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The Forgotten "Old-Darwinian" Synthesis: The Evolutionary Theory of Ludwig H. Plate (1862–1937)[1]

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The German zoologist and geneticist Ludwig Plate was a pupil and successor of the "German Darwin" Ernst Haeckel as the director of the Institute of Zoology at Jena University. Plate campaigned for a revival of the original Darwinism. His research program, which he labelled "old-Darwinism", proclaimed the synthesis of selectionism with "moderate Lamarckism" and orthogenesis. This article reconstructs and analyses Plate's "old-Darwinian" synthesis and sheds light on Plate's controversial biography, especially his conflict with Haeckel.

1 Introduction

The zoologist and geneticist Ludwig Hermann Plate (1862–1937), pupil and successor of Ernst Haeckel (1834–1919) at Jena University, is one of the most important figures in the 'pre-synthetic' period (first third of the 20th century) of continental European evolutionary biology. Plate campaigned for a revival of the "original Darwinism" combining selectionism with neo-Lamarckian ideas, and was seen by many contemporaries worldwide as a proper advocate of Darwinism. Thus, a prominent Russian biologist, geographer and anti-Darwinist Leo S. Berg (1876–1950) saw Plate as his main scientific opponent [Berg, 1922, 1926]. The American paleontologist Henry F. Osborn (1857–1935), who sought a compromise between selectionist and neo-Lamarckian methodologies, likewise honoured Plate with the title "prominent selectionist" [Osborn, 1926]. Another of Plate's contemporaries, the Swedish anti-Darwinian historian of science Erik Nordenskiöld (1872–1933) claimed that Plate's Selektionsprinzip (1913) contains "all that can be adduced in modern times in defence of the old Darwinism. And as its champion Plate has done a great service, thanks to his wealth of knowledge, his strong convictions, and his honesty" [Nordenskiöld, 1928, p. 572]. Nordenskiöld classified him as a middle-way Darwinian, who opposed the imperious dispositions of his master Haeckel and choose a course pursued by Darwin himself.

Selectionists counted Plate as one of their most important theoretical opponents as well. For example, in the works of the Russian evolutionary morphologist Alexej N. Sewertzoff (1866–1936) Plate is one of the most cited authors [Sewertzoff, 1931]; [Levit et al., 2004].

The majority of German evolutionary biologists referred to the Jena zoologist either for supporting for their own views or as a serious theoretical opponent. The sympathizers and "architects" of the German evolutionary synthesis also did not pass over Plate's work in silence (see, e.g. [Heberer, 1943]). This can be exemplified by the German zoologist Bernhard Rensch, who indisputably belongs to the leading figures in the German "synthetic" movement. As Thomas Junker [2004, p. 166] stresses, Rensch is said to be the most cited author in Ernst Mayr's *Systematics and the Origin of Species* [1942]. Ironically, in the first edition of his *Neuere Probleme der Abstammungslehre* [1947] Rensch cites Mayr only five times in contrast to 23 references to Plate. Even Darwin with 19 references appears behind Plate in this central "synthetic" book by Rensch.[2] In the third edition (1972) Rensch, increases Mayr's citations to 14, but Plate is still in the lead with 18 references.

Plate's empirical as well as his theoretical works both had an enormous impact during his life-time and are still cited in the morphological literature (e.g. [Reynolds, 2002]; [Vorster & Starck, 2003]). He was translated into Russian early on [Plate, 1928].

Yet, despite Plate's extraordinary importance for a historical reconstruction of the "pre-synthetic" period in 20th century evolutionary biology, only a few authors have so far described and analyzed Plate's evolutionary theory [Uschmann, 1959]; [Penzlin, 1994]. Therefore, the primary objective of this paper is to show the "true colours" of the German "old-Darwinian" movement as it is represented in the works of Plate. Furthermore we will briefly discuss the problem of the radical decrease of interest in Plate's ideas after WWII even in the German-speaking world, which, in our view, can be partly explained by the peculiarities of Plate's biography and personality and, partly, by theoretical developments in evolutionary biology.

2 Biographical sketch

Ludwig Hermann Plate (fig. 1) was born on August 16, 1862 in Bremen (Germany) as the son of a teacher. In 1882 he started to study mathematics and the natural sciences in Jena, Bonn and Munich [Plate, 1935]. He had developed an interest in evolutionary theory already by attending Ernst Haeckel's lectures in Jena. However, "the proper training in zoology" Plate owes to his teacher Richard Hertwig (1850–1937), who lectured in Munich and Bonn and who impressed the young scientist very much. Hertwig later encouraged him to write a doctoral thesis [Plate, 1935]; [Böhm, 1994]. Plate gained his doctorate in 1886 from Jena University after submitting his thesis on *Rotatoria* (*Rotifera*) [Plate, 1886] and passing the oral exams in chemistry (for J. G. A. Geuther, 1833–1889) and zoology/botany (for E. Haeckel). Already two years later (1888) Plate obtained his habilitation[3] in zoology at Marburg University and soon established himself as an expert in the fields of zoology and the theory of descent. In 1898 he started to teach zoology at the Veterinarian College [Tierärztliche Hochschule] in Berlin and after a short period of service as a curator at the Museum of Marine Science (Berlin) he was offered a full professorship in zoology (1905) at the Agricultural College [Landwirtschaftliche Hochschule] in Berlin.

