical revision of Haeckel's biogenetic law during the first third of the twentieth century. In Germany, meanwhile, Franz, personally acquainted with Sewertzoff, developed a closely related theory [15]. Franz claimed priority in formulating the theory of the differential impact of deviations arising at different stages of embryonic development on the course of morphogenesis and, consequently, on the direction of phylogenetic evolution.

These two closely related and similarly structured theoretical systems experienced profoundly different fates. In Germany, Franz, who joined the NSDAP (*National Socialist German Workers' Party*, the ruling party in Germany under Adolf Hitler's dictatorship from 1933 to 1945) as early as 1930 (well before Hitler's assumption of power) sought to align his biological theories with National Socialist ideology [29, 33, 34]. During the Nazi rule, he even elaborated a biological interpretation of the *Führerprinzip*, the ideological principle legitimizing Hitler's absolute dictatorship [18, 30].

In contrast, in the USSR, Sewertzoff continued to develop his theory along Darwinian lines, founding a scientific school and training his pupil Ivan Schmalhausen in this tradition [1, 35, 39]. Schmalhausen (also spelled Shmal'gauzen, Schmalgauzen) subsequently adapted Sewertzoff's theoretical system with several improvements, integrating it into Soviet biology and later into the international Evolutionary Synthesis [6, 35, 38, 54–56]. Although the Sewertzoff-Schmalhausen theory came under attack from Lysenkoists after the Second World War, it survived ideological pressure.

In the present paper, we outline the two theories and provide an explanation for how two similarly structured and partly synonymous theories could have developed in such divergent directions (Fig. 1).

Alexei Sewertzoff—biographical sketch

Alexej Nikolajevich Sewertzoff was born on March 12 in Moscow into a family of scientists (Fig. 1). His father, Nikolaj Alexeevich Sewertzoff (1827–1885) was one of the first biologists in Russia to actively propagate Darwinian ideas [37, 41]. In 1875 he visited Darwin in Down House and was encouraged by Darwin to continue his zoogeographical studies [51, p. 45]. Growing up in this environment, Sewertzoff was predisposed toward evolutionary biology. After entering Moscow University in 1885, he studied under Mikhail A. Menzbier, a pupil of his father and a leading Darwinist of the time.

Between 1896 and 1897, Sewertzoff conducted research in France, Germany, and Italy, studying with Carl von Kupffer, Walther Flemming, and Anton Dohrn [45]. His Ph.D. dissertation (1898) examined head segmentation in stingrays. He became associate professor of zoology at Jurjev (now Tartu) University in 1899 and, three years later, full professor at Kyiv University, where he organized a new laboratory and began comparative embryological and paleontological studies. During this period, he already introduced the term “phylembryony,” which later



Fig. 1 Alexei Nikolaevich Sewertzoff: Portrait

became the foundation of his phylembryogenesis theory [37, 40]. Among his students in Kyiv was Ivan Schmalhausen, who would later play a central role in the Russian version of the evolutionary synthesis [40].

In 1911 Sewertzoff accepted a professorship at Moscow University, where he established a laboratory of evolutionary morphology. His major theoretical works, *Essays in Evolutionary Theory* (1912) and *Contemporary Tasks of Evolutionary Theory* (1914) [47], and his studies on lower vertebrates earned him the Karl von Baer Prize in 1919 [46, 48]. Following the Russian Revolution, he was elected a full member of the Academy of Sciences (1920) and successfully promoted evolutionary biology within the new Soviet scientific institutions. He founded the Department of Zoology (1922) and later the Institute of Evolutionary Morphology (1934), precursor of the present A. N. Severtsov Institute of Ecology and Evolution.

Sewertzoff’s visits to Weimar, Jena, Vienna, Munich, and Stockholm (1925–1927) brought him into contact with leading European morphologists and evolutionists. His major book *Morphological Regularities of Evolution* was published in German by Gustav Fischer Verlag in Jena [48]. Sewertzoff was also personally acquainted with Ludwig Plate, Haeckel’s successor in Jena, and even published with him [51, p. 338]. He died in Moscow, having established himself as a renowned scientist and passed on his scientific legacy to numerous pupils, most notably Schmalhausen.

Alexei Sewertzoff—theoretical contributions

In a posthumous paper devoted to Sewertzoff’s scientific legacy, Schmalhausen emphasized that Sewertzoff’s principal merit was that he sought the regularities of the evolutionary process, attempting to derive them from data on concrete phylogenies. Sewertzoff initially proceeded from Haeckel’s biogenetic law, which “undoubtedly gives an incorrect interpretation of the facts” and is closely connected with the idea of the inheritance of acquired characters. Only Sewertzoff, writes Schmalhausen, “on the basis of an enormous amount of factual material, succeeded in achieving clarity on the question of the relationship between phylogenesis and ontogenesis and in formulating a number of clear propositions in his theory of phylembryogenesis” [53]. Schmalhausen listed many scholars, among them Franz, Ludwig Plate, Gavin de Beer, Walter Garstang, Edward Drinker Cope, Louis Dollo, and Henry Fairfield Osborn, who likewise sought morphological regularities (laws) of evolution; however, they either addressed only particular aspects of the problem or adhered to non-Darwinian positions [53].

