Valentin Haecker (1864–1927)

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Abstract

The German zoologist Valentin Haecker (1864–1927) is one of the forerunners of experimental biology, genetics, and developmental physiology. In his

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"Entwicklungsgeschichtliche Eigenschaftsanalyse," published in 1918, Haecker tried to describe the earliest stages in the development of the phenotype (*Phenogenetics*). His major objective was to embrace two central concepts of Mendelian genetics, phenotype and genotype, within a well-articulated theory. Haecker realized that a proper analysis of how the genotype gives rise to the phenotype requires joint efforts of morphology, physiology, and experimental embryology. In this sense, Haecker's theory of phenogenetics became not only indispensable for the future acquisition of knowledge in epigenetics but also in the field of evo-devo.

Keywords
Phenogenetics · Developmental genetics · Valentin Haecker · Pluripotency · Neo-Lamarckism

Life

Ferdinand Carl Valentin Haecker was born on September 15, 1864, in Ungarisch-Altenburg (today Mosonmagyaróvár, Hungary) as the son of the Professor of Agriculture Christian Ludwig Haecker and his wife Julie Charlotte Schübler. During his childhood, Haecker concentrated on the exact and natural sciences. Since 1870 he went to the elementary school in Altenburg. In 1873 his father died unexpectedly from a stroke. A year later, the family moved to Stuttgart, where Haecker continued his education at a secondary school. In 1879 he joined a Convent School in Maulbronn (Neckarkreis). After two years his class moved to Blaubeuren (Swabian Alb), where he passed through a difficult examination and got his matriculation examination in 1883. After the school, Haecker served one mandatory year in the German army as a lieutenant. In the fall 1884, together with his brother Walter, he enrolled first at the Convent of Tübingen (Stift), and later at the Tübingen University to study mathematics and natural sciences. At the University of Tübingen, Valentin attended lectures of Theodor Eimer (1843–1898), a founder of the orthogenesis theory. Being moved for a while to Straßburg, he graduated in the spring of 1889. After receiving his PhD with Eimer with a dissertation "About the Colours of Bird's Feathers" in 1889, he spent a decade in Freiburg with the co-founder of neo-Darwinism August Weismann (1834–1914), first as an assistant, and later as a Privatdozent, after defending his habilitation thesis. In 1895 he became Professor of Zoology. Based on the research conducted in Freiburg, Haecker published his first book, *Praxis and Theory in the Cell- and Fertilization Studies,* in 1899. Two of his later books, *Bastardization and the Formation of Gamete* (1904) and *About Memory, Heredity and Pluripot*ency (1914), were dedicated to Weismann's 70th and 80th birthdays and resumed his research of the Freiburg period as well (Fig. 1).

In 1900, when Haecker was 36 years old, he became the Chair of Zoology at the Technical University in Stuttgart as a successor of Carl Benjamin Klunzinger (1834–1914). In Stuttgart, he lectured for students of agriculture and veterinary medicine and became interested in Mendelism. During this period, Haecker

Fig. 1 Valentin Haecker as Rector at Halle University (University Archive Halle, Rep. 40, Nr. I, HI 36)

evaluated the Radiolaria collection of the Valdivia-expedition (1898–1899) with Carl Chun (1852–1914). In 1903 Haecker married Johanna Lucia Anna Kühn. The couple had two children: a daughter, Hertha, and a son, Rudolf. In 1908 Haecker joined the editorial board of the newly founded journal *Zeitschrift für Induktive Abstammungs- und Vererbungslehre* (ZIAV). His research interests in Stuttgart focused on axolotls neoteny. In 1909 he moved to Halle as a Full Professor of zoology at the Philosophy faculty. He was elected as a member of the Leopoldina Academy in 1910.

While teaching at the University of Halle, Haecker supervised Bernhard Rensch (1900–1990) and Gerhard Heberer (1901–1973), two PhD students who later became leading figures of the Modern Synthesis in Germany (Reif et al. 2000). In 1922 Rensch published his paper on dwarfism and gigantism in the domestic fowl. Two years later Heberer published his PhD thesis devoted to the study of sperm formation in copepods. Among all Haecker's students, Rensch was especially well trained in the analysis of speciation and phylogeny. Rensch recognized early on the potential and the great theoretical importance of new systematics. His studies significantly contributed to a new field of genetics created by Haecker, the so-called "Phenogenetics" (developmental genetics), devoted to analyze developmental processes resulting in different phenotypic characters. On the other hand, Haecker was convinced that there were strong evidences in favor of nongenetic, Lamarckian mechanisms of modification explaining, for instance, "the geographic color differences of birds and mammals – more brownish in Western and more grayish in Eastern Europe" (Rensch 1998, p. 294). In 1911 the first edition of Haecker's *General Genetics* (*Allgemeine Vererbungslehre*) came out of print, and in 1918 his major work *Developmental Genetics* (*Phänogenetik*) was published. Besides, jointly with the philosopher Theodor Ziehen (1862–1950), Haecker wrote a book on the inheritance and development of musical talents (Haecker and Ziehen 1923). Finally, Haecker summarized his views on Goethe's morphological works in a book (Haecker 1927a).

