Empirical Genetic Laws Published in Brno Before Mendel Was Born

V. Orel and R. J. Wood

The Sheep Breeders Society of Brno held debates from 1816 to 1819 on the relative benefits of inbreeding and crossing races, and how to associate various wool traits (elasticity, fineness, density, length, and color) into effective combinations. Members differed on the value they attached to inbreeding. J. M. Ehrenfels believed that constancy of inheritance was under climatic influence and that inbreeding would do nothing but increase the rate of degeneration in a race removed from its ancestral climate. E. Festetics and R. André believed a race's properties to be intrinsic, capable of being "concentrated" by inbreeding. Ch. C. André agreed on the potential value of inbreeding, but also stressed the usefulness of crossing to generate heterogeneity "in reciprocal reaction" to produce "new products with more significant, stronger actions, construction and forms." He called upon Festetics to define more clearly his own position, which he did in four "genetic laws" (1819). He connected heredity with health and vigor, rejected a climatic influence on heredity, recognized that different traits had to be integrated into a "healthy whole," and stressed that inbreeding could be practiced safely only when accompanied by stringent selection of breeding stock. The quest for a theoretical underpinning of breeding practices is discussed in relation to Mendel's motivation for his hybridization experiments with peas.

Some years before Mendel arrived at the monastery of St. Thomas in Brno, Moravia, where he would conduct his famous hybridization experiments with peas, intensive discussions were taking place in the city on the nature of heredity in sheep. Freudenberger (1977) has pointed out how Brno had become a major industrial center for the manufacture of fine woolens at the end of the 18 century, the most important in the Austrian monarchy. In the economic climate thus created, sheep breeders began to discuss urgently with representatives of the textile industry and wool business how they might increase production and quality (Orel and Wood 1981; Wood and Orel 1982). The demand for reliable rules of breeding led those concerned to form an association in order to meet together and address the problem. The Sheep Breeders Society, founded in 1814, had among its varied membership, factory owners, businessmen, economists, and later the two principal Moravian professors of agriculture, J. K. Nestler (1783–1841) of Olomouc University and F. Diebl (1770–1859) of the Brno Technical Institute. Seeking answers to practical problems, they began to ask basic questions about heredity, probing a subject about which very little was known. The answers they demanded could be provided only by themselves or other breeders, perhaps in foreign countries, based on the experience of selective breeding and crossing (Orel 1977, 1996). In this article we shall review these questions and the controversies that arose from them.

Genetic Laws

Discussions taking place within the society in its early days, in the period 1816–1819, reveal that members were already examining the transfer of parental traits to progeny, although they rarely then used the term "heredity" (*Vererbung*). Neither natural historians nor physiologists of the time could explain the fertilization process and the origin of the embryo. Heredity was thus a deep mystery, inseparable from the process of generation (*Zeugung*), the enigmatic sequence of embryological events that resulted in a new individual.

"*The Society of Friends, Experts and Supporters of Sheep Breeding for the achievement of a more rapid and more thoroughgoing advancement of this branch of the*

From Barvicova 51, 60200 Brno, Czech Republic (Orel) and the School of Biological Sciences, University of Manchester, Stopford Building, Manchester M13 9PT, UK (Wood). Address correspondence to Dr. R. J. Wood at the address above.

Journal of Heredity 1998;89:79–82; 0022-1503/98/$5.00

economy and the manufacturing and commercial aspects of the wool industry that is based upon it," which was the full name of the Sheep Breeders Society, held annual meetings that attracted breeders and others not only from Moravia and other Austrian provinces, but also from neighboring countries. The type of sheep of most concern to the society was the Merino breed, "noble" sheep as they were called, imported from Spain and kept either in "pure noble flocks" or used to upgrade local "common" sheep by crossing. At the 1816 meeting J. Petersburg (1757–1839), estate manager to the Archbishop of Olomouc, and a progressive sheep breeder, raised a question of how to maximize the yield of high-quality wool. The traits to be considered included elasticity, fineness, density, length, and color, the qualities required by the industry (Petersburg 1816). R. André (1792–1825), who had just produced a practical handbook on sheep breeding (1816) based on the techniques of Moravia's foremost breeder F. Geisslern (1751–1824), responded by underlining the lesson of experience, that striving for high-volume production of wool had so far proved incompatible with achieving the highest quality.

