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PERSPECTIVES

The emergence of genetics from Festetics' sheep through Mendel's peas to Bateson's chickens

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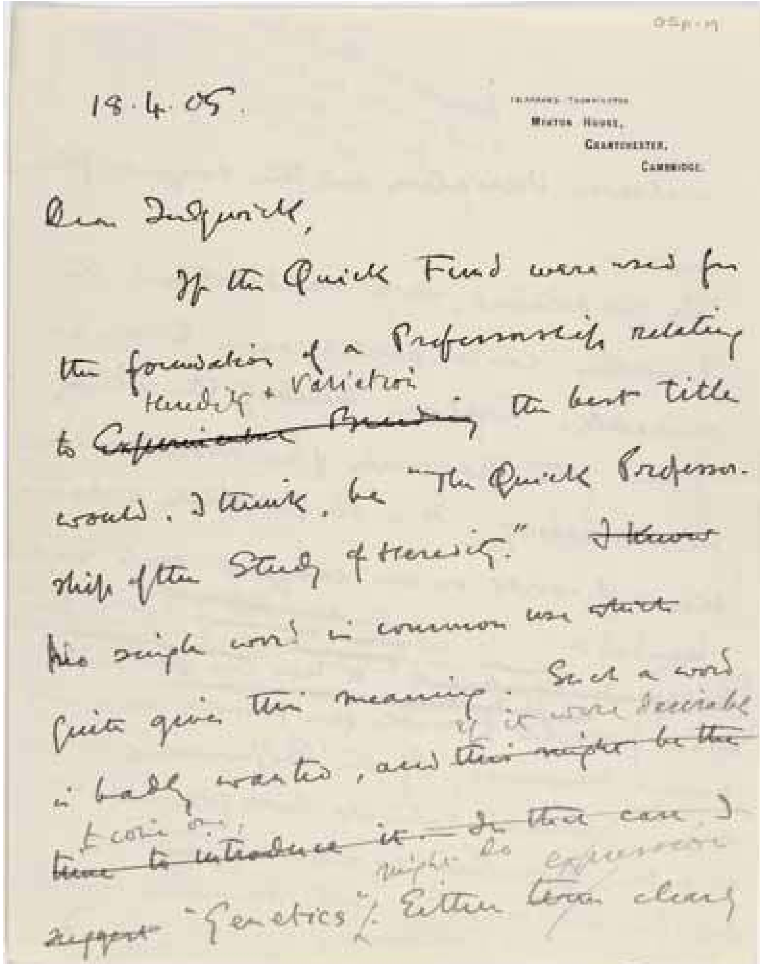
It is now common knowledge—but also a misbelief—that in 1905 William Bateson coined the term 'genetics' for the first time in his letter to Adam Sedgwick. This important term was already formulated 81 years ago in a paper written by a sheep-breeding noble called Imre (Emmerich) Festetics, who still remains somewhat mysterious even today. The articles written by Festetics summarized the results of a series of lasting and elegant breeding experiments he had conducted on his own property. Selecting the best rams, Festetics had painstakingly crossed and backcrossed his sheep to reach better wool quality. These experiments later turned out to reveal a better understanding of inheritance outlining genetics as a new branch of natural sciences.

The question often emerges as to why genetics started so late, relative to other sciences.

In its evolution towards genetics as a well-established scientific field in its own right, the history of 'heredity' has many plots and characters. This history was often littered with what appeared to be dead ends, which were, then later ironed out to linear threads. Those geneticists, who wrote science history burdened by religious prejudices and political perplexities, often followed this crooked road. For the latter, the best example could be seen in the 1940s through the work of T. D. Lysenko (1898–1976), who transformed a set of neo-Lamarckian hereditary theories into Lysenkoism—a 'soviet pseudoscience'. Lysenko rejected Mendelian inheritance, believing in the 'physiology of inheritance', including the inheritance of acquired characters. His theory received official support from Stalin in 1936. From then on, opponents of Lysenkoism in the Soviet Union were dismissed from their jobs; or even sentenced to death as enemies of the state, as in the case of the first genetic resource scientist, Nikolai I. Vavilov (1887–1943). After the Second World War, in the East and in the Central European Soviet satellite states, Lysenkoism became the official 'science of heredity' and, by some accounts, set this science back more than a century (see Soyfer 2001). It is an irony of history that the question 'What is inherited, and how?' was first discussed in the modern scientific sense exactly in this part of Europe.

