Heredity before Mendel

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> For he that knows the way of nature will more easily observe her deviations: and on the other hand he that knows her deviations will more accurately describe her ways.
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> \- Francis Bacon, *Novum Organum* (1620)

The effects of heredity had been apparent since time immemorial, and man had taken advantage of them ever since he first kept animals or cultivated crops, deliberately choosing for breeding those individuals he liked best or which gave the best yields. He must soon have realized that the characteristics of parents tended to be passed on to their offspring, and that his own species was no exception. But it remained a mystery why one offspring was like its mother and another like its father, while the only resemblance some of them bore was to one or other of the grandparents. Variable traits such as height often seem to appear in the children as the average of those of their parents. This observation gave rise to the notion of 'blending' inheritance subscribed to by ancient philosophers and natural historians. Hippocrates of Cos (460-377 BC), considered to be the founder of medical science, propounded a theory according to which minute particles from every part of the body entered the seminal substance of the parents, and by their fusion gave rise to a new individual exhibiting the traits of both of them.

Hippocrates' theory of pangenesis still dominated the ideas of natural scientists in the nineteenth century, culminating in Darwin's attempt to explain heredity. A more concrete conception of heredity was developed by Aristotle (384-322 BC). He supposed that every part of the new organism was contained within the semen, which was formed by sanguineous nutriment. It acquired the active power to shape a new embryo. The menstrual blood of a woman passively contained each and every part of her body, which was shaped into a new organism by the action of the principle of motion of the sperm. In this conception, the sperm produced qualitative changes in the matter of the female organism, and thus Aristotle was the first to attribute to the mother an essential role in the process of generation. These ideas formed the starting-point for ancient speculation on the nature of heredity.

The pragmatic Romans accepted the speculative views of the Greeks, as could be seen in the writings of the influential physician Galen (AD 131-201). They paid more attention to the problems of growing plants and breeding farm animals. In this connection they described local breeds of animals and varieties of cultivated plants, and even some aspects of breeding practice, including progeny testing.

In the early centuries of the Christian era St Augustine (AD 345-430) paid serious attention to questions of generation in his writings. He tried to bring the teaching of Aristotle into line with Christian theology, accepting the Old Testament cosmology as a revelation that the world was created (creatio ex nihilo). According to St Augustine, God had endowed matter with certain powers of self-development, leaving free the operation of natural causes in the production of plants and animals. But heredity only emerged as a problem of natural science much later.

HEREDITY IN LATTER-DAY SCIENCE

By combining the findings of astronomy and physics, the French philosopher and natural scientist Descartes presented a new view of the world, based on the principles of mechanics. Natural scientists started to believe that everything in nature could be investigated and explained in terms of the existence and regrouping of minute particles of matter. Even living organisms were considered as structures subject to the laws of mechanics. After Isaac Newton offered a mathematical explanation of the force of gravity, scientists began an objective investigation of the macrocosm of the Universe, and later of the structure of the Earth. The living world, too, soon caught their attention, and one of the questions they considered was the 'enigma' of generation. The English physician William Harvey (1578-1657) linked his speculation on the origin of birds' eggs with the mysteries of generation and heredity, assuming that new individuals arose through a fusion of the formless substance of both parents. This notion of epigenesis was in conflict with the long-held idea of the pre-existence of life-forms.

In the seventeenth century naturalists began to use the microscope to study the development of the embryo, leading to apparent confirmation of the idea of pre-existence. Leeuwenhoek (1632-94) supposed, on examining the sperm of animals and man under the microscope, that he could see Samentierchen (minute animals). He thought that these were preformed embryos whose nutritional needs were catered for by the egg. Around the same time Malpighi (1628-94), on studying the development of avian embryos, likewise supposed he had found a preformed embryo in the egg, which he said began development on coming into contact with sperm. These notions gave rise to the contradictory theories of preformation known as the ovistic and the spermistic respectively.

A new concept of generation was introduced by the French physicist and zoologist RÚamur (1683-1757). He supposed there were organic molecules in the seminal substances of the parents, into which a new order was introduced after their fusion, through the action of a special force which thus gave rise to a new individual. The inheritance of traits was connected with this process. These ideas were further developed by the mathematician and astronomer Maupertius (1698-1759). Influenced by Newton's idea of attraction and repulsion, he investigated the transmission of the traits of parents to their offspring. He also studied the inheritance of polydactyly in man, which RÚaumur, too, had found interesting. He assumed that there existed in the seed of parents some sort of fluid elements which came from all parts of the body, and on fusing together formed a new individual with traits from both parents. Maupertius tried to explain the normal development of an embryo, and the origin of monsters (teratology), a problem dealt with in the second half of the eighteenth century by other naturalists. His views contradicted the idea of preformation-a position also reached by Buffon, though for somewhat different reasons.

Wolf (1734-94) undertook a systematic observation of the process of growth and development of plants and later of the chicken embryo in the egg, and supposed he had discovered a 'law of organic bodies.' In his thesis Theoria generationis, Wolf (1759) concluded that the developing parts of the chicken embryo were formed from the structureless soluble yolk grains on the basis of a special force he called the vis essentialis. He saw the basis of the development of an organism in the process of nutrition; for him the essence of conception was perfect nutrition provided by the extreme nutritive value of semen. Gaissinovitch (1990) shows how Wolf even argued in the unpublished notes on his thesis that semen was 'necessary to form the initial basis of the embryo' and served to create 'the first fermenting movement.' Wolf went on to carry out more work which refuted the preformation theory, and tried to prove the existence of epigenesis, even trying to offer a confused explanation of variation and heredity.