Central to Sewertzoff’s evolutionary morphology is a twofold program: (i) a causal account of the directions of morphological evolution, and (ii) a developmental mechanism—phylembryogenesis—by which directional

change in adult form is produced [46, 48, 49, 52]. Ernst Haeckel sought not only to demonstrate the very reality of evolution but also to establish its dysteleological character: the absence of any predetermined or divine goal in the evolutionary process. Sewertzoff, while critically revising Haeckel's developmental scheme, aimed to remain firmly within the Darwinian framework of a non-teleological and causally determined evolution [37, 39]. Sewertzoff rejected orthogenesis (the concept of directed evolution) and sought instead to classify evolutionary change according to its morphophysiological consequences and its relation to environmental interaction [48, 52].

To preserve the notion of progress within a non-teleological framework, following Haeckel in this respect, Sewertzoff distinguished between biological (ecological) progress, defined in demographic and biogeographical terms such as increase in population size, range expansion, and cladogenesis, and morphophysiological progress, denoting an increase in the degree of organisation and the “vital energy” of organisms [48, 50, 52].

These two forms of progress, he emphasized, are not necessarily correlated and may occur independently of one another. On the level of morphophysiology Sewertzoff identified four principal directions (modes) of evolution. (1) Aromorphosis—rapid, large-scale innovations that increase the organism's degree of organisation and capacity to exploit resources (e.g. origin of hair, occurrence of the vertebrate heart). In Sewertzoff's own words: “Periods of aromorphosis can be seen as nodal points in the evolutionary process, after which phases of intensified adaptive radiation occur” [52, p. 87]. According to Schmal-hausen, aromorphosis correlates with Franz's “perfecting” [54, p. 23], but this is only one of the modes of evolution (2) Ideoadaptations—specialised, restricted adaptations that fit organisms to particular environments without raising overall organisational level:

“Periods of aromorphosis are typically followed by periods of divergent ideoadaptation” [52, p. 87]. (3) Coenogenesis—embryonic or larval adaptations beneficial to early life stages but not retained in the adult. (4) Morphophysiological regress (degeneration)—simplification or loss of structures associated with secondary shifts [48, 52]. Sewertzoff emphasised that evolutionary trajectories usually combine these modes and that aromorphoses are relatively rare and short compared with prolonged ideoadaptive phases, an observation he invoked to account for apparent gaps in the fossil record (Fig. 2).

Sewertzoff regarded his concept of aromorphosis as standing in clear opposition to the “law of improvement” proposed by Franz, who made the idea of biological progress the central element of his theoretical system [12, 18]. Following the tradition of Goethe and Haeckel, Franz emphasized the evolutionary significance of processes of centralization and differentiation, which also played a central role in his *Führerprinzip*-concept (see below for details). Sewertzoff, by contrast, maintained that there is no direct correlation between centralization and the intensity of life processes, arguing that the latter constitutes the decisive criterion of any aromorphosis, but aromorphosis is only one of evolutionary directions [50, 52].

Sewertzoff's theory of evolutionary directions classifies the principal modes of progress and regress in evolution but, by itself, does not specify the underlying mechanism of change. This developmental mechanism was provided by Sewertzoff's theory of phylembryogenesis, which explained how modifications of ontogeny generate the morphological transformations corresponding to these evolutionary directions [40, 46].

The first documented attempt to formulate the basics of the phylembryogenesis theory was made by Sewertzoff in his 1910 talk to the XIIth congress of Russian naturalists and physicians, where he also coined the term phylembryogenesis [51, p. 185]. In 1912, Sewertzoff published

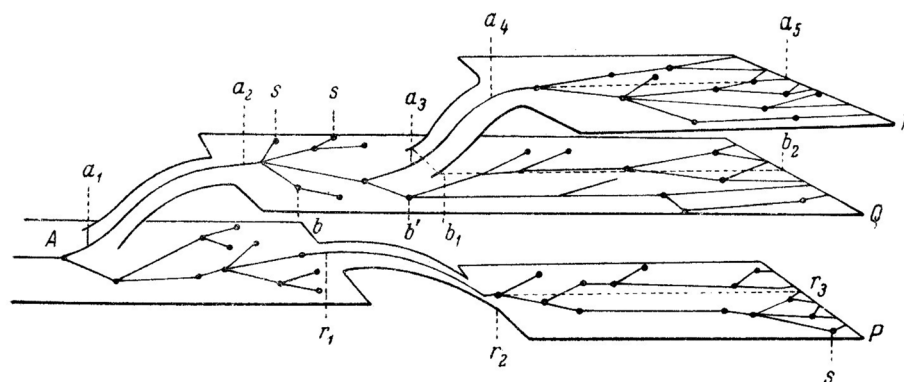


Fig. 2 Sewertzoff's Scheme of Evolution. The scheme suggests that at a certain stage in the evolutionary process an animal form A goes through aromorphosis (a_1 – a_2 ; a_3 – a_4), which is followed by ideoadaptations (b , b') and specializations (s), occurring when a new form is confronted with various novel environments. The idea of morphophysiological regress is reflected in the scheme by the transition r_1 – r_2 , which is likewise followed by ideoadaptations (r_2 – r_3) and specializations

the detailed version of his theory [46]. Although Franz [15] claimed priority for the idea of biometabolic *modi*, Sewertzoff had been more than ten years ahead of Franz in developing the theory (Fig. 3).