Three years later (1908) Haeckel decided to retire from his position as director of the Institute of Zoology and Jena University offered Plate to take Haeckel's chair. After some period of negotiations and with the active support of Haeckel himself, Plate accepted the position in January, 1909 and held it until his retirement [Uschmann, 1959, p. 201].

Plate was an active field biologist and undertook several expeditions to South America, the USA, Greece and the Bahamas, where he studied marine zoology.

Fig. 1. Portrait of Ludwig H. Plate (1862–1937)

According to Plate himself these expeditions played a significant role in the development of his interest in evolutionary theory and delivered materials for comparative anatomical studies [Plate, 1935, p. 85]. His special interest before he came to Jena was in rotifers and molluscs. In Jena, Plate extended his morphological interests to other groups including insects, spiders, reptiles, amphibians, birds and mammals, while combining morphological studies with research in genetics and evolutionary theory [Böhm, 1994]. Plate was seriously involved in genetic studies already during his Berlin period (e.g. [Plate, 1900, 1905, 1906]) and continued them in Jena [Plate, 1911/12; 1913]. These studies resulted in Plate's own theory of heredity, the final version of which he expressed in some of his latest papers (e.g., 1932) and finally summarized in the three volumes of his *Vererbungslehre* (Genetics), comprising more than 3000 pages [Plate, 1932–38].

For his scientific services Plate was awarded membership by the Leopoldina Academy (Halle/Saale) (1933) as well as by the science academies in Budapest and Stockholm. He was also honoured with the *Coburger Ritterkreuz I* and the *Roter Adlerorden IV*.[4]

Yet Plate's biography also has highly controversial aspects. Thus immediately after taking office Plate came into personal conflict with Ernst Haeckel [Schmidt, 1921].

This conflict was described in detail by the biologist Adolf Heilborn, who belonged to the circle of Haeckel's closest friends [Heilborn, 1926]. In this book with an affected title *Die Leartragödie Ernst Haeckels*[5] and in a series of articles in the newspapers, Heilborn blamed Plate for making the last ten years of Haeckel's life into the "decade of Haeckel's martyrdom", which lead to his isolation in his home 'Villa Medusa' [Ibid., pp. 1, 53]. Heilborn's view of the situation was supported by Gustav Schwalbe (1844–1916), Richard Hertwig, Max Verworn (1863–1923), and many others. The quintessence of Heilborn's accusations is unfair financial claims against Haeckel (whom Plate accused of embezzling the institute's money and using the institute's library for private needs) as well as insulting behaviour towards Haeckel (e.g., Plate forced Haeckel out of his rooms in the Phyletic Museum).

Plate publicly repudiated these charges [Plate, 1920, *Die Umschau*, 6 Jan., pp. 109–111] and presented his own version of the story. He did not reject the very fact of the conflict with Haeckel and repeated his accusations. For example, Plate incriminated Haeckel for wasting 5200 Mark: "Haeckel had purchased masses of books both written by him and complementing him and given them away to his friends and favourers" [Ibid., p. 109].[6]

To defend his good name Plate started a legal process. Quite detailed information about it can be found in the newspaper *Jenaer Volksblatt*.[7] The hearings proceeded openly in Jena; tickets were even sold for the "show". The newspaper reported that sympathies were in favor of Heilborn from the beginning, and Heilborn also won the case. The judge stated that "Haeckel experienced a tragedy" [Ibid., p. 7] and declared Plate guilty.

The court of the second instance, however, decided in favour of Plate and Heilborn was sentenced to paying 900 Mark.[8] Plate has proudly written in his autobiography that he won the process against the "Jewish anthropologist", again blaming Haeckel for slandering him in an "unbelievable form" [Plate, 1935, p. 84].

Yet Heilborn's version of the story finds support in the recently published letters between Haeckel and his younger contemporary, friend and popularizer Wilhelm Bölsche (1861–1939). It is true that Haeckel was initially very optimistic about Plate's engagement in Jena. In a letter dated December 29, 1908 he wrote that Plate is in all aspects the best successor for the chair [Nöthlich, 2002, p. 214]. However, already on July 27, 1909, Haeckel reports about the hard and long conflict with Plate and complains that directly after accepting the office Plate told him in an "extremely <u>brutal</u> form" (Haeckel underlined the word "brutal"), that he (Plate) is the only director of the Phyletic Museum and Haeckel must obey his instructions. Furthermore, Haeckel reports that Plate searched his archives in his absence and blamed him for misuse of university funds (buying books for private needs). "The details of his 'inquisition' are hair-raising", Haeckel concludes [Ibid., p. 218]. In another letter (June 24, 1912) Haeckel mentions a boycott against Plate as a reaction to his "brutal behaviour" against his predecessor [Ibid., p. 245].

Nevertheless Plate's activities as director of the Phyletic Museum were very successful and Haeckel agreed, despite the personal conflict, that the Museum was established in accordance with his initial ideas [Penzlin, 1994].

Yet Plate's conflict with Haeckel was not the only dark side of his biography. He was also known as a convinced anti-Semite and supporter of the German nationalist movement long before the national socialists came to power. Already in 1904, together with the champion of "racial hygiene" Alfred Ploetz (1860–1940) and the lawyer Anastasius Nordenholz, Plate founded the journal *Archiv für Rassen- und Gesellschaftsbiologie*, which became a major tribune of theoretical racism.