The problem of heredity itself is deeply rooted in European science. 'Uncertain also what could come to birth … and by what law?' (*Incertum quique iam constet quid possit oriri… finite potestas denique cuique*) was a question asked as early as 50 BC by Titus Lucretius Carus in *De rerum natura* (Character of the Atoms 1. 594–595). Fundamental evidences were accumulating over centuries by breeders, who were witnesses to the phenomena of heredity. It is easy to believe Dunn's (1965) interpretation that experimental breeding gave rise to the principles of genetics. Of all domesticated animals, sheep with their uniquely valuable coat, milk and meat attracted particular attention. This animal constitutes far more than its widespread, fluffy picture might concede; its domestication traces back to 11,000–9000 BC in Mesopotamia. Ovine symbols have been around in different religions, evoking an animal important in different cultures.


18.4.05.

Merton House,
Grantchester,
Cambridge.

Dear Sedgwick,

If the Quick Fund were used for the foundation of a Professorship relating Heredity & Variation to ~~Experimental Breeding~~ the best title would, I think, be "The Quick Professorship of the Study of Heredity." ~~I know~~ No single word in common use ~~exactly~~ quite gives this meaning. Such a word is badly wanted, and if it were desirable ~~this might be the time to introduce it. In that case I~~ to coin one, ~~suggest~~ "Genetics" might do. Either expression ~~term~~ clearly

Figure 1. First page of a 1905 letter written by William Bateson, first Director of the John Innes Institute, to Adam Sedgewick, Cambridge professor. The transcription of the letter is the following: 'Dear Sedgewick, if the Quick fund were used for the foundation of a Professorship relating to Heredity and Variation the best title would I think, be 'The quick professorship of the study of heredity.' No single word in common use quite gives this meaning. Such a word is badly wanted, and if it were desirable to coin one, 'Genetics' might do. Either expression clearly …' Published with permission from the Bateson estate. Courtesy of the Cambridge University Library.

The importance of wool as a generator of wealth is incomparable to anything else in history (Wood and Orel 2001). Breeders produced an enormous number of crossbreeds based on trial-and-error logic in the hope of obtaining a better variety. Nevertheless, the sheep (*Ovis aries* Linnaeus, 1758) has become, as we argue here, the very first model organism of genetics. In the scientific melting pot of the Sheep Breeders' Society (SBS) in Brünn (Brno, now in Czech Republic), debates flourished from 1809 almost until Mendel read his paper in 1865 to the Natural History Society (*Naturforschenden Vereines*).

Teaching genetics started until recently with depicting Gregor Mendel (1822–1884) as an eccentric monk, a lone genius experimenting with peas and making one of the greatest discoveries in human history. Later his mathematical formulae were given to students as the 'Mendelian laws' rediscovered by Hugo de Vries, Carl Correns and Erich von Tschermak in 1900 (see Bateson 1902 for references). It is now common knowledge – but also a misbelief—that in 1905 William Bateson (1861–1926) coined the term 'genetics' for the first time in his letter (figure 1) to Adam Sedgwick (1854–1913)—and not to his great-grandfather Adam Sedgwick (1785–1873), who had been Darwin's professor. However, there are some flaws in this concept.

The first is the term 'Mendelian Laws'—better translated as rules (*Regel*). Mendel has never claimed any laws to his credit. The term was conferred by Correns (1900) and was later taken up by Morgan (1919). Nowadays, the laws are accepted as: (i) the law of the segregation of 'factors' i.e. genes; (ii) the law of independent assortment; and (iii) the law of dominance. Any change to this concept (usually followed by geneticists who are ignorant of exact details and priorities) is against the accepted nomenclature.

The second is the controversial nature of the rediscoveries of Mendel's work (Fisher 1936). For example, de Vries (1900) in his paper did not cite Mendel, but simply tried

Figure 2. Count Emmerich Festetics (1764–1847) around 1810; plexiglass plate engraving by Gy. Simon based on a contemporary canvas (Simon 1990 in Portrait Gallery of Scientists, Natural History, Vas County, Bio Tár nr. 8, Szombathely-Budapest).

to take credit for the entire idea himself. After de Vries's death (1935), one of his students, Stomps (1954) reported that de Vries had in fact received a copy of Mendel's paper from Martinus Beijerinck (1851–1931); thus, he certainly knew that the idea was not his own. Beijerinck wrote to de Vires in early 1900 with the reprint: 'I know that you are studying hybrids, so perhaps the enclosed reprint of the year 1865 by a certain Mendel, which I happen to possess, is still of some interest to you'. Even worse, de Vries possibly saw Mendel's paper for the first time around 1897 due to Liberty H. Bailey's reference to Mendel (Bailey 1892), but failed to understand it (see Meijer 1985).