Phylembryogenesis supplies the developmental mechanics for these directional outcomes. Sewertzoff replaced Haeckel's simple recapitulation with a triadic scheme of ontogenetic reorganisation through which evolutionary novelties in adults arise: (i) Anaboly—extension of morphogenesis by addition of new late developmental stages (Fig. 3); (ii) Deviation—changes in middle stages of ontogeny that produce partial recapitulation or altered adult trajectories; (iii) Archallaxis—modifications of the earliest embryonic stages, which abolish recapitulation and can produce fundamentally new adult structures (Fig. 4) [48, 49]. Crucially, archallaxis implies that evolutionary novelty can originate in non-regulable embryonic variation and become fixed only by selection, an argument that committed Sewertzoff to a selectionist explanation [37, 39]. As noted by his wife and biographer Ludmila, Sewertzoff concluded in 1929–1930 that progressive evolution may also proceed via a third pathway, deviation, as earlier proposed by Fritz Müller, namely a modification of embryonic development at intermediate stages of morphogenesis [49, p. 35] (Fig. 4).

Sewertzoff further linked these developmental modes to his hypothesis of correlation: organs differ in their directness of environmental coupling and can be classified as ectosomatic (directly interacting with environment) or endosomatic (internal). Long-term environmental change primarily acts on ectosomatic features, inducing correlated changes in endosomatic systems [48, 49]. Thus environmental directionality operating on ectosomatic traits, filtered through developmental reorganisation (phylembryogenesis) and fixed by natural selection, produces the observed directions of morphological evolution.

Sewertzoff's mentorship was the decisive formative influence on Ivan Schmal-hausen's intellectual development (Fig. 5). Their collaboration in Kyiv from 1902 onward grounded Schmal-hausen in Sewertzoff's evolutionary morphology, especially the correlation theory and the concept of phylembryogenesis [40]. Sewertzoff's evolutionary morphology became the nucleus of Schmal-hausen's evolutionary theory. Schmal-hausen expanded his morphological principles into a general theory of evolutionary dynamics, providing it with genetic foundation and integrating them into the emerging Modern Synthesis [40]. As noted by Gilbert [22], among the most ambitious attempts to synthesize evolutionary theory with genetics and development were those of Schmal-hausen and Conrad Hal Waddington. Waddington himself emphasized that the main value of *Factors of Evolution* "lies in the particular point of view which

Schmal-hausen has derived from his studies as an embryologist, and which differentiates him from most of the other recent writers on evolution" [59].

The modes of phylembryogenesis identified by Sewertzoff inspired Schmal-hausen in developing a concept of adaptive transformations [44]. In general terms, Schmal-hausen demonstrated that phylogeny is itself a historical series of ontogenies, however, it represents only those ontogenies that have actually been realized, that is, selected [54, p. 68]. Evolution tends to go where development can go, and that is why, for Franz, Sewertzoff, and Schmal-hausen, the theories of evolutionary directions go hand in hand with the reformulation of the biogenetic law.

Schmal-hausen, like Sewertzoff, was familiar with Franz's theory of perfecting and explicitly criticized it for one-sidedness: "The morphological problem of the organism's integrity in its historical development has not been developed at all. In any case, it is far from being encompassed by the principle of 'centralization' formulated by H. Bronn, E. Haeckel, and V. Franz" [54, p. 212] (Fig. 5).

In sum, Sewertzoff provided a unified programme: a taxonomy of evolutionary directions grounded in organismal and ecological criteria, together with an explicit developmental account (phylembryogenesis) showing how changes in timing, sequence, and position of embryonic events can generate adult morphological novelties. This synthesis made evolutionary morphology compatible with Darwinian selectionism and prepared the conceptual ground later consolidated by Schmal-hausen in the Evolutionary Synthesis [40].

Victor Franz—biographical sketch

Victor Franz was born on April 5, 1883, in Königsberg (now Kaliningrad, Russia). After completing his *Abitur* in 1902, he studied natural sciences, with a focus on zoology, at the University of Breslau (now Wrocław, Poland) from 1902 to 1905. Under the supervision of Willy Kükenthal, he completed his doctoral dissertation on the anatomy and histology of the shark eye [7] and was awarded the Ph.D. on November 2, 1905. In 1906 Franz briefly worked at the Zoological Institute in Halle (Saale) before joining the Biological Station on Helgoland, where he conducted marine biological research under Friedrich Heincke until 1910. He subsequently moved to Ludwig Edinger's Institute of Neurology in Frankfurt am Main, where he deepened his comparative anatomical studies [34] (Fig. 6).

In 1913 Franz accepted a position as editor in the natural sciences department at the Institute for Bibliography in Leipzig, where Hans Meyer, Ernst Haeckel's son-in-law, was also active. Following military service on the Western Front during the First World War, he was