Botanists began experimenting with plant crossing in connection with the demonstration of sex in plants, and they considered their results from the viewpoint of the idea of generation and later of fertilization. Most natural scientists saw a supernatural order in nature, with the organisms created at the start of the Universe simply replacing themselves, and forming an unbroken chain from the lowest forms up to man. It was considered a closed system, devised according to the Creator's plan. Then an examination of fossil remains revealed forms of plants and animals which no longer existed, and natural scientist began looking for an explanation. When, in 1735, Linnaeus published his system of classification of living nature, he believed the number of species to be the same as it was at the Creation. But subsequent experimental crossing of plants convinced him that hybridization gave rise to combinations of parental traits. He thought the genus rather than the species to be the basic unit of creation, and now admitted the possibility of new species appearing in nature and disappearing from it. He formed an open system, interpreting it in harmony with the Creator's design.

Most natural scientists accepted Linnaeus' classification system, and began to consider the question of whether new species came into being and, if so, how. Hybridization became a problem connected, inter alia, with the classification of forms of plants. In 1749, J.G. Gmelin, professor of chemistry at the University of T³bingen, gave J.G. K÷lreuter (1733-1806) the idea of experimenting with the artificial fertilization and crossing of plants, supposing that he would refute experimentally the ancient and still current dogma of the constancy of species. K÷lreuter (1761-6) published a three-part report on experimental plant crosses involving thirteen genera and fifty-four species. His results have been analyzed by E. Mayr (1986). K÷lreuter introduced hybridization as a method of investigation of the old enigma of generation. As an essentialist, he believed that the uniform, fluid semen material of two parents, which blended in an intermediate condition in the progeny, was 'designed by the Creator for joining.' As an outstanding observer in nature he was convinced that when a species was fully grown and began to develop flowers, the male and female fluid semen again had to segregate (Olby 1986). According to this conception he was able to confirm experimentally the controversial sexuality of plants, and described the uniformity of hybrids and the results of reciprocal crosses and the segregation of parental traits in the hybrid progeny. He put exceptions to his theoretical expectation down to the irregular mixing of semen from both parents. K÷lreuter saw his explanation as agreeing with the Aristotelian theory of generation through the semen of both parents, in contradiction to the still widely held theory of preformation. In publishing the results of his experiments K÷lreuter became a supporter of the theory of epigenesis, according to which the newly-formed germ is homogeneous, and differentiates only as it develops.

Another unique feature of K÷lreuter's theory was his explanation of the variable degree of sterility of plant hybrids as being due to a disturbed balance of the semen stuffs of the two parents, and to the influence of the environment. In repeated fertilization of hybrids with paternal pollen, K÷lreuter wished to explain how the hybrids reverted to the original paternal form. His conclusion was that his experiments had not refuted the dogma of the constancy of species. These were the first carefully performed experiments with artificial fertilization of various forms of plants, in which the author described in the hybrid progeny segregation of three types of offspring, those like the hybrid, and those like each of the parental forms. He sought an explanation on the level of contemporary alchemy, in analogy with salt formation.

After K÷lreuter's death voices were raised in opposition to the idea of sex in plants, so in 1822 the Berlin academy of sciences offered a prize for new research elucidating the question. The winner was A.F. Wiegmann (1828), an apothecary from Brunswick, who crossed experimentally various species of peas. He described hybrid forms which were similar to the maternal or paternal plants, or combined the traits of the two. But he also observed traits which bore no resemblance to those of either parent, and failed to reach the nub of the problem. In 1830 the academy of sciences at Haarlem in The Netherlands offered a similar prize. The conditions laid down for its award stipulated that the work should explain the manner in which hybridization could be exploited in the breeding of plants.

The prize was won in 1837, by the German botanist F.C. Gõrtner (1772-1850). In 1849 he published an extensive monograph on plant hybridization, reviewing the published findings of other researchers as well as reporting his own experimental results. In performing over 10000 artificial fertilizations in 700 plant species, yielding 250 different hybrids, he demonstrated, in agreement with K÷lreuter's findings, that hybrids exhibited decreased fertility. Gõrtner also rejected the notion that natural hybridization gave rise to new plant species, thus confirming the constancy of species, and in accordance with German Naturphilosophie he asserted that form and essence were the same. His starting-point was the inborn character of the traits of the plant and the fact that their preservation and reproduction were assured by fertilization. When pollination with foreign pollen took place, in Gõrtner's view, the traits of the plant were altered, since the pollen had a life-giving and, at the same time, a form-building force. From this point of view, according to Gõrtner (1849, p.250) 'the explanation of the formation and creation of bastards from elements and characters of the parent stock is as important for the physiology of the plants as for systematic botany.'

In his monograph Gõrtner distinguished between hybrids from various points of view, explained in more detail in Chapter 5. For the most part he considered, like K÷lreuter before him, hybrid plants in whose progeny alternative traits appeared to be the result of a process of reversion of hybrid forms to the stock species. However, he also pointed to the occurrence of new trait combinations, which could be used for creating new varieties of cultivated plants. In some species Gõrtner also drew