Plate's nationalism brought him into conflict with liberal public organizations. For example, on January 6, 1920 the Weimar Government was forced to react on the conflict between Plate and the student organizations and the social-democratic members of the Jena Municipal Council. Plate was blamed for using his position for the purposes of political propaganda against the social democrats and in favour of nationalism and anti-Semitism.[9] Three years later the Jena organization of republican students wrote a letter to the State Ministry, where they repeatedly accused Plate for excusing the Pogroms in his lectures and for blaming Jews for propaganda of sexual immorality and social democracy.[10] Although, by contrast to many other German biologists [Junker, Hoßfeld, 2002] Plate was neither a member of the SS nor of the NSDAP, he explicitly expressed his anti-Semitic convictions and his loyalty to the national-socialist ideology not only in lectures and conversations but also in his publications (e.g. [Plate, 1934, p. 280]).

Plate's support of the national-socialist movement was also implemented in real life. For example, he supported the appointment of the Nazi-ideologist Hans Friedrich Karl Günther[11] ("Rasse-Günther") (1891–1968) as a full professor of social anthropology at Jena University against the will of the Rector and University Senate.[12] In his statement on Günther's appointment Plate wrote: "He has rendered great services by opening thousands of eyes to racial differences and helping people to come to the conclusion that Germans must be proud of their heredity, which should be kept off from the low-graded genetic sets [Plate means – nations – *Auth.*]".[13] Plate also publicized these views in several newspaper articles.[14]

A part of the national-socialist ideology which Plate passionately supported, was the idea to encourage women to focus on their roles as wives and mothers and at the same time restricting their professional activities. Plate actively maintained this anti-feminist view, which can be illustrated by the long-lasting conflict between him and the only female professor at Jena University, Mathilde Vaerting (1894–1977).[15] Plate publicly attacked both Vaerting personally and the feminist movement in general.[16] The conflict resulted in official removal of Vaerting from her office on July 1, 1933 following a decision by the Gauleiter Fritz Sauckel (head of the Weimar district [Gau]).[17]

In summary, Plate's difficult personality along with his explicit loyalty to the national-socialists explains, at least partly, the abrupt decrease of citations of his work in the post-war era. This is in sharp contrast to his indisputable impact in the first third of the century.

Plate officially held the chair in Jena until 1935 and died soon thereafter on November 16, 1937.

3 Plate's views on the mechanisms of evolution

Plate thought he had proposed a concept combining all valuable theoretical movements and new disciplines of the biology of his time. He developed a research program which he called "old-Darwinism" during more than thirty years of experimental and theoretical investigations (e.g. [Plate 1913b, 1925, 1932–1938]). Except Darwin and himself, Plate counted Ernst Haeckel, Richard Semon (1859–1919), Wilhelm Roux (1850–1924), Richard Hertwig, Fritz v. Wettstein (1895–1945), Berthold Hatschek (1854–1941), Jan Paulus Lotsy (1867–1941), Franz Weidenreich (1873–1948) and even the future "co-architect" of the evolutionary synthesis Bernhard Rensch to the old-Darwinians. According to Plate, old-Darwinism follows exactly the initial ideas of Charles Darwin, at the same time adapting and processing all healthy and empirically verifiable scientific achievements. Old-Darwinism, in Plate's view, was the only evolutionary theory able to unite all fruitful theoretical approaches (Lamarckism, selectionism, orthogenesis) with the most innovative fields of experimental biology, such as genetics.

The basic assumption of Plate's "old-Darwinian" synthesis was that pure selectionism based on random variation and natural selection cannot explain the whole panoply of evolutionary events:

- "Darwinism is a 'chance-theory' in that it takes into account variations occurring by chance in the individuals of a certain species" [Plate, 1913, p. 222].
- "However the harmonious modification of numerous features is much easier conceivable from the Lamarckian standpoint…" [Ibid., p. 224].[18]

Below we show how Plate integrated these two, from our modern viewpoint incompatible, theses into his theoretical system.

3.1 Plate's general views on the struggle for existence and natural selection

The struggle for existence is, according to Plate, a universal phenomenon: "Strictly speaking, there are as many fighters for existence as there are organisms" [Plate, 1913, p. 226].[19]

Plate distinguished two forms of the struggle for existence: the struggle with inanimate nature (temperature, light, humidity, dryness etc.) and animate forces (other organisms). The first case is not necessarily accompanied by natural selection and evolutionary progress,[20] whereas the rivalry in the second case is caused by overpopulation and automatically leads to the selection of the fittest. However, natural selection is more than just the consequence of overpopulation.

Plate's classification of natural selection follows that of Lloyd C. Morgan (1852–1936) with a few modifications.

The first category of natural selection Plate called "*natural elimination*": Natural elimination consists of the "non-selective elimination" resulting from catastrophic events and the "selective or individual elimination" (Personal elimination) of insufficiently adapted individuals. As a general rule, "non-selective elimination" has little influence on evolutionary processes, but in certain cases it can influence the course of phyletic history, for example, when the individuals, which survived a catastrophe, transfer part of the species-characters to their offspring (Plate, 1913, p. 233).