Thirdly, and most importantly, Mendel was not a lone genius since many of the central principles of heredity were formulated before Mendel was born, also in Brno where Mendel later worked, and through the study of sheep rather than of peas (Festetics 1819a; Orel 1989; Szabó and Pozsik 1989; Poczai *et al.* 2014) (figure 2).

Bateson was among the first to realize the very importance of Mendelian rules in the study of variation and evolution (figure 3). In early May of 1900, he made a pilgrimage to Brno and realized: Mendel described 35 years ago what he was trying to explain with his experiments in breeding chickens (Bateson 1894). He was both shocked and elated and started to reflect on how he should introduce Mendel to the English-speaking world. He consequently became the most diligent public relations man for Mendel's ideas (Bateson 1902). Bateson was, however, unaware of the melting pot of heredity research that had been carried out in the first decades of the 19th century in the Habsburg Empire (chiefly in Moravia, Austria and Hungary). At that point, no other early 20th-century scientific community did either. If he was shocked by Mendel's results, he might have been electrified to realize

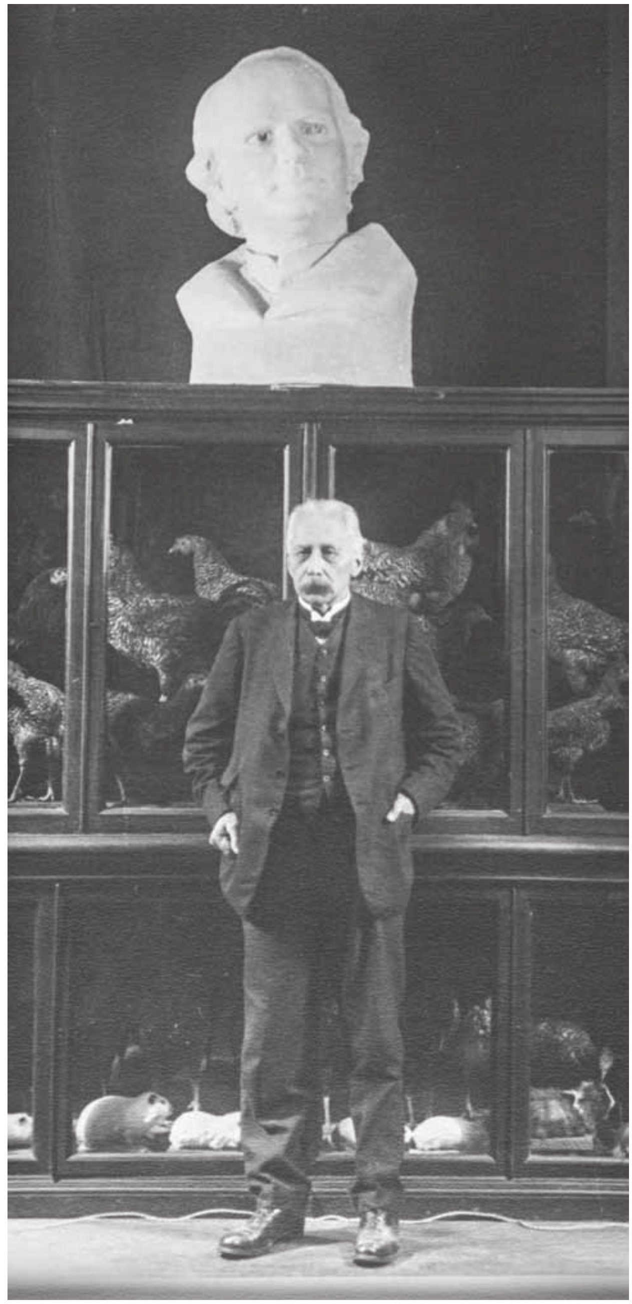


Figure 3. Photograph of William Bateson standing under the statue of Gregor Mendel in the State Darwin Museum, Moscow, 1925. John Innes Archives reference number WB/A.34, courtesy of the John Innes Foundation.