Within a year, Baron J. M. Ehrenfels, a prominent Austrian breeder, was calling attention to the worrying fact that, in his experience, wool in the monarchy was actually declining in quality. On the basis of "his theoretical and practical knowledge," he explained the decline in terms of what he saw as the three major harmful factors: (1) selection of animals for breeding on the basis mainly of their physical appearance, (2) a stress laid upon the total volume of wool that an individual sheep produced rather than its quality, and (3) the practice of pairing sheep "in the closest consanguineous relationship." His recommendation was for a new order of priority in selection criteria: (1) wool fineness, (2) wool length, and (3) wool quantity. With this approach he confidently expected to produce better wool than that purchased directly from Spain (Ehrenfels 1817). Ehrenfel's article was published in the weekly *Oekonomische Neuigkeiten und Verhandlungen* (*ONV*), edited by Ch. C. André (1763–1831), secretary of the society.

A report of the 1818 meeting of the Sheep Breeders Society, written by an unnamed participant, was published in *ONV* (Anonymous 1818). In a footnote, Ch. C. André explained that the author was a doctor of philosophy who had worked for 4 years in agricultural economics. The society's president, E. Bartenstein wrote an independent account of the proceedings (Bartenstein 1818). The anonymous author reported a strong difference of opinion among the participants in what he characterized as the "theoretical part" of the meeting. The major protagonists were Ehrenfels and Count E. Festetics (1760–1847), a Hungarian expert. Festetics, supported by Bartenstein, defended the practice of inbreeding as beneficial because it could result in more constant inheritance. This was directly against Ehrenfel's opinion that constancy of inheritance was an effect of climate. As proof of his view, Ehrenfels cited the Merino breed. In its native territory of Spain, constancy in wool characteristics was achieved under the direct influence of the Spanish climate. Removed from Spain the breed showed evidence of degeneration (*Rückschläge*), with a reduction in wool quality. Ehrenfels believed that the application of inbreeding to such stock would have exactly the opposite effect to that expected by Festetics. By acting against the "main plasma" of animal organization (*Hauptplasma der thierischen Organisation*) it would account directly, he believed, for a decrease in wool fineness. Divergent opinions were also expressed on how to combine fine wool with a heavy fleece. André, in his note, revealed his concern that differences of opinion could arise simply from imprecise terminology, a subject he also considered in a separate publication (Ch. C. André 1818). For a start he hoped that they might be able to agree on what they meant by "inbreeding." He was convinced that unconditional close mating of sheep of the same blood carried on for several generations must result in organic weakness. On that, at least, he was in agreement with Ehrenfels. He considered it to be a "physiological law of nature" (*physiologisches Naturgesetz*). Hence inbreeding had to be practiced with great subtlety before it would be possible to approach with confidence toward an ideal outcome. "We are here interfering with the innermost secrets of nature," he wrote.

To clarify matters André asked Festetics to summarize his view of the problem. In an article that André published, accompanied by some notes written by himself, Festetics (1819a) acknowledged that he had been commissioned "to uncover the truth" about consanguinity, discussed with his "esteemed friend Baron Ehrenfels," which he believed must have a pure physiological (*rein physiologisch*) basis. He agreed with André that the unconditional application of close inbreeding was bound to lead to organic weakness. Could it be, asked Festetics, that the inbred subject was prevented from integrating its functions in agreement with natural law, and from reproducing its inherent properties in the correct relative order within the organism, which otherwise would have been healthy? Was it not a disruption of all that is connected with the "conservation of self" (*Erhaltung seiner selbst*)? With such arguments Festetics too was moving to a position from which he could claim that intense inbreeding would disrupt the accuracy of hereditary transmission.

In order for characteristics to remain stable between generations, Festetics believed that a "robust constitution" (using the French/English word *Constitution*) was required, determined partly by an inborn component (*theils angeboren*) and partly by upbringing (*durch Erziehung*). When within the offspring of a healthy father there appeared individuals of low quality, then the constitution of these animals must have been weakened. But what if both parents had been carefully selected for vigor as well as for the particular traits desired? Any deviation from the parental type would then be classed as a "freak of nature" or "sport" (*Spiel der Natur*). Festetics (1819a) connected such events with the observed fact that grandparents sometimes possessed traits that did not appear in their immediate progeny but might reappear in the second or later generations.