The regular evolutionary progress is, however, due to "individual" or "selective" elimination, which Plate organized into three sub-kinds: elimination through inanimate forces (e.g., climatic factors, salinity), elimination through natural predators (including parasites and bacteria) and "intra- and inter- speciational" elimination (within a species in the first case and resulting from the struggle between species in the second). Individual elimination can proceed both in a "negative" (the slow bunnies will be eliminated) and in a "positive" form (e.g., sexual selection) [Plate, 1913, p. 235]. While the intensity of intra- and inter-speciational struggle for existence is intimately connected with the degree of overpopulation, elimination through inanimate forces (for example, the so called "constitutional" struggle for existence (Konstitutionalkampf), which Plate made responsible for the removal of weak and ill individuals through inanimate forces, can proceed in small populations [Ibid., p. 238].

As necessary preconditions for natural selection Plate lists variability, heritability, geographical isolation and overpopulation, although he seems to be convinced that overpopulation is an important but not necessary precondition [Ibid., p. 437].

In Plate's latest works [Plate, 1932, 1933] we can find all the basic factors of evolution then adapted by the Evolutionary Synthesis. Thus Plate claimed that random mutations and recombination deliver the bulk of raw material for evolution. Natural selection and geographical isolation have, according to him, important roles in evolution as well (e.g. [Plate, 1933, p. 1045]). Also what is now known as "population thinking" is of great importance for Plate and he analyses the "laws of populations" using mathematics [Ibid., pp. 1047–1052].

Yet Plate admitted additional evolutionary factors which go beyond the classical theses of Darwinism. Thus he accepted both macro- and directed mutations, orthogenetic restrictions and the inheritance of acquired characters.

3.2 Plate on the inheritance of acquired characters and its place in old-Darwinian evolutionary theory

Plate defines 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].[21] 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. Plate attached great importance to the idea that inheritance of the 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" [Ibid., p. 440].

In 1913 Plate still believed that it is possible to deliver direct experimental evidence for "somatic heredity" (Plate's term for the inheritance of acquired features). He pointed out, for example, the butterfly experiments of Maximilian R. Standfuß (1854–1917). Standfuß [1899] had shown that subjecting the chrysalises of *Vanessa urticae* to low temperatures (0–18°C) leads to an increase of fuscous-coloured butterflies. Crossing these fuscous-coloured butterflies with each other produced several male butterflies (4 out of 2000 initial chrysalises) with presumably inheritable fuscous-coloured wings. The experiment was however disturbed by an insect-infection and is considered of doubtful value. Plate described and analysed many experiments of this kind in the hope that some decisive experiments could solve the problem of "somatic inheritance".

However, already in his 1922 textbook *Allgemeine Zoologie und Abstammungslehre* Plate claimed that the crucial issues of heredity are too complicated to be once and for all solved by experiments and must be approached both empirically and theoretically. In this book Plate provided several important arguments for the inevitability of Lamarckian explanations in any evolutionary theory [Plate, 1922, p. 9]:

- Only Lamarckism explains the appearance and eventual disappearance of vestigial features: because they are neutral or insignificant in the initial stages they are inaccessible for natural selection (example: the disappearance of pigmentation on the underside of pleuronectids [flounders] resulting from the lack of light).
- The degeneration of characters sometimes proceeds inexpediently.
- The homologies demonstrate that a number of complex organs (like the compound eye) occur independently in different families; one cannot admit that a purely random series of mutations would lead to the same result in all known cases.
- A variety of evolutionary modifications would be impossible without simultaneously (co-adaptively) changing features; for example, the ganglia of arthropods were concentrated around the brain in such a way that some strands grew short, while some nerves became longer during evolution.
- Studies of regeneration processes show that there is no impenetrable barrier between somatic cells and germ cells.

Despite this defence of Lamarckism Plate's objective was not to dethrone natural selection, but, on the contrary, to defend it by showing that it can co-exist with Lamarckian evolutionary mechanisms. Accordingly, Plate made great efforts to define the exact ratio of Lamarckian and selectionist mechanisms in evolutionary processes [Plate, 1913, pp. 549–608]. For this purpose he analysed the concept of adaptation.

Adaptation by means of natural selection, Plate argued, can be achieved in three different ways. In the majority of cases natural selection operates under the permanent pressure of overpopulation leading to spatial diffusion of organisms (*extensive effect*). In the case of monotonous environmental pressure, natural selection acts as a conservative force eliminating pathological and deficient individuals (*conservative effect*) [Ibid., p. 552]. However, in changing environments natural selection operates as a breeding and directing force in that it preserves a number of variations and guides the "flow of life" in the certain directions. In the latter case natural selection slowly increases the degree of adaptedness and therefore determines the qualities of future generations (*prospective effect*). "In all three cases", Plate concluded, "the struggle for existence and natural selection operate positively; this means that they create circumstances which would not occur in their absence; and nothing is more incorrect than to describe these factors as purely negative" [Ibid., p. 553].[22] So natural selection by Plate is a *creative force* and in this respect he is in accord both with Darwin himself and with our contemporary understanding of Darwinism (compare [Harwood, 1993, p. 107]).

The crucial distinction between the purely selectionist, old-Darwinian and purely Lamarckian mechanisms of evolution, Plate claimed, lies in their views of adaptation. When exposed to an absolutely new environment, organisms, in most cases, either react purposefully, i.e. adapt to the new circumstances, or go extinct. Lamarckians in this situation would believe that the majority of organisms will react purposefully and directly adapt to the new environment, whereas pure selectionists would negate any possibility of direct adaptation and claim that adaptation proceeds by the "indirect way of natural selection". Old-Darwinians in this situation would propose that different individuals react differently and only a few of them react "purposefully" in the Lamarckian sense, while most organisms simply disappear [Plate, 1913, p. 561–574].