that the term 'The genetic laws of nature' (*Die genetischen Gesetze der Natur*) was coined not 35 years before him, but 81 years earlier in a series of papers written by a sheep-breeding count based in Western-Hungary called Emmerich (Imre) Festetics (1764–1847), who remains somewhat mysterious even today. The articles written by this noble (Festetics 1815, 1819a, b, c, d, 1820a, b, c, 1822), summarized the results of a series of lasting and elegant breeding experiments he had conducted on his own property in Vas-county (mostly in Kőszegpaty). Selecting the best rams, Festetics had painstakingly crossed and backcrossed his best sheep to reach better wool quality. These experiments later turned out to reveal a better understanding of inheritance, outlining genetics as a new branch of natural sciences.

After working with closed-race sheep (in)breeding for 16 long years, Festetics in April 1819 published a paper titled 'About inbreeding' (*Über Inzucht*). The German language paper was submitted to the scientific journal *Oekonomische Neuigkeiten und Verhandlungen* (ONV; Economic News and Announcements) edited by Christian Carl André (1763–1831) 'secretary' of the SBS right in Brno—the town where Mendel later set to work with an autogamous (inbreeding) species of peas (*Pisum sativum* L.). By the time Festetics had published his paper, Mendel was not born either. Interestingly, this pivotal paper (Festetics 1819a), the one that Bateson had missed during his pilgrimage, was stored in the same abbey library that he had visited in Brno; in a library headed by Mendel for long years.

After his visit to Brno, Bateson had Mendel's paper translated into English and—five years later—he coined the term 'genetics' (Bateson 1928). The quotation found everywhere, is based on the previously mentioned personal letter. It is unproductive here to discuss Bateson's priority, because he was in fact the most influential Englishman in the rediscovery of factorial inheritance demonstrated by Mendel decades earlier. His legacy in genetics is secured, inter alia, through his codiscovery of a genetic linkage, together with Reginald Punnett (1875–1967) and Edith Saunders (1865–1945), and by coining other important terms like 'epistasis', and by founding the *Journal of Genetics* with Punnett in 1910 (Bateson 2002).

What is much more important, though, is William Bateson's concept on the nature of heredity. Bateson (1902, preface I) in his fundamental book formulated explicitly that: 'The object of this book is to give a succinct account of […] heredity made by the application of Mendel's method of research. […] recognized as parts of a consistent whole […] as a branch of physiological science.' This is the notable dilemma, which formed the exact basis for the controversy almost a century earlier in Brno in the so-called 'Sheep Breeding Debate' (Wood and Orel 2001; Szabó 2017) between baron J.M. Ehrenfels (1767–1843), —arguing for physiology—and count Emmerich Festetics, who categorically distinguished heredity from physiology. He created the term 'genetic' (figure 4) as early as 1819 to clearly distinguish his rules of heredity, or 'genetic laws', from the 'physiological laws' of the adepts of Ehrenfels. This is an often-missed link in the history of genetic rediscoveries and especially in the restoration of Festetics' work to the scientific community.

The Greek term '*Genetikos*' (γενετικός) in its original sense means, 'connected with emergence', with formation. Used in its current scientific sense, 'genetic' as an adjective denotes genes, e.g., genetic mutation, genetic disorder etc. 'Genetic' as an original concept stems from German idealism and 'philosophy of nature' (*Naturphilosophie*), which persisted into the 18th and 19th centuries and struggled to realize the hypothetical union of nature and spirit. The philosophy of nature was associated with Romanticism (or the Age of Reflection c. 1800–1840) and considered the natural world as a type of giant organism, which should be observed and studied to fully understand its deepest secrets. Johann Gottfried von Herder (1744–1803), in his holistic view, extended this concept to languages where a language is one universal organism never finished; it is rather an ever-changing dynamic process with 'genetic' differences. In Herder's concept, 'genetic' refers to relationships between two languages with common ancestry. Another nature-philosopher the German naturalist and poet Johann Wolfgang von Goethe (1749–1832) used the term 'genetic' to denote a deterministic link between some morphological phenomena in a series of archetypal plants from which all forms could be derived (Brem 2015). This was an idea that framed the question of evolution for Charles Darwin (1809–1882) and Alfred Russel Wallace (1823–1913).