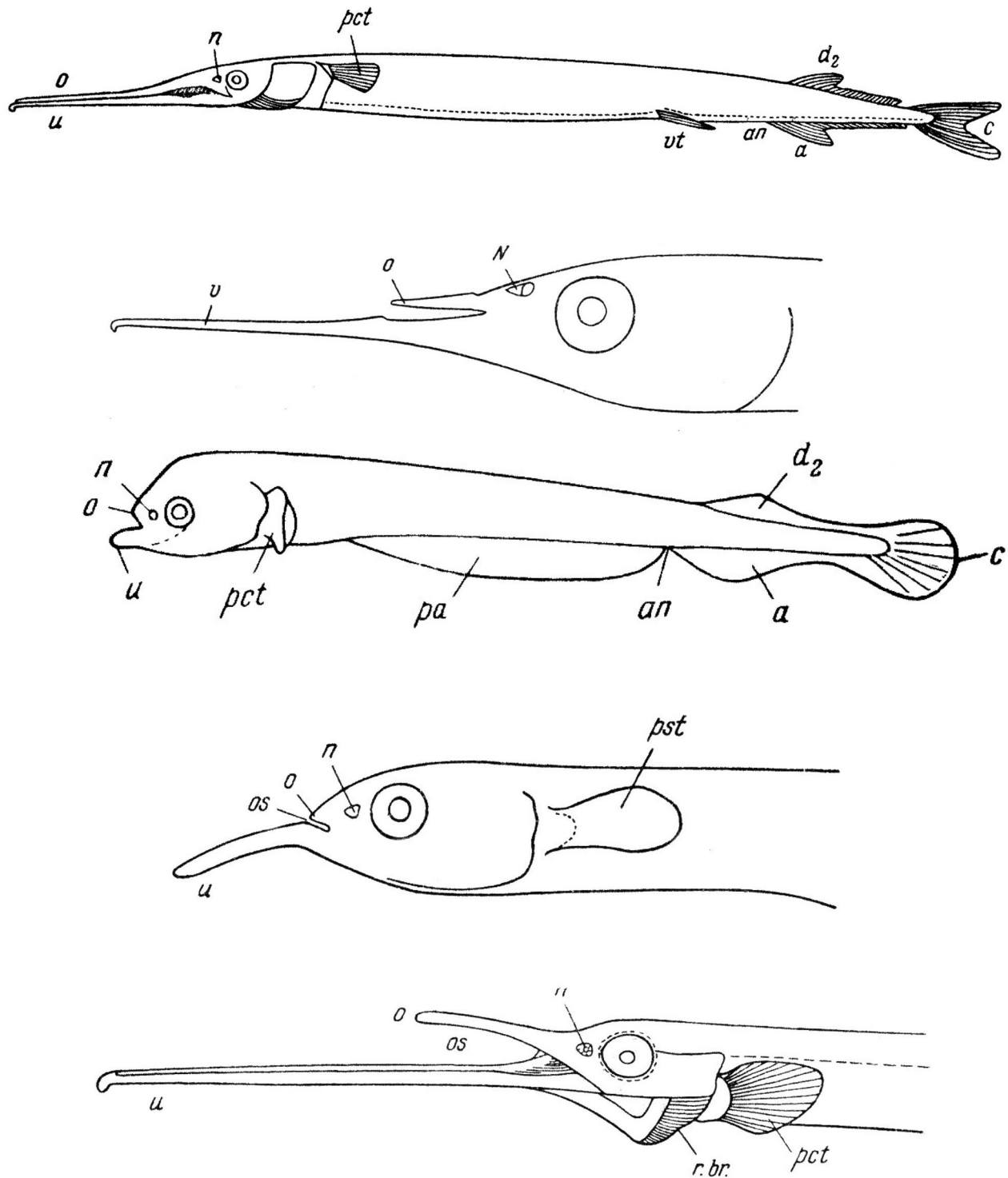


Fig. 3 The development of *Belone acus* as an example of *anaboly* as an example of Sewertzoff's very detailed empirical research. **A** Adult *Belone acus*. Lower (U) and upper (O) jaws are strongly elongated. **B** Head of an adult *Haemiramphus*. The upper jaw (O) is much shorter than the lower jaw (U). **C** A 10 mm larva of *Belone acus*. **D** A 21 mm larvae of *Belone acus*. **E** A 9,1 cm *Belone acus*. a ¼ anal fin; an = anus; C = caudal fin; d2 ¼ posterior dorsal fin; N ¼ nasal pit; Os ¼ mouth; p. a. = preanal fin; pct = pectoral fin; r. br. = Radii membranae branchiostegiae; vt = ventral fin. (from: Sewertzoff, 1949, p. 403)

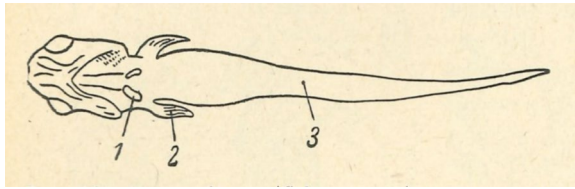


Fig. 4 An illustration borrowed by Schmal-hausen from Sewertzoff (Sewertzoff, 1939, p. 516) with minor modifications, used as an illustration of *archallaxis*. A goby larva (*Gobius capito*) with primordia of the pelvic fins: (1) pelvic fins, (2) pectoral fins anteriorly, (3) anal opening; view from the ventral side. "The pelvic fins are located in the same secondary position as in the adult fish. Their displacement from the anal opening forward, beneath the head, historically occurred through the displacement of the very earliest primordia. An example of evolutionary transformations through modification of the organ primordium (*archallaxis*)" (Schmal-hausen, 1969, p. 358)



Fig. 5 Ivan Schmal-hausen: Portrait

appointed Ritter-Professor of Phylogeny at the University of Jena, a position he would hold for the remainder of his career. Franz was promoted to *außerordentlicher Professor* in 1924 and, in 1936, assumed the chair of Phylogenetic Zoology, Heredity, and the History of Zoology. Between 1935 and 1945 he also served as Director of the Ernst Haeckel House [28].



Fig. 6 Victor Franz: Portrait

Franz published more than 200 papers and monographs and supervised over 30 doctoral students. Among his major works are *Die Geschichte der Organismen* (1924), *Morphologie der Akranier* (1931), and his contribution on *Die Geschichte der Tiere* in Gerhard Heberer's anthology *Die Evolution der Organismen* (1943) [14, 16, 20]. His anatomical research achieved enduring recognition through the description of several previously unknown sensory structures, notably the bulbous organ of mormyrids and the shadow-perception organ of amphioxus, both of which still bear his name in modern zoological terminology. He also described the snail *Viviparus menzelli Franz* near Phöben (Potsdam).