In other words Plate believed that direct adaptation is an auxiliary mechanism of evolution: "Without doubt such direct adaptation occurs very rarely and in the overwhelming majority of cases adaptation proceeds in the indirect way of natural selection […]" [Ibid., p. 572].[23]

Plate excluded "direct adaptations" both for the very complex adaptations[24] and for the cases which he labelled "simple active adaptations". For example, the simple teeth of lizards would never turn into the hooked teeth of snakes by means of direct adaptations, and can be explained only by natural selection [Ibid., p. 597]. At the same time one cannot explain the appearance of the complex characters of the highest adaptive value (such as the vertebrate eye) solely by random variation and natural selection.

Therefore, Plate resumed, only "Darwinism and Lamarckism together can deliver a fair explanation of the origin of species including the emergence of adaptations, whereas each theory alone is unable to do this" [Ibid., p. 603].[25]

3.3 Orthogenesis and orthoselection

Plate viewed the concept of directed evolution (*orthoevolution*) as one of the most important principles of evolutionary theory [Plate, 1922, p. 11]. At the same time, his attitude towards orthoevolution was the most sophisticated part of his theoretical system. On the one hand, as we have seen above, Plate consistently advocated the idea of random variations: "Variability is unlimited and manifests itself also by the extremely specialised forms. Even the elephant varies in all its organs and in all possible directions" [Ibid., p. 10].[26] On the other hand, he championed orthogenesis, which propagates just the opposite idea, namely that variation is restricted and canalised [Popov, 2003].

To make his position clear Plate separated *facts* from the *hypotheses* explaining these facts. Plate argued that any principal form (Stammform) gives rise to only a few side branches and never produces an innumerable variety of side branches. He also claimed that almost all phylogenetic branches look more or less like straight lines and do not oscillate zigzag-like between progress and degradation.

There are two ways to explain these facts. The first is *orthogenesis*, which, according to Plate, means that certain external factors influence and modify all individuals in such a way that natural selection has almost nothing to select from [Plate, 1913, p. 508; 1922, pp. 10–11; 1925, pp. 115–116]. The second way is *orthoselection*, which asserts that, although individual variations are random, only a few phyletic directions are progressive (in any sense of the word) and therefore persist under selective pressure [Plate, 1913, p. 508]. The difference in principle between orthogenesis and orthoselection is that *orthogenesis* is usually associated with Lamarckism, whereas *orthoselection* implies the Darwinian idea of random mutations processed by natural selection. Plate's objective was to revise these concepts and to incorporate them into the „old-Darwinian" synthesis.

Both mechanisms (orthogenesis and orthoselection) can work simultaneously and independently and Plate's orthogenesis is in no way a universal evolutionary pattern. He wrote: "Definitely directed variation and selection are not mutually exclusive, but can work together. It does not matter to selection, if a certain change is in the same direction as the one before or not, if the change continues in the same direction or not." [Plate, 1913, p. 510].[27] He was convinced of exactly following Darwin's initial ideas here [Ibid., p. 511].

In the *Vererbungslehre* (1932–38) Plate attempted to substantiate his view on the problem of directed evolution with the help of genetics, which dominated his late works. A significant theoretical challenge was to separate the directed evolution on the gene level from orthogenesis and orthoselection at higher levels.

Orthoselection on the level of separate genes operates among the "superior number of variations" [Plate, 1933, p. 1088], since nature creates in the course of time more and more new genes thereby varying characters „downwards or upwards" [Ibid., 1933, pp. 1088–1089]. This is a purely selectionist explanation of directed evolution.

Orthogenesis on the level of separate genes takes place under constant external environmental pressure due to the heritable cytoplasmatic reactions and polyallely (see below, chapter 3.4.). This is a Lamarckian explanatory model.

On the level of complex features (whole organs) orthoselection acts not on the various alleles of a certain gene, but on their sets (radicals – see below) or on the whole genotype [Plate, 1933, p. 1095]. The latter can lead, for example, to an immediate selective advantage for the whole race. Nevertheless also on this level orthoselection cannot explain the whole panoply of phenomena, because "there are cases, when selection is excluded", for example the complete disappearance of vestigial organs or the excessive development of certain features [Ibid. p. 1095–1096].

Orthogenetic evolution on this level (whole organs) means the occurrence of new characteristics by the process of capturing "freely mendeling genes" by the "Erbstock", as described below. In any case this kind of orthogenesis is thought to be the response to the continuous stimuli over the course of phyletic history (e.g. the light-sensitive spot on the skin evolved into a retina and further to the human eye due to the continuous light stimulus).

3.4 The hypothesis of variable inheritance and the "Erbstock"-hypothesis

The "Erbstock"– and variable inheritance hypotheses reflect Plate's way of synthesising genetics with evolutionary theory. A detailed discussion of both hypotheses can be found in the *Vererbungslehre* [1932–38]. Plate has explicitly emphasised that the basic objective of this voluminous work was to overcome the scepticism of the geneticists towards evolutionary theory and to provide genetic foundations of the theory of descent [Plate, 1932, pp. III, VII].

The basis of Plate's theory of heredity is his concept of mutations (table 1).

The table illustrates Plate's idea that new features which appear in the course of phylogenetic history, can have various degrees of heritability. A certain degree of

Table 1. Plate's Classification of Mutations [based on: Plate, 1933, p. 1004].