Emmerich Festetics can be personified as an explorer of heredity of the Romantic Era. He was the first geneticist stemming from *Naturphilosophie* and was definitely ahead of his time. This philosophy is evident in how he spoke about his work: 'For your own part, work tirelessly, if you want to understand the rules imposed by nature upon itself'. The spirit of the Romantic Era was overloaded by lasting dilemmas of heredity, but no contemporary thinker viewed heredity as genetics, as Festetics did in his own day. His contemporaries' views on nature were merely physiological (in the best case). Festetics (1819a) is clear: new genetic malformations (*lusus naturae*) are mostly deleterious in the breeding of pure lines, characteristics acquired by nurture are not inherited and heredity is not a physiological phenomenon, therefore it needs a new name. Festetics also formulated the rule of dominance and segregation, as one of the contrasting characters may dominate in the first hybrid generation but will not amalgamate definitely; instead, both reappear separately in the second hybrid generation (46 years later—also in Brno—Gregor Mendel provided the exact mathematical proof of this observation).

Festetics also clearly stated that his 'laws' are valid for all living organisms until the opposite is demonstrated. Later, the same question motivated Bateson, who tried to prove

169

Oekonomische

Neuigkeiten und Verhandlungen.

Nr. 22. April 1819.

61. Debatten. Schafzucht.

Weitere Erklärung des Herrn Grafen Emmerich Festetics über Inzucht.

(Verglichen Beilage Nr. 2—4 1819.)

Die Bemerkungen, mit welchen Herr Rath André in der 4ten Beilage der Ökon. Neuigk. meine Erklärung über die Inzucht, selbst in der nächsten Blutverwandtschaft zu begleiten für gut fand, flossen aus jenem rastlosen Streben, nach welchem er jede wichtigere Streitfrage bis zur Evidenz beleuchtet wissen will. Gerne folge ich diesem Wink, und werde dort, wo ich vielleicht weniger verständlich geblieben, oder meine Meinung nicht erschöpfend sagte, das Nothwendige noch nachtragen.

Zuerst muß ich bitten, in der 2ten Beilage Seite 20, Spalte links den §. 5. die 4te und 5te Zeile folgendermaßen zu lesen: „Abkömmlingen eine Aenderung für sich gehet; oder waren die Voraltern nicht mit" rc. rc.

Diese 5 Paragraphen enthalten meiner Meinung nach, die genetischen Gesetze der Natur. Diese sind es, die bestritten werden müssen, sonst stehet mein System. Denn ich sage in demselben

a. die Thiere von Gesundheit und robuster Constitution pflanzen, und vererben ihre charakteristischen Eigenschaften fort.

b. Eigenschaften der Voraltern, welche von den Eigenschaften ihrer Nachkommen unterschieden sind, kommen in folgenden Generationen wieder zum Vorschein.

c. Bey Thieren, welche durch viele Generationen die nämlichen sich angeeignete Eigenschaften besessen haben, fallen mit unter Abkömmlinge, die abweichende Charactere haben. Dieß sind Varietäten, Spiel der Natur, zur Fortpflanzung, wenn die Vererbung der Eigenschaften der Zweck ist, untauglich.

d. Bedingniß bleibt bei der Inzucht die scrupulöseste Auswahl *) der Stammthiere. Nur jene, die die geforderten Eigenschaften in auffallendem Maß besitzen, können in der Inzucht Gutes wirken.

Nach diesen Prämissen komme ich immerhin auf jenen Satz zurück, daß wenn ich bei den Thieren eine besondere Eigenschaft festhalten, in der Descendenz vererben, und constant machen will, eine vorsichtig geführte Inzucht rathsam sey, ohne Gefahr zu laufen, daß organische Schwächung eine nothwendige Folge werden müsse. Die angeführten Analogien können mich nicht bereden, im mindesten von meiner Behauptung nachzugeben.

Schon erwähnte ich in meiner Erklärung, daß die Fortpflanzung des Menschen und der Thiere dem größten Unterschiede unterliegt, daß bei dem Menschen das Intellectuelle sehr ins Spiel trete. Aber ich frage: kann bei dem Menschen die Inzucht mit scrupulöser Beobachtung meiner Bedingnisse gehandhabt werden, besonders dort, wo Convenienz Schwächlinge zusammen verbindet, wo Herz und Sinn sich ewig fremd bleiben? Mein kräftiger Widder in seinem Harem ist gewiß in einer ganz anderen Lage, und doch fallen von ihm Lämmer, welche in der Inzucht den Stamm ver-

*) Hiermit ist meines Erachtens der Hauptpunkt entschieden. Der Herausgeber.
Ökon. Neuigk. Nr. 22.