On the matter of inbreeding and its supposed influence on the orderly transmission of traits, Festetics proceeded to consider the example of man himself. He drew upon his knowledge of small inbred communities reproduced by consanguineous mating in certain Hungarian villages, colonized by different nationalities, where he observed both harmful and beneficial effects of inbreeding, in mental as well as physical traits. Returning to consanguineous pairing of animals, he acknowledged that such matings could, in some circumstances have beneficial consequences, leading to a more uniform inheritance of desired traits. Robert Bakewell's principle of "breeding in and in" (Wood 1973) had been at that time most successfully applied by certain German cattle breeders. Since 1803 Festetics himself had been reproducing noble sheep, introduced from prominent breeding farms, together exclusively to create a "closed race" (*abgeschlossene Rasse*). His conclusion was in favor of continuing to apply inbreeding to

this degree within the flocks because he could no longer "be sure of buying rams of better quality." This was precisely the opinion attributed to Bakewell by George Culley in his book *Observations on Livestock* (1786), which appeared in a German translation in 1804, published in Leipzig.

In a footnote to Festetics's article André contrasted the procedure of inbreeding with that of crossing, after which he stated what he believed to be a natural law in favor of crossing, in the following terms: "It is not in the homogeneous (condition) but the heterogeneous, in reciprocal reaction, that new products with more significant, stronger actions, constitution and forms are generated." He called upon Festetics to formulate his own rules about when and where to use the inbreeding technique. Festetics (1819b) responded to this call. He stated that he had agreed to present his 15 years of experience to the experts in Brno in the full expectation that growth in knowledge would eventually allow the formulation of "systematic laws" for the guidance of breeders in coming surely and quickly to the most useful ways of wool improvement. Responding to André's suggestion he summarized his knowledge on the subject under the heading "genetic laws" (*genetische Gesetze*) with the following four points:

1. Animals of healthy and robust constitution are able to propagate and pass on their characteristics.
2. Traits of grandparents may sometimes disappear in their immediate progeny and then reappear in later generations.
3. Animals that possess the same suitable traits can sometimes have offspring with divergent traits. Such progeny are variants, freaks of nature, unsuitable for propagation if heredity is the aim.
4. The precondition for the successful application of inbreeding is scrupulous selection of stock animals. Only those animals possessing the desired characteristics in notable excess can prove effective in inbreeding.

In a footnote to the term *scrupulous selection*, André added: "In my opinion this is decidedly the main point."

By defining his genetic laws, Festetics alluded to heredity without reference to its physiological basis, although he saw it being connected with health and robustness. He was fully aware that heredity of wool quality involved different traits, although he stressed that these had to be integrated into a healthy whole. Based on extensive practical experience, his laws can be designated as empirical. The traits that breeders were concerned with, that one might recognize as having a definite identity, could appear in different combinations. But his theory is far from Mendel's experimentally based concept of discrete trait pairs, and there is no application of mathematics in the explanation of trait segregation and recombination.

Festetics's laws arose from practical questions. Does inbreeding lead to degeneration, that is, a breakdown of heredity? Or does it lead to exactly the opposite effect, to more certain heredity? The answer was clear to him. It depends precisely on whether the parents are carefully paired for the same strongly selected traits, which must include those relating to health, reproductive capacity and a robust constitution as well as those directly concerned with wool quantity and quality, and other economically significant features. Festetics, who reflected the views of Geisslern, the "Moravian Bakewell," had come to a similar conclusion as English sheep breeders, influenced by the original Robert Bakewell: that inbreeding could be critically valuable for strain improvement and was relatively safe to apply as long as it was practiced with discretion and accompanied by stringent selection. Inbreeding accompanied by selection resulted in lines breeding more or less true to type.

The correspondence between Festetics's laws and Geisslern's practical achievement was confirmed by R. André (1819). His personal experience in residence at Hoštice, Geisslern's breeding farm, assured him of the validity of Festetics's laws and of the value of inbreeding as the principal instrument for preventing organic weakness. He noted how the breeders of Arab horses had reached the same conclusion, experiencing no detriment to their breed. The highest aim of breeding was organic robustness, expressed in terms of homogeneity for desired characteristics. Such animals, the product of inbreeding, which he referred to as *Racethiere*, transmitted their uniform characteristics to their offspring with impressive regularity.