Origin of mutation	Hereditary rigidity [Erbfestigkeit, Erbkraft]	Morphological effect	Cells in which mutation occurs
Gene mutations: different alleles of a certain gene (A↔a): - suddenly: nucleogenic - gradually: plasmogenic	Weak-mutations; strongly depend on the environment; gradually reversible	Small-mutations	Mutations of the germ cells
Neo-mutations: appearance of a new gene: + → A → a - suddenly: nucleogenic - gradually: plasmogenic	Labile mutations; 50% are reversible;[28] with all probability do not depend on the environment.	Step-mutations; modifications are clearly identifiable, but are of moderate nature; the majority of mutations belong to this category;	Somatic mutations
Chromosomal mutations	Proper mutations; keep almost constant; very rarely reversible.	Saltations (sports)	
Amphi-mutations are the products of cross-breeding, when two genotypes join.	Blastovariations of the Erbstock; extremely stable; modifications are only phyletically identifiable.		

heritability is reflected by the term *Erbkraft* (inheritance-power), which varies on the weak-strong scale. Natural selection operates in such a manner that individuals and groups possessing a useful character with stronger heritability (starke Erbkraft) will gradually win dominance over the softly mutating competitors [Plate, 1936, p. 93]. On the contrary, in the case of harmful mutations natural selection is directional against their strongest forms. With "strength of heritability" Plate means the ability of a new character to persist in the population over generations (the more generations, the higher is the degree of inheritance-power).

Correspondingly, Plate proposed an inclusive definition of mutations covering all modifications of the genotype causing heritable characters to appear suddenly [Plate, 1933, p. 1004]. The ultimate purpose of these theoretical efforts was to substantiate genetically the theory of natural selection, and at the same time to reformulate the concept of the inheritance of acquired properties in terms of 1930s genetics.[30]

The whole scale of strength of heritability looks as follows [Plate, 1933, p. 1013]:

Somation – weak mutation – labile mutation - proper mutation – blastovariation

The first four degrees correspond to various alleles of a certain gene A, which Plate lettered as $A°, A', A'', A'''$. He explained the strengthening of heritability by the succession of the diverse alleles of a particular gene. This concept, which explains different degrees of heritability by the multi-allelic structure of genes, Plate called the hypothesis of variable inheritance-power of polyallelic genes [Plate, 1936].

The most rigid last degree in the above scheme "*blastovariations*" ("blastos", Greek – bud, embryo) is of a principally different nature and will be explained by the variation of the *Erbstock*, which is a qualitatively different kind of heredity to genotype-heredity.

Plate formulated the *Erbstock*-hypothesis in 1924 and then developed it further. The hypothesis proceeds from the true assumption that chromosomes contain genes bearing hereditary information. All genes together form a genotype. However, genes do not bring about the organs themselves, but rather their properties. For instance, Plate argued, we do not know any gene for *Drosophila*'s eye as it is, but we can identify more than 80 genes determining its colour, form, the number of ommatidia and so on. There are no genes for general body constitution, head, thorax, brain etc., whereas there are various genes determining, for example, colour, form and structural details of the *Drosophila* head. Along these lines Plate concluded: "It appears to me as the inevitable inference that the variety features have other genetic roots as compared to the features of general organisation and higher systematic categories" [Plate, 1933, p. 931].[31] In other words Plate supposed that there are carriers of hereditary information crucial for establishing general structural patterns and representing another level of genetic information than the ordinary genes. In this respect Plate's ideas seem to be similar to the "systemic mutations" of Richard Goldschmidt's (1878–1958), whose early works Plate had critically analysed. However, their concepts differ significantly. Goldschmidt defined systemic mutations as "a change of intrachromosomal pattern" [Goldschmidt, 1940, pp. 206]. Plate told, by contrast, about the imaginable *out-of-chromosomal* supergenes, which control the characters of genus, family and higher taxa.[32] The name "Erbstock" was invented by Plate to contrast it to the "Mendelstock", i.e. the genotype consisting of ordinary genes.

The "Erbstock" is made up of rigid sets of genes situated in the cell's nucleus but outside of chromosomes and undergoing only slow modifications [Plate, 1933, p. 933]. Plate called these clusters of hereditary entities "radicals" and defined them as "groups of correlatively connected genes" [Plate, 1933, p. 935]. "Radicals" operate only jointly, as a whole (this is why they are called radicals). They are responsible for shaping most essential structural characters. "Radicals" are phyletically much older than ordinary genes and do not obey Mendel's laws, because individual genes lose their independency by getting attached to the radicals. Their rigidity explains the constancy of species. Radicals have only few possibilities to vary and therefore also explain *orthogenesis* [Ibid., p. 1141]. Although radicals are very conservative structures, they are neither absolutely irreversible nor totally closed and in the course of phylogeny gradually incorporate new "ordinary genes". This is the crucial point of the Erbstock-hypothesis: ordinary genes inevitably join the Erbstock in the course of phylogeny, thus serving as the basis of evolutionary progress.