Politically, Franz became an early member of the NSDAP (1930) and sought to align biological concepts with Nazi ideology [33, 34]. After 1945, he was dismissed from his professorship for his active involvement in the National Socialist regime and died in Jena on February 16, 1950.

Victor Franz—theoretical contributions

Victor Franz received a comprehensive education in histology, morphology, and physiology under Arnold Lang and Willy Kükenthal, which equipped him for interdisciplinary work in evolutionary biology [7, 34]. Early in his career, he belonged to the group of biologists known as the “Vervollkommnungsnegierer” (“negators of perfection”), who denied that evolution was inherently progressive [8, 9]. After 1910, however, Franz reconsidered this view and sought to provide the concept of *Vervollkommnung* (“improvement” or “perfecting”) with a rigorous scientific foundation [10–12]. In doing so, he placed himself within a distinctly Jena tradition that originated with Goethe, was further developed by Ernst Haeckel, and continued by Ludwig Plate, Haeckel’s successor and Franz’s senior colleague in Jena [19, 30]. Franz realized that he was working in Haeckel’s tradition and defined himself as Haeckel’s academic grandson.

Building upon Haeckel’s morphological principles, Franz developed a concept of “improvement” or “perfecting” (1911) and later formulated his “law of the superiority of differentiation and centralization” (1920). He interpreted biological progress as a process of structural refinement and functional integration, in which differentiation and centralization jointly defined the “degree of perfection” of an organism [12]. At the beginning of the twentieth century, Franz thus revived a discussion initiated by Goethe and later Haeckel, which had meanwhile lost significance [12, p. 75]. Seeking to transform this idea into a universal biological principle, he elaborated it most fully in his programmatic main work *Die Vervollkommnung in der lebenden Natur*, which traces the history of the concept of perfection from biblical teachings and Aristotle through the Middle Ages to its position within the modern scientific landscape.

Like many other German morphologists of the first half of the twentieth century, Franz paid particular attention to the ideas of Goethe and Kant. However, unlike proponents of the structuralist (idealistic) research programme, such as Adolf Naef, he focused primarily on Goethe’s theory of perfection. In this context, Franz analyzed the concept of metamorphosis. He considered Goethe a gifted artist with extraordinary intuition rather than a scientist in the strict sense and maintained that Goethe could not be regarded as a precursor of evolutionary theory; nevertheless, Goethe’s works provided clear criteria of perfection in terms of differentiation and centralization, which Franz integrated into his own concepts [10, 11]. In Franz’s own words: “The view that the more perfect living being is the one with more differentiation and centralization, we find, with slightly different words, in Goethe, 1807” [21]. Franz here referred to the introduction to *Zur Morphologie*, “Die Absicht eingeleitet,” dated 1807, where Goethe, among other things, stated that “the more

imperfect the creature is, the more its parts are alike or similar to one another, and the more they resemble the whole” (cited from: [23]). From Kant, he adopted the objective, “ecological” criterion of perfection, he argued. Darwin, according to Franz, played a questionable role within the framework of a natural theory of perfection, since he was cited as a source both by proponents and opponents of the theory [12].

Franz’s own concept of perfection follows entirely his interpretation of Goethe and Kant, although he additionally incorporates Darwin’s principle of the struggle for survival. He distinguishes a morphological concept of higher development (Goethe), centered on differentiation and centralization, from Kant’s “ecological” approach, which he considers compatible with Darwin’s natural selection. It is noteworthy that Franz, in doing so, attempts to create a value-free methodology, while at the same time claiming that it could contribute to contemporary ethical debates. Within the framework of the latter, Franz formulated a “common ideal,” which, in his view, was urgently needed by the “defeated, impoverished, and internally divided” German nation [12, p. 126].

Between 1920 and 1935 he published a series of works addressing the theoretical interrelations between embryology, morphology, and evolution [13, 15, 17, 18]. In his monograph *Ontogenie und Phylogenie* (1927), he introduced four “biometabolic modi”: prolongation, abbreviation, deviation, and culminating deviation, as mechanisms of evolutionary modification in ontogeny [15]. As well as Sewertzoff’s *modes*, these were intended to refine the biogenetic law by providing a developmental and physiological explanation for the evolutionary transformation of form (Fig. 7).

As well as Sewertzoff, Franz not only reformed the biogenetic law but also proposed his theory of directions of evolution. The central point of Franz’s fundamental work on the history of organisms, in which he applies the criteria of perfection to detailed morphological analyses of phylogeny, is the idea that the process of perfection is constituted through centralization and differentiation [14]. In a work published 11 years later, he additionally introduces the concept of “superiority,” which reinterprets Franz’s idea of gradual perfection: “Since 1920, I have shown that in the history of organisms, increasing differentiation and centralization is always associated with growing superiority or success in the struggle for existence, as evidenced by the increasing ecological relief ...” [18, p. 2]. Franz now explicitly expresses the idea that his theory of perfection could find practical-political application. Against this background, his theory of evolutionary progress supported the ideology of National Socialism in Germany [33]. Franz refers to the Gauleiter of the Bayerische Ostmark and Bavarian Minister of Culture, Hans Schemm, who defined National Socialism