During the First World War, Haecker was preoccupied with the harmful effects of the war on the environment. For example, he pointed out that several plant species had shown the ability to regenerate after being effected by battles. He believed in spontaneous regeneration and hold that nature was a regulatory force which could preserve and rejuvenate the German nation. In 1923, Haecker lectured on human racial and family issues. Richard W. Darré (1895–1953), who advocated the restoration of the peasantry (Weindling 1989, p. 330), attended his lectures on agriculture.

In 1926 Haecker became the rector of Halle University. His inaugural lecture was entitled "Environment and Heredity." A year later, on December 12, 1927, he suddenly died from a stroke in Halle (Hoßfeld et al. 2017, 2018).

Work

Barthelmess and Harwood have shown that the interest in Mendelism grew rapidly in Germany around 1900 (Barthelmess 1952; Harwood 1993). The "rediscovery" of Mendel's laws in 1900 is seen worldwide as a turning point in the development of modern genetics. In the first half of the twentieth century, it was generally held that the "rediscovery" took place several times. Four (not three) European biologists – the German plant physiologist Carl Correns (1864–1933), the Dutch botanist Hugo de Vries (1848–1935), the Austrian plant breeder Erich von Tschermak-Seysenegg (1871–1962) along with his brother, the Austrian physiologist Armin von Tschermak-Seysenegg (1870–1952) – independently and simultaneously rediscovered the Mendelian laws (Simunek et al. 2011a; Simunek et al. 2011b).

In the years immediately following the rediscovery of Mendel and until the First World War, the three Mendelian laws were modified and supplemented to explain more complex patterns of inheritance. The quantitative analysis of inheritance was extended to include both plants and animals. The Danish geneticist Wilhelm Johannsen (1857–1927) coined the term "gene" in his book *Elemente der exakten Erblichkeitslehre ("Elements of exact Genetics")* to refer to discrete hereditary units located with the cell, as well as the notions of genotype and phenotype (Johannsen 1909).

In 1901 Carl Correns began to teach the new "science of heredity" (Vererbungswissenschaft), first in Tübingen, and later in Leipzig and Münster. Other German biologists such as Erwin Baur (1875–1933), Richard Goldschmidt (1878–1958), and Valentin Haecker followed him since 1910 (Harwood 1993, p. 35). In parallel, a variety of genetic textbooks came out of print: Johannes Paulus Lotsy (1867–1931) with Vorlesungen über Deszendenztheorie ("Lectures in Evolutionary Theory", 1906, 1908), Erwin Baur with Einführung in die experimentelle Vererbungslehre ("Introduction to Experimental Genetics", 1911), Richard Goldschmidt with Einführung in die Vererbungswissenschaft ("Introduction to General Genetics", 1911), V. Haecker with Allgemeine Vererbungslehre ("General Genetics," 1911), Ludwig Plate (1862–1937) with Vererbungslehre ("Genetics," 1913), Arnold Lang (1855–1914) with Die experimentelle Vererbungslehre in der Zoologie seit 1900 ("Experimental Genetics in Zoology since 1914"), Heinrich Ernst Ziegler (1858–1925) with Die Vererbungslehre in der Biologie und in der Soziologie ("Genetics in Biology and Sociology", 1918), or Johannes Meisenheimer (1873–1933) with Vererbungslehre ("Genetics", 1923). In addition, several new biological journals were founded such as *Archiv für Rassen- und Gesellschafts-biologie* (*Archive for Race and Society Biology*), *Archiv für Zellforschung* (*Archive for Cell Research*), *Zeitschrift für Pflanzenzüchtung* (*Journal of Plant Breeding Research*), or *Zeitschrift für induktive Abstammungs- und Vererbungslehre* (*Journal for the Inductive Study of Evolution and Heredity*). As a result of this development, several geneticists with an interest in botany or zoology acquired chairs at different German universities. Haecker moved to Halle (1909), Correns went to Leipzig (1902) and later to Münster (1909), Plate (1909) became Haeckel's follower in Jena, and Baur received a chair in Berlin (1911). Haecker was a key figure in the growth of genetics of that time, but he also had interests in various fields of biology such as ornithology, animal physiology, marine biology, developmental genetics, and philosophy (Haecker 1965; Immelmann 1965a, b; Rensch 1965; Osche 1965; Heberer 1964; Heberer 1965; Kosswig 1965). Along with R. Goldschmidt (see for instance Goldschmidt 1927), he was the second German geneticist interested in the early stages of ontogenesis. Haecker evidently influenced Conrad Hall Waddington (1905–1975), who appealed to Haecker's hypotheses in his article "The Epigenotype" (1942) or, without citing him, in his book Genetics and Development (1962). Waddington noted:

> For the purpose of a study of inheritance, the relation between phenotypes and genotypes can be left comparatively uninvestigated; we need merely to assume that changes in the genotype produce correlated changes in the adult phenotype, but the mechanism of this correlation need not concern us. Many geneticists have recognized this and attempted to discover the processes involved in the mechanism by which the genes of the genotype bring about phenotypic effects. The first step in such an enterprise is [. . .]to describe what can be seen of the developmental processes. For enquiries of this kind, the word 'phenogenetics' was coined by Haecker. The second and more important part of the task is to discover the causal mechanisms at work, and to relate them as far as possible to what experimental embryology has already revealed of the mechanics of development. We might use the name 'epigenetics' for such studies, thus emphasizing their relation to the concepts, so strongly favourable to the classical theory of epigenesis, which have been reached by the experimental embryologists. We certainly need to remember that between genotype and phenotype, and connecting them to each other, there lies a whole complex of developmental processes. It is convenient to have a name for this complex: 'epigenotype' seems suitable. (Waddington 1942, p. 18)

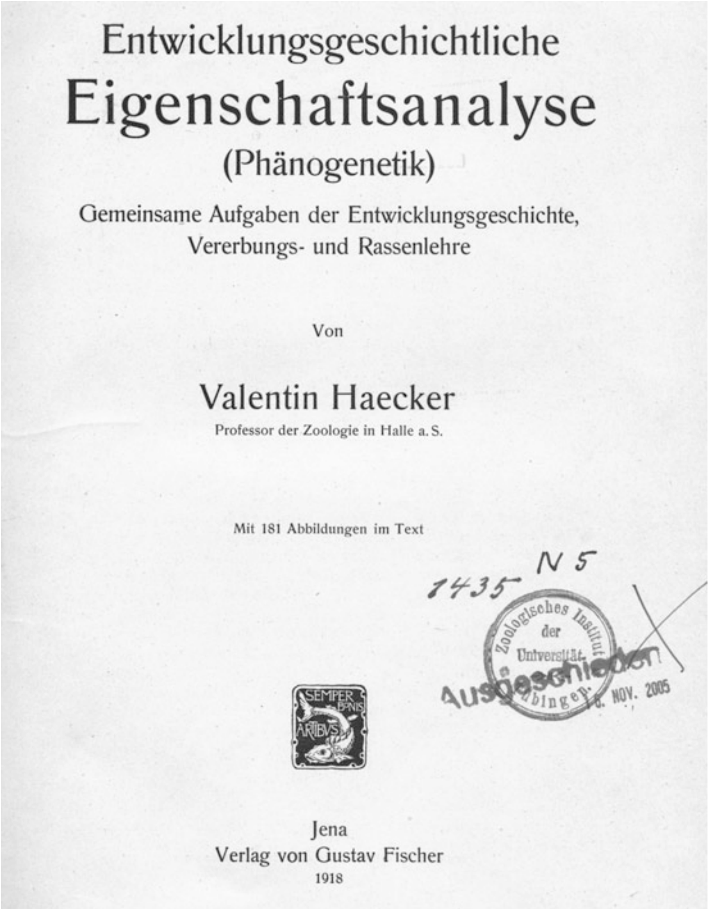
Haecker's Lamarckism

Many German biologists, in particular zoologists and paleontologists, defended Lamarckian evolutionary mechanisms between 1900 and 1940. They believed in the inheritance of acquired characters and a direct effect of the environment on organism's inheritance. For example, the zoologist and geneticist Ludwig Plate (1862–1937) campaigned for a revival of the original Darwinism. His research program, which he labeled "old-Darwinism," proclaimed the synthesis of selectionism with "moderate Lamarckism" and orthogenesis (Rensch 1983, 1998; Harwood 1993; Levit and Hoßfeld 2006). Plate defined the inheritance of acquired characters as follows: "The inheritance of an acquired character means only that a newly occurred character was in the first generation somatogenic whereas in the subsequent generations it becomes blastogenic" (Plate 1913, p. 439). In modern terms, this means that there is a variety of features, which have been phenotypic in a certain generation and became inheritable in all subsequent generations (Levit and Hoßfeld 2006). Plate attached great importance to the idea that the inheritance of acquired characters should not necessarily be combined with the Lamarckian idea of use or disuse of a certain organ: "It is no matter whether somatic modifications are caused by a use or disuse of an organ or by temperature, nutrition or other factors" (Plate 1913, p. 440).

Haecker, as well as Plate, advocated Lamarckian evolutionary mechanisms, but by contrast to Plate, he concentrated on the description of the phenotype and paid little attention to selectionism; there is not a single reference to natural selection in Haecker's book of 1918. At the cell biology level, he paid much attention to the chromosome theory:

> Haecker acknowledged the importance of the chromosome theory but remained dissatisfied with several of its features throughout his life. Many of his criticisms were also voiced by Bateson: the cytological evidence for crossing-over was inadequate; vastly different kinds of organisms sometimes possessed the same number of chromosomes; sex chromosomes were less likely to be the cause of sex differences than merely indicators of the real cause; and the evidence for purity of the gametes was unconvincing (Harwood 1993, p. 42).

In his *Allgemeine Vererbungslehre* ("General Genetics"), Haecker postulated that speciation was caused by the selection of hereditary varieties in August Weismann's sense. Haecker was convinced that the inheritance of acquired characters should be regarded as improbable, because a chain of causal events which phenotypically altered the soma and the genes could never be identical with a causal chain leading from altered genes over embryonic stages back to the characteristics of the soma (Rensch 1983, p. 32). He argued that "If one assumes that different 'virtual possibilities of individual development' exist, then 'a parallel activation' (*Parallelaktivierung*) of latent general potentialities in genetic and somatic cells by means of the altered chemical processes takes place" (Haecker 1921, p. 154). He also believed that "constitutional concussion" of genetic and somatic cells could cause a parallel reduction of the resistance against illness. Thus, in 1918 he



Entwicklungsgeschichtliche
Eigenschaftsanalyse
(Phänogenetik)
Gemeinsame Aufgaben der Entwicklungsgeschichte,
Vererbungs- und Rassenlehre

Von

Valentin Haecker
Professor der Zoologie in Halle a. S.

Mit 181 Abbildungen im Text

SEMPER APERTIS ARTIBVS

Jena
Verlag von Gustav Fischer
1918

Fig. 2 Title Page (1918)

postulated that a "parallel induction" of somatic and germ cells would be possible only "when characteristics acquired by the parents preexisted already in the virtual potential of the plasma" (Haecker 1918, p. 324).

Haecker saw as a candidate for a neo-Lamarckian evolutionary mechanism the so-called "parallel-induction," namely, the simultaneous impact of the environment on soma and germ cells, (1921, 150 ff.) as well as the "ideocynesis," defined as the influence of external stimuli on the ideoplasm (1921: 163 ff. and graft (1921, p. 170). The final version of Haecker's Lamarckism can be found in two books of him (1914, p. 8, 1921, p. 148) (Fig. 2).

Haecker's Phenogenetics

One of Haecker's objections to the Mendelian chromosome theory was its failure to bridge the gap between hereditary units and phenotypic traits. His research program, which he called *Phänogenetik* ("phenogenetics"), had precisely the objective to build this bridge between the genotype and the phenotype (see the chapter "▶ Genotype-Phenotype Map"). He outlined this program in a study of 1918. In the preface, Haecker described a new research field that should explore "in terms of morphogenetics and developmental physiology" the appearance of the organism's "external characteristics" (Haecker 1918, p. 4; Deichmann 1996, p. 164).