Plate believed that the Erbstock-hypothesis opens a way for a molecular-genetic explanation of the variable degree of heritability. Discussing the differences in the "inheritance-power" he wrote: "One can suppose that these differences depend, first of all, on the chemical-physical composition of genes or radicals. Just as a number of chemical compounds easily disintegrate, while many others are rigidly bound, so are the biomolecules, some of which are simply reversible, whereas others are hardly – or not at all – reversible after a mutation; as to the radicals, I assume, they can regress to the earlier, more simple stages (radicals)” [Plate, 1933, p. 1013].[33]

Whatever the exact molecular mechanism, Plate maintained that the selective pressure in a population and the variable inheritance ensure that the individuals with a stronger inheritance-power will get selective advantages as compared with individuals with soft inheritance. In this way the general degree of heritability of certain characters increases in a certain population over time. This happens due to the multi-allelic nature of the majority of genes: a series of alleles gives an impression of directed mutations: “Mutations are vital responses to the external stimuli appearing in many cases as various allelic forms” [Plate, 1933, p. 1043].[34] New “alleles”, Plate argued, represent a transformation (Umwandlung) of a certain gene as a response to a certain continuous stimulus of the cytoplasm [Ibid., p. 961]. Another way to respond to an environmental stimulus would be to constitute a new gene. The latter case Plate called „plasmogenic neomutations“ [Ibid, p. 960].

Under the stimuli Plate understood temperature, X-rays, luminosity and other environmental factors. The stronger and longer the stimulus, the higher the degree of expected heritability. This is the basic mechanism of Lamarckian inheritance in Plate’s theory.

The inheritance of acquired characters is only conceivable over several generations, and only if a population is exposed to certain environmental influences. However, Plate emphasised that *Lamarckian and orthogenetic hereditary mechanisms coexist with random mutations*, which are essential for evolution [Plate, 1936, p. 120; 1933, p. 963]. All these factors contribute over time to the formation of the “Erbstock”, which is the genetic foundation for macroevolutionary processes. Therefore Ilse Jahn [Jahn, 1990, p. 472] is completely right in referring Plate to the champions of macroevolution, especially considering the fact that, besides blastovariations, Plate also supported the idea of “ordinary” de Vriesian “sports” (macromutations).

4 Epilogue

Plate was without doubt one of the most influential evolutionary biologists of the first third of the 20th century. His evolutionary theory, which looks eclectic for the current reader, reveals a relatively transparent logical structure in the internalistic perspective. Plate consistently developed his “old-Darwinian” research program over more than thirty years. His basic objective was to unite the newly established genetics with the morphologically and paleontologically based evolutionary theory. The central tenet of this “old-Darwinian synthesis” was to incorporate neo-Lamarckian mechanisms, orthogenesis and natural selection into a universal, genetically based theory. From this standpoint “old-Darwinian synthesis” appeared to be more inclusive than the “Darwinian synthesis” (Synthetic Darwinism or Modern Synthesis) which developed in parallel. Plate's theory in its latest version embraced the standard set of “Darwinian” factors of evolution (random variations, recombinations, natural selection, and geographic isolation) combined with “population thinking” and an emphasis on the “ectogenetic” (adaptive) character of evolution. However, parallel to this now classical subset of concepts, Plate also admitted neo-Lamarckian mechanisms wholly abandoned by the Modern Synthesis. Plate's sophisticated genetics based on contrasting "Erbstock" and genotype (hypothesis of "radicals") was later likewise proven false.

Curiously the influence of Plate's early programmatic book [Plate, 1913] in the international context was much stronger than the impact of his last pretentious multi-volume work aspiring to be the fundament for a new era in evolutionary theory [Plate, 1932–38]. This can be partly explained by the isolation of Germany during the NS-regime, but was to a certain extent connected with the over-complicacy and over-extendedness of Plate's latest book. The controversial character of his personality, his explicit commitment to national-socialism along with the growing influence of the Synthetic Darwinism on the international scientific community contributed to the decrease of Plate's influence both inside and outside of post-war Germany.

Notes

1 Our research was supported by the *Deutsche Forschungsgemeinschaft* (HO 2143/5–2).

2 The disproportions in references partly be explained by the difficulties Rensch had in getting foreign literature. Rensch reports that he received Mayr's *Systematics* (1942) only after he had read the 1st proofs of his book. This does not explain, however, the higher rate of references to Plate.

3 Habilitation was and is in Germany a procedure of getting *venia legendi* (the right to teach independent courses) and consists of a second dissertation and proof of teaching abilities.

4 Universitätsarchiv Jena [UAJ], Personalakte Plate, Bestand D, Nr. 3000.

5 The title alludes to Shakespeare's tragedy 'King Lear'.

6 German original: „Haeckel hatte massenweise seine eigenen Bücher oder Schriften, die ihn lobten, auf Institutskosten angeschafft und an Freunde und Gönner verschenkt."

7 *Jenaer Volksblatt*, Nr. 266–267, 11th and 12th of November, 1920.

8 *Jenaer Volksblatt*, Nr. 152, 2nd of July, 1921.

9 See "Die Stellungnahme der Universität zur Resolution des Jenaer Gemeinderats vom 20. November 1919 und die Beschwerde gegen die politische Betätigung des Professors Plate 1919" – UAJ, Bestand BA, Nr. 947.

10 See Thüringisches Hauptstaatsarchiv Weimar [ThHStAW], Personalakte Plate, Bereich Volksbildung 23373.

11 See [Hoßfeld 1999] and [Hoßfeld/John et al. 2003].

12 See UAJ, N, Nr. 46/1, Brief vom 21. März 1930, Bl. 159–166.

13 „Er hat das grosse Verdienst, Tausenden den Blick für Rassenunterschiede geöffnet und ihnen die Erkenntnis gebracht zu haben, dass wir Deutsche stolz sein sollen auf unser Erbgut und es vor Überfremdung und Vermischung mit minderwertigeren Anlagen behüten müssen." Ibid.; for further information see also [Hoßfeld 2003, S. 519–574]; [Hoßfeld 2004].