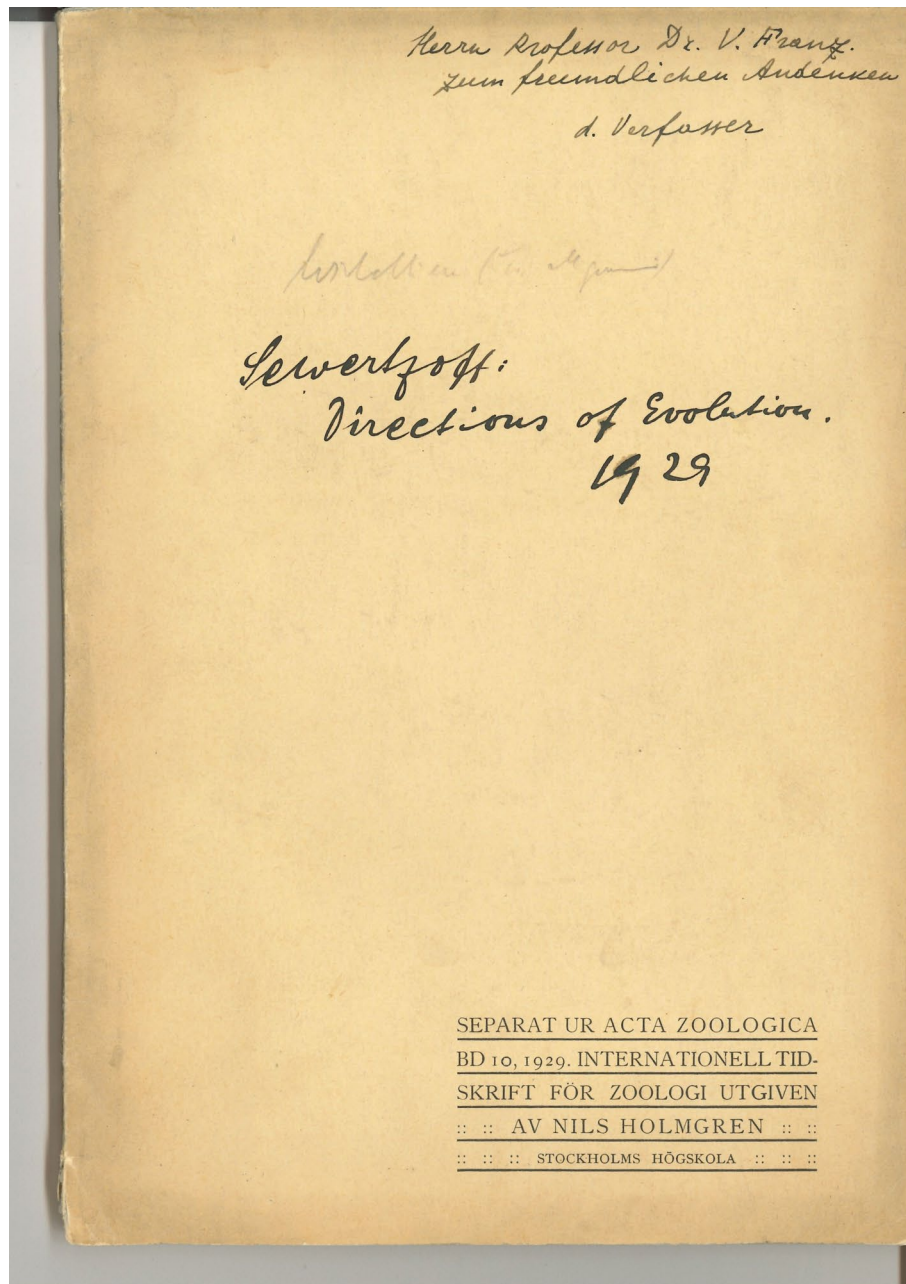


Fig. 7 Sewertzoff's Book "Directions of Evolution" with a handwritten dedication to Franz

as "politically applied biology" and he draws parallels between organism and state, which he equates with a "living organism of strict differentiation and centralization." Finally, Franz attempts to explain political events in terms of his evolutionary theory: "[...] And it is especially clear to us Germans today that such an organism can come so close to disintegration through the autonomy of its parts or partial functions that a strong centralizing force is required to save it. This occurred in the German March Revolution of 1933" [18, p. 77].

Franz's mature views were presented in *Biological Progress: Theory of the Phylogenetic Perfection* [*Der biologische Fortschritt: Theorie der organismengeschichtlichen Vervollkommnung*] (1935), which offered a concise exposition of his theoretical system [18]. In 82 pages, he summarized his key concepts of centralization, differentiation, and energetic improvement, arguing that the advancement of organisms could be understood as an increase in organizational "vital energy." He exemplified his theory with comparative studies on the vertebrate eye, which, in his view, showed progressive improvement

from lower to higher vertebrates. In the concluding sections of his 1935 book, he explicitly aligned his notion of perfection with the *Führerprinzip* of the *Third Reich*, equating biological “advancement” with racial purification and the selective promotion of “high-quality families” [18]. Franz’s conception of biological progress acquired a distinctly ideological dimension during the 1930s. In 1937, Franz published a programmatic paper, “*Progress or Theory of Perfection, Built Upon Haeckel’s Phylogenetic History*” [*Vervollkommnungstheorie, der Aufbau auf Haeckels Stammesgeschichte*]. Drawing on the “Darwin-Haeckelian theory of descent” [27], he connected his theory of progress to “ethical” issues, explicitly embedding racist ideas: “A new supreme goal now stands before us: racial awareness. The uniformity of the race allows us to live in accordance with the Nordic-German ideals of honor, martial valor, loyalty among men, strict morality, clarity, and attachment to the homeland” [19]. Franz extended his law of progress to attack “individualism,” which he portrayed as incompatible with the new direction Germany was taking under Hitler’s totalitarian leadership [19]. His theory of biological progress served to legitimize the regime, as he argued that the improvement of a nation depended on the selective breeding of its most “culturally advanced” racial components [19].