Generation and Heredity

The debate on inbreeding and heredity continued within the society as new evidence arose from practical experience. Fresh articles appeared on the pages of *ONV* and, after 1821, in the society's new journal *Mittleilungen*. That was the year when Ch. C. André, editor of *ONV*, moved to Stuttgart. Shortly afterward, his role as prime mover in the breeding debate passed to his pupil J. K. Nestler, Professor of Agriculture, Science and Natural History at the Moravian University of Olomouc. In 1827 Nestler presented his students with a new course in Scientific Plant and Animal Breeding, which he later published (Nestler 1829; Orel 1978). Moravian breeders then began to make freer use of the word heredity (*Vererbung*) to describe what they observed in the transmission of different traits. Their lack of success in revealing any consistent pattern to heredity despite extensive examination of their breeding records, was a frustration to them (Orel 1977; Orel and Wood 1981; Wood and Orel 1982).

Sharing a central position with Nestler in a final attempt at finding an explanation of heredity was F. C. Napp (1792–1867), abbot of the Augustinian monastery in Brno, shortly to become Mendel's mentor. Nestler and Napp took a leading part in debates on heredity at the society's annual meetings in 1836 and 1837. Nestler, in his opening address to the 1836 meeting, proposed to consider the concept of heredity quite separately from the enigmatic process of generation. While not wishing to deny the significance of the generative process, he presented heredity as the most important problem in breeding. The final debate was concluded by Napp, posing the physiological question to which they still had no answer: "What is inherited and how?" (Bartenstein *et al.* 1837). Reacting to the discussion, Nestler (1837) wrote a series of articles entitled "Heredity in sheep breeding," in which he explained how he had tried to analyze the problem. The exercise had led him to place major emphasis on inbreeding as a means of creating new breeds. He was to expand on this theme in a later article, "On inbreeding" (Nestler 1839), but even in 1837 he had become convinced of its overwhelming significance in relation to heredity. Without this technique, he insisted, "Bakewell could never have existed nor could one exist in the future." Nobody within the society now doubted that various traits were inherited and that inbreeding, carefully applied, could make inheritance more certain. But what lay behind these traits? The mystery represented by Napp's question seemed no closer to being solved. Soon afterward sheep breeding became less significant in Moravia, as abundant quantities of excellent, cheaper

wool became available from Australia. And Napp's question remained unanswered.

Mendel's motivation for his experiments on peas has been the subject of much published discussion and controversy in recent years (Bowler 1989; Corcos and Monaghan 1990, 1993; Falk and Sarker 1991; Hartl and Orel 1992; Monaghan and Corcos 1993; Olby 1979; Orel 1996; Orel and Hartl 1994; Sandler and Sandler 1986; Sapp 1990). Was he trying to establish the laws of heredity attributed to him or was he primarily, or merely, concerned with the formation of hybrids? Monaghan and Corcos (1993) reach the conclusion that the influence of practical breeders on Mendel would not have stimulated him to think in theoretical terms at all. They believe that the Moravian breeders, "like most of the breeders of plants and animals before and after them, were not concerned with the theoretical underpinning of their practice." The evidence presented here indicates that the sheep breeders of Moravia were for many years looking for theoretical explanations and that their interests centered on heredity, as they repeatedly stated. Festetics made an important empirical statement when he defined his genetic laws, published in Brno 3 years before Mendel was born. They had sufficient theoretical interest to stimulate years of discussion and abortive attempts to find an explanation of heredity, a fitting prelude to Mendel's research.

References

Anonymous, 1818. Wirksamkeit der Ackerbaugesellschaft in Brünn. ONV 297–310.

André R, 1816. Anleitung zur Veredelung des Schafviehes. Nach Grundsätzen, die sich auf Natur und Erfahrung stüzen. Prague: Calve.

André R, 1818. Terminologie für Woll-Industrie. ONV 319.

André R, 1819. Meine Ansichten und Bemerkungen über organische Schwäche, besonders bei feinwolligen Schafen: veranlasst durch den Aufsatz des Herrn Grafen Emmerich von Festetics im Jännerheft 1819. ONV 161–162.

Bartenstein E 1818. Bericht des Herrn Präfes Baron Bartensteins an die k.k. Ackerbaugesellschaft. ONV Ausserordentliche Beilage 11:81–84.