14 See *Deutsche Zeitung*, Nr. 127, 35. Jg., 1. Juni 1930 – Für Hans Günther. Einspruch gegen den Protest des Rektors und Senats der Universität Jena. (Verf. L. Plate); *Jenaische Zeitung*, Nr. 127, 2.6.1930, S. 4 – Um die Professur Dr. Günthers. Für Hans Günther. (Verf. L. Plate).

15 See UAJ, Bestand BA, Nr. 957, Bl. 40, Akte Dienststrafverfahren gegen M. Vaerting 1930 – UAJ, Bestand BA, Nr. 957; see also Plate's article against Vaerting with the title "Ein Beispiel sozialistischer Leichtfertigkeit", *Deutsche Zeitung* vom 19. Juli 1927.

16 See UAJ, Anlage zu Bestand BA, Nr. 957, Nr. 12; see also [Plate 1930] and [Naumann 2001].

17 See [Hoßfeld/John et al. 2003, S. 1108].

18 German original: "der Darwinismus ist eine 'Zufallstheorie' d.h. er rechnet mit den bei den Individuen einer Art 'zufällig vorhandenen Variationen'." […] „Jedoch ist die harmonische Abänderung zahlreicher Merkmale vom Lamarckschen Standpunkt aus bedeutend leichter zu ver-

stehen und kann daher als ein indirektes Zeugnis zugunsten der Vererbung somatischer Variationen angesehen werden."

19 German original: "Es gibt also streng genommen in der Natur ebenso viele Kämpfer ums Dasein, wie es Organismen gibt."

20 Vervollkommnung [completion] in the vocabulary of Plate.

21 German original: "Eine Erwerbung einer erworbenen Eigenschaft kann also nur bedeuten, daß eine neu aufgetretene Eigenschaft in der ersten Generation nachweislich somatogen, in den späteren hingegen blastogen ist."

22 German original: "Nach diesen drei Richtungen wirken der Kampf ums Dasein und die Selektion positiv, d.h. sie schaffen Zustände, welche ohne ihr Vorhandensein nicht sich ergeben würden, und nichts ist daher unrichtiger, als diese Faktoren als rein negative zu bezeichnen."

23 German original: "Aber es muß betont werden, daß solche direkten Anpassungen zweifellos nur selten auftreten, und daß in der überwiegenden Mehrzahl die Anpassung auf indirektem Wege unter Mithilfe der Selektion erfolgt […]"

24 Plate wrote, for example: "Wenn ich demnach mit Darwin die Möglichkeit direkter Anpassung zugebe, so muss ich doch besonders betonen, daß auf diesem Wege nie komplizierte Anpassungen entstehen konnten, weil hierzu eine ganze Kette zweckmäßiger Variationen gehört" [Plate, 1913, p. 574].

25 German original: "Darwinismus und Lamarckismus zusammen geben eine befriedigende Erklärung der Artbildung einschließlich der Entstehung der Anpassungen, während jede Theorie allein dies nicht vermag."

26 German original: „Die Variabilität ist schrankenlos und zeigt sich auch bei den spezialisiertesten Formen. Selbst der Elefant variiert an allen Organen nach den verschiedensten Richtungen."

27 Plate used the expression "definitely directed variation" (variation in a certain direction) as it was used by many champions of orthogenesis, for instance, by Theodor Eimer (1843–1898). Plate's words in German: "Bestimmt gerichtete Variation und Selektion schließen sich nicht aus, sondern können zusammen wirken, denn für die Zuchtwahl ist es gleichgültig, ob eine bestimmte Abänderung in der selben Richtung wie eine frühere Auftritt, diese gleichsam fortsetzt, oder nicht."

28 Comment from: Plate, 1936, p. 93.

29 Plate, 1933, p. 1005. Plate's *amphimutations* correspond to *recombinations* in modern terms.

30 Plate wrote: "Meine hypothetische Reihe verschiedener Erdkraftstufen ist zweifellos als eine Stütze des Lamarckismus gedacht" [Plate, 1935, p. 119].

31 German original: "Es scheint mir ein zwingender Schluß zu sein, dass die Varietätsmerkmale eine andere genetische Wurzel haben als die Merkmale der Organisation und der höheren systematischen Kategorien."

32 Plate was not alone in attempting to separate chromosomal and out-of-chromosomal (e.g., cytoplasmic) inheritance. The analogous concept of "Grundstock" was widely spread in the German speaking world (Harwood, 1993, p. 109).

33 German original: "Es ist anzunehmen, dass diese Unterschiede in erster Linie abhängen von der chemisch-physikalischen Beschaffenheit des Gens oder Radikals. So wie manche chemische Verbindungen leicht, andere schwer oder gar nicht nach der Mutation in den ursprünglichen Zustand zurück; von den Radikalen nehme ich an, daß sie auf frühere einfachere Zustände (Radikale) zurückschlagen können."

34 German original: "Die Mutationen sind vitale Reizantworten, die bei vielen Genen in mehreren, allelen Formen auftreten können." It is important to stress that Plate does mean here all mutations. Mutations, according to him, can appear as a response to the external stimuli, but there are also random mutations.

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