According to Haecker, phenogenetics always begins with the so-called "differential diagnostics," i.e., with histological, morphological, and physiological studies of differences between species or races. All his phenogenetic investigations were descriptive, such as color differences in different races of mammals, axolotls, birds, and plants (Chaps. 7–13) as well as the stripe patterns in various species (Chap. 14), or the growth of the skin (Chaps. 16–18). This "phenoanalysis" is followed by a "phenogenetic descriptive" investigation of variations of a certain trait. The traits in question are traced back to a "phenocritical phase," the point of bifurcation in which the developmental stage manifests an initial divergence of the trait. Phenogenetics in the narrow sense is the study of diverging developmental pathways, and it must penetrate into the deeper ("phenocritical") causes of the observed divergence (Haecker 1918, p. 4 ff.). This process can proceed epigenetically externally or internally, and in that sense phenogenetics is a subdiscipline of developmental mechanics (*Entwicklungsmechanik*) and developmental physiology (*Entwicklungsphysiologie*).

In 1918, Haecker also discussed the problems of asymmetry, such as handedness in humans, which he considered an inherited trait. He also looked at other phenogenetic problems in the anomalies of extremities in animals and humans such as polydactyly, syndactyly, and brachydactyly. Haecker was also particularly interested in the phenogenetics of skull form and face shapes and was most involved in the study of abnormalities of the lower jaw. From a developmental history perspective, he viewed skull and face shape, as well as certain regions of the face, as "compound characters" (*komplex-verursacht*) in William Bateson's sense (Haecker 1918, p. 279), i.e., the development of these regions is seen as a product of the interaction of various developmental processes that occur under the influence of the neighboring organs (Lehmann 1965) (Fig. 3).

The Problem of Pluripotency

The study of pluripotency (*Pluripotenz*) and its evolutionary causes was one of the tasks of phenogenetics. Haecker first used the term *Pluripotenz des Artplasmas* ("Pluripotency of species specific plasm") in his book *Über Gedächtnis, Vererbung und Pluripotency* (1914, p. 40) and explained the hypothesis in detail in his later work on "The manifestations of pluripotency" (*Pluripotenzerscheinungen*) (Haecker

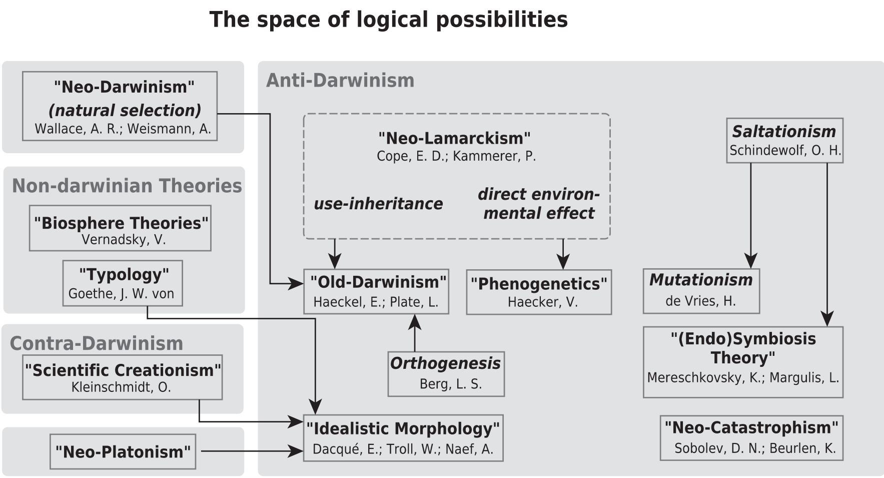


Fig. 3 The whole panoply of alternative evolutionary theories available in the first half of the twentieth century. Some of these theories persisted into the 1950s and 1960s. Neo-Lamarckism, saltationism, typology, and orthogenesis played major roles in the discussion of evolutionary mechanisms and were very influential in paleontology. Names in the boxes are prominent proponents of each theory (Levit and Hoßfeld 2011, 2013)

1925). In general, Haecker's theory of pluripotency postulated a relatively plastic concept of hereditary material suitable to account for the inheritance of acquired characters (Harwood 1993, p. 131 – Haecker 1918, Chap. 25; 1911/1921 Chaps. 14–17). In 1925 he published the most complete definition of the term:

> In a narrow (evolutionary) sense, *I understand by pluripotency* an *essential abilit*y of every organism (not only of species and races, but also of any individual germ and any cell at the embryonic stage of any individual) to develop under certain circumstances in directions *deviating from the basic typ*e. Therefore, pluripotency is a presence of a greater, *although not unlimited number*, of potencies or developmental possibilities than determined by a *property grounded in a normal, material, structural constitution of a species specific - but for the most part common to many species - plasm* (1925, pp. 1–2. Haecker's italics. Our translation).