In his final paper, published after World War II only a few months before his death in the newly founded GDR, Franz reiterated and further developed his central claims while, as expected, removing any explicit references to Nazi ideology [21]. In this paper, with the long and somewhat pretentious title “*On the Current State of the Theory of Biotechnical Progress in the History of Plants and Animals*,” [Zum jetzigen Stand der Theorie vom biotechnischen Fortschritt in der Pflanzen- und Tiergeschichte] Franz explicitly cites Sewertzoff as one of the few authors whose views he considered “akin” to his own. Franz introduces here the theory of progress as the “the crowning keystone” of evolutionary theory. Franz’s central idea is that in no habitat does a true biocoenotic equilibrium exist over the long term, that is, there is no balance in the reproductive pressures among the species that inhabit it. Instead, certain species always gradually increase, genuinely reproducing, to the detriment of others, which decline [21]. From a purely technical perspective, as if they were machines, organismal species differ in their “degree of perfection”, i.e. in how effectively they secure survival and reproduction with minimal energy expenditure. Predators of large prey outperform small-prey hunters, Franz argues, as they expend less effort per unit of gain. Progressive organisms allocate more resources to high-yield functions (e.g., vision over touch) and exhibit increasing centralization and differentiation of both structure and control. Differentiation is for Franz the progressive specialization of parts within an organism, such

that distinct structures and functions emerge from an originally more homogeneous organization. The increasing coordination, regulation, and control of differentiated parts through integrative centers or higher-order organizational units is called centralization. In another place Franz commented: “The ascendent is that form which, in comparison with the other, is constructed in a regular and particularistic manner (for example, strict metamorphism as opposed to interpenetrating structures)” (Fig. 8) [15]. Warm-blooded animals, with their advanced sensory systems and centralized nervous organization, exemplify greater “biotechnical” efficiency [21]. Franz, again, advances his favored idea that evolutionary success depends on centrally organized differentiation, shorter internal transport and control pathways (nerves, blood flow), and the harmonious integration of parts; in contrast, uncoordinated differentiation produces “bizarre” forms that are evolutionarily unstable. In other words, increasing centralization and differentiation of structure and control remains Franz’s central point, now detached from any Nazi parallels, though still analogized to state-building: “The greater the differentiation and centralization, the more state-like the organism becomes, and the more it constitutes a whole in the sense of indivisibility” [21]. Franz claims this framework restores scientific legitimacy to the concept of evolutionary “advance” while avoiding teleology or metaphysics, Franz argues. Avoiding, this time, a direct “application to humans,” he nevertheless feels justified in urging humans to “avoid excessive differentiation (fragmentation) and seek harmonious balance through centralization.” This indicates that he still considered his concept applicable to social processes [21]. Although Franz claims to reject teleology, his evolutionary model repeatedly and predictably moves toward centralization, differentiation, functional economy, and integration, and he extends this directional logic to both biological evolution and society. In this sense, his conception of evolution remains teleological in a weak, structural sense and ultimately moves beyond the explanatory domain of biology into society, ethics and politics.

Franz’s theoretical system thus combined an evolutionary morphology inspired by Goethe and Haeckel with an explicitly hierarchical and biologically determinist worldview. Unlike Sewertzoff’s Darwinian and explicitly non-teleological approach in the Soviet context, Franz sought to reconcile developmental biology, evolutionary theory, and even political ideology with a very broadly construed idea of progress (Fig. 8).

Conclusions

Both Franz and Sewertzoff formulated closely aligned evolutionary-morphological concepts, each grounded in two central ideas: that evolution proceeds along