Bartenstein E, Teindl F, Hirsch J, and Lauer C, 1837. Protokol über die Verhandlungen der Schafzüchter-Versammlung in Brünn in 1837. Mittheilungen 201–205, 225–231, 233–238.

Bowler PJ 1989. The Mendelian revolution. The emergence of the hereditarian concept in modern science and society. Baltimore: Johns Hopkins University Press.

Corcos AF and Monaghan FV, 1990. Mendel's work and its rediscovery: a new perspective. Plant Science 9:197–212.

Corcos AF and Monaghan FV, 1993. Gregor Mendel's experiments on plant hybrids, a guided study. New Brunswick, New Jersey: Rutgers University Press.

Culley G 1786. Observations on livestock. London (German translation, 1804, Leipzig).

Ehrenfels JM 1817. Ueber die höhere Schafzucht in Bezug auf die bekannte Ehrenfelsische Rasse. Belegt mit Wollmustern, welche bei dem Herausgeber in Brünn zu sehen sind. ONV 89–94.

Falk RA and Sarkar S, 1991. The real objective of Mendel's paper: a response to Monaghan and Corcos. Biol Philos 6:447–451.

Festetics E, 1819a. Erklärung des Herrn Grafen Emmerich von Festetics. ONV 9–12, 18–20.

Festetics E, 1819b. Weitere Erklärung des Herrn Grafen Emmerich von Festetics über Inzucht. ONV 25–28.

Freudenberger H, 1977. The industrialization of a central European city, Brno and the fine woolen industry in the 18th century. Wiltshire, England: Edington.

Hartl DL and Orel V, 1992. What did Gregor Mendel think he discovered? Genetics 131:245–251.

Monaghan FV and Corcos AF, 1993. The real objective of Mendel's paper: a response to Falk and Sarkar's criticism. Biol Philos 8:95–98.

Nestler JK, 1829. Ueber den Einfluss der Zeugung auf die Eigenschaften der Nachkommen. Mittheilungen 47: 369–372, 48:377–380, 50:394–398, 51:401–404.

Nestler JK 1837. Ueber die Vererbung in der Schafzucht. Mittheilungen 34:265–269, 35:273–279, 36:281–286, 37:289–293, 38:300–303, 40:218–320.

Nestler JK, 1839. Ueber Inzucht. Mittheilungen 16:121–128.

Olby RC, 1979. Mendel no Mendelian? Hist Sci 17:55–72.

Orel V, 1974. Scientific millieu in Brno during the era of Mendel's research. J Hered 644:314–318.

Orel V, 1977. Selection practice and theory of heredity in Moravia before Mendel. Folia Mendeliana 12:179–221.

Orel V, 1978. Heredity in the teaching programme of Professor J.K. Nestler (1783–1841). Acta Univ Palack Olomuc fac rer nat 59:59–98.

Orel V, 1996. Gregor Mendel, the first geneticist. Oxford: Oxford University Press.

Orel V and Wood R, 1981. Early development in artificial selection as a background to Mendel's research. Hist Philos Life Sci 3:145–170.

Orel V and Hartl DL, 1994. Controversies in the interpretation of Mendel's discovery. Hist Philos Life Sci 16: 423–464.

Petersburg J, 1816. Aeusserung des Repräsentanten für den Olmützer-Kreis Herrn Wirtschaftsrath Petersburg über die acht aufgestellten Haupt-punkte. ONV 113–115.

Sapp J, 1990. The nine lives of Gregor Mendel. In: Experimental inquiries (Le Grande HE, ed). Amsterdam: Kluwen; 137–166.

Sandler I and Sandler L, 1986. On the origin of Mendelian genetics. In: Proceedings Science As a Way of Knowing III—Genetics, American Society of Zoologists, 753–768.

Wood RJ 1973. Robert Bakewell (1725–1795) pioneer animal breeder and his influence on Charles Darwin. Folia Mendeliana 8:231–243.

Wood RJ and Orel V, 1982. The sheep breeders' legacy to Gregor Mendel. In: Gregor Mendel and the foundation of genetics (Orel V and Matalova A, eds). Brno, Czechoslovakia: Moravian Museum; 57–70.

Received May 16, 1994
Accepted May 5, 1997

Corresponding Editor: Glen E. Collier