Figure 4. Title page of Festetics' paper in *Oekonomische Neuigkeiten und Verhandlungen* (ONV; Economic News and Announcements) published in April of 1819. The reference to the 'genetic laws of nature' (*Die genetischen Gesetze der Natur*) is marked with a rectangle. Below Festetics' four laws the text can be translated as the following: (a) healthy and robust animals are able to propagate and pass on their specific characteristics; (b) the traits of grandparents that are different from those of the immediate progeny may reappear in later generations; (c) animals possessing desirable traits that have been inherited over many generations can sometimes have offspring with divergent traits; such progeny are variants or freaks of nature and are unsuitable for further propagation if the aim is the heredity of specific traits; and (d) a precondition for the successful application of inbreeding is scrupulous selection of stock animals. (In my opinion this is the main point. Footnote inserted by C.C. André).

that the patterns that Mendel achieved in his peas could be applied across the entire living world. For lack of a university position in Cambridge and any kind of funding, he bred all sorts of animals e.g. chickens, pigeons and mice in a disused church. He hired volunteers from students of Newnham College—mostly women often known as Bateson's ladies—to observe the transmission of hereditary traits, without knowing that these questions had already been investigated a century ago.

Count Festetics was able to finance his own breeding experiments with sheep; selling wool provided him enough income to carry on his work for almost two decades. He also went further in his papers by stating that the same genetic laws apply to human beings. He may even be regarded as a founder of gene-ethics due to his statement that inbreeding in humans is deleterious because selection is inapplicable. He did this without referring to blood as the physiological basis of heredity, although he pointed out that this is related to health and robust body structure, which is partly influenced by an external component (*Erziehung*) and by an innate (*Angeboren*) component. He concluded that well-conducted inbreeding and selection can fix the desired characters and that distant hybridizations are unprofitable in the breeding of pure lines. He was able to draw a parallel between natural selection and artificial selection by stating that the breeder and nature act similarly during selection.

In contrast, Darwin was completely misguided even in his basic concepts by believing in 'blending inheritance' directed by the main plasma secreted from blood, a phenomenon he later called pangenesis (Darwin 1868). Darwin presented first his 'theory' proving inheritance through natural selection (but without any genetic background), while Mendel was the first in providing mathematically supported 'facts' for the same by means of plant hybridization (without any perspective towards artificial selection, 'breeding', and evolution). Neither of them connected the two processes. This was later, first attempted by William Ernest Castle (1867–1962), who tried to unite Mendelian inheritance with Darwin's theory, stating that species become distinct from one another when one species acquires a new Mendelian factor (Castle 1903), and finalized later by Theodosius Dobzhansky (1900–1975) by the sentence 'Evolution is a change in the genetic composition of populations' (Dobzhansky 1937).

Festetics clearly focused on heredity, without any references to blood as the true bearer of hereditary factors. Nevertheless, he carefully derived his four points from his experiences and observations in the early 19th century, when even basic biological mechanisms of reproduction were not understood. Experimental procedures were omitted and the application of mathematical models in search of heredity was not yet conceived, rather just intuited by Festetics (1820a), as he said in a meeting on 5th May 1819: 'I believe in the beginning of a new epoch of scientific breeding defined with mathematical precision' (Salm 1820). It would have been impossible for Festetics to draw further conclusions, based on his inbreeding experiments studying qualitative traits such as wool quality and density. It was not until 1931 that Castles's graduate student Sewall Wright (1889–1988) summarized the genetic basis for quantitate natural variation and the bases of the theory of population genetics had only been worked out during the preceding 30 years.

Whatever the reasons that Festetics' work had been forgotten requires further research, focusing mainly on the following questions: Was his work truly inaccessible? Was it unconvincing and incomprehensible to most contemporary scientists? Did his new terminology, which applied the phrase genetics to inbreeding, produce any reference in the scientific literature, despite the fact that interest at that time was wide-ranging in the recognition and understanding of the 'laws of nature'?

Festetics based his laws strictly on empirical observations and he was able to provide valuable guidance at a practical level, which was just what was needed at that time. Further, however, he was able—after the fact—to formulate lasting theoretical statements in his pivotal papers as well.

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