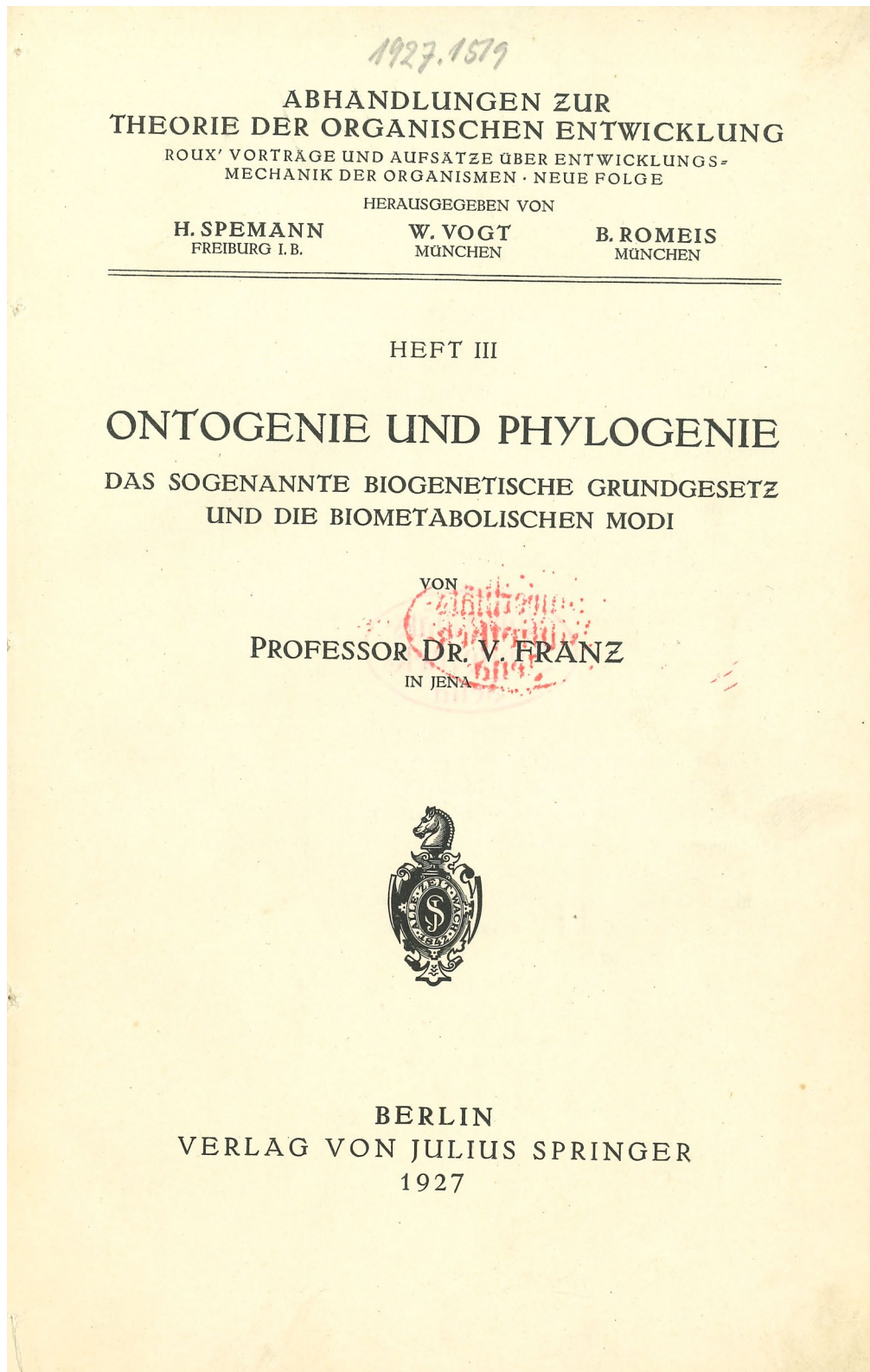


Fig. 8 Cover of Victor Franz's "Ontogeny and Phylogeny", where the concept of four "biometabolic modi" of phyletic change was introduced

certain directional trends and that Haeckel's biogenetic law requires revision. Yet the subsequent trajectories of their theories diverged markedly. Sewertzoff's ideas were further developed and incorporated into the Modern Synthesis by his student Ivan Schmal-hausen, securing Sewertzoff's status as a foundational figure in evolutionary morphology and developmental biology. His scientific legacy is widely regarded as a significant advance in both fields.

Franz's theoretical contributions, by contrast, were largely forgotten and today attract interest only among professional historians of science. Several factors explain this strong difference in posthumous reception. Franz openly supported the Nazi regime and sought to use his theory as a biotheoretical foundation for Hitler's dictatorship, a move made possible by his overextension of the explanatory power of comparative morphology, which he attempted to transform into an instrument of political ideology. Early in his career he adopted certain metaphysical assumptions, most notably the notion of "perfectioning" [Vervollkomm-nung], which he continued to refine throughout his scientific work. Yet Franz's "modi" and his theory of perfection cannot truly be regarded as full-fledged theories; they remained brief sketches lacking detailed morphological analysis and in-depth empirical research. On a strictly "technical" level, Franz's principle of centralization represents only one among many evolutionary modes, yet he falsely elevated it to a universal evolutionary law, as Schmal-hausen explicitly noted. In that sense, Franz echoed the intellectual overreach of his "academic grandfather" Haeckel, who likewise elevated the biogenetic law to an absolute principle.

Sewertzoff, by contrast, developed a highly detailed, diverse, and empirically grounded theory of development and evolution. His ideas were presented in extensive volumes that gradually moved from rich descriptive material toward broad theoretical generalizations. His writings contain no explicit metaphysical framework; he rejected simplistic models of ascending evolution and helped lay the foundation for modern perspectives on evolutionary progress. As a result, Sewertzoff's theory was ill-suited to political instrumentalization or to serving as a justification of social ideology. His pupil Schmal-hausen resisted ideological pressure within the USSR as well and carried forward his teacher's line of research.

In a certain sense, the relationship between Sewertzoff and Franz parallels that between Kowalevsky, Metchnikov, and Haeckel. The latter was criticized by the former for excessive speculation in his theoretical constructions and, like Franz, eventually sought to adapt his theory to contemporary political purposes toward the end of his life.

Acknowledgements

We sincerely thank Prof. Andreas Hejnol (Jena) for his generous support and guidance during the preparation and publication of this paper. We are also grateful to the anonymous reviewers for their insightful and constructive comments, which substantially improved the manuscript.

Author contribution

GL and UH contributed equally.

Funding

Open Access funding enabled and organized by Projekt DEAL. This research received no external funding.

Data availability

No datasets were generated or analysed during the current study.

Declarations

Competing interests

The authors declare no competing interests.

Received: 21 November 2025 / Accepted: 16 January 2026

Published online: 10 February 2026

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