Under the term *Artplasma* ("species specific plasm"), Haecker understands a hereditary material in the very broad sense, whereas the germ plasm was for him identical with nuclear substance of germ cells and germ line cells. Pluripotency enters the stage when the *Artplasma* jumps into another state of equilibrium. If a pluripotency occurs in the germ cells, it is called a "germ plasmatic pluripotency," while if it takes place during the ontogenesis of embryonic organs, it is a "somatic pluripotency." In that sense, Haecker maintained that transitions from heritable variations of germ cells to nonheritable variations of soma were possible (1925, p. 3). In such cases as atavisms and rudiments, pluripotency manifests itself in the ontogenetic development. The Russian botanist Nikolai I. Vavilov (1887–1943) spoke in this respect on *homologous* series and formulated his famous "Law of Parallel Variation," establishing a parallel variability of homologous characters in taxonomically near species (Kupzow 1975), however, without citing Haeckers paper of 1924 (Haecker 1924).

Contributions to General Biology

In addition to his work in genetics and developmental biology, Haecker also conducted research in the field of reproductive biology with a focus on copepods. He was also interested in ornithology as well as in the study of Radiolari. From his work in reproductive biology, his Titisee study from 1901 is most worth mentioning. Here he made a significant contribution to understanding the complex geographical and ecological distribution as well as the reproductive cycle of zooplankton in mountain lakes (Haecker 1901, Elster 1965, Hoßfeld 1996). The study of ornithology also played an important role in Haecker's life and work. In fact, he produced 22 publications on the subject (Immelmann 1965a, pp. 71–72). His book *Der Gesang der Vögel, seine anatomischen und biologischen Grundlagen* (*The bird song and its anatomical and biological foundations*), published in 1900, was based upon comparative phylogenetic perspectives. Upon looking at the phylogenetic development of song, Haecker was able to determine the phylogenetic basis of these sounds as being dependent upon different factors such as season or changes in the thyroid gland and then illuminated the connection between this and the birds' reproductive life and flight-songs. Haecker also produced a number of works on bird migration and their feathers as well as the correlation between the bird colors and phenogenetics (1921, 1924, 1927b). In 1908, he presented a comprehensive evaluation of a collection of Radiolari materials, edited in volume no. 14, which had been gathered from 1898 to 1899 by a German deep-sea expedition in Valdivia, led by Carl Chun (Haecker 1908).

Legacy

Valentin Haecker numbers among the crucial figures in the history of German genetics of the first half of the twentieth century along with Richard Goldschmidt, Erwin Baur, and Ludwig Plate. His contributions to developmental physiology and experimental biology in general are indisputable as well.

Haecker himself championed the idea that experimental biology was of great importance for applied biomedical research and anthropology. This was due to the fact that experiments are possible in almost all fields of biology, whereas they might be difficult in medicine. Haecker was arguably the first who realized the importance of genetics for medical research.

His main contributions to genetics were the foundation of the theory of phenogenetics and his conceptual work on pluripotency. Although his phenogenetics was a neo-Lamarckian theory, it bounded together the findings of various biological disciplines and answered the questions on the relationships between the phenotype and the genotype. Therefore, Haecker's phenogenetics was indispensable not only for the growth of developmental genetics, but also in the field of evo-devo. Although neo-Lamarckian in its essence, Haecker's phenogenetics reflected on many important aspects of relationships between phenotype and genotype and, in this sense, contributed to the growth of developmental genetics. From today's viewpoint, Haecker's phenogenetics appears as an experimental embryology which, using such methods as alteration or switching off and on of certain genes in order to test the reactions of various organs to different genetic perturbations, appears as a pioneer of contemporary developmental genetics (Freye 1965a, b; Hoßfeld et al. 2017). Haecker recognized very clearly that genetics should closely cooperate with morphology, physiology, and experimental embryology. Currently, one proceeds from the assumption that the interplay of the genotype and environmental factors determines the phenotype. Haecker as well as current biologists rejected any influence of phenotype on genotype. His neo-Lamarckism was constrained solely to the idea of direct environmental influences on development. The latter makes his approach akin to modern epigenetics. Today it is known that environmental impact can simulate genetics effects (phenocopy) (Hallgrímsson and Hall 2011; Hendrikse et al. 2007; Graw 2010).

Cross-References

► Conrad Hal Waddington (1905–1975)
► Developmental Plasticity and Evolution
► Eco-Evo-Devo
► Genotype-Phenotype Map
► Parallelism
► Richard Goldschmidt (1878–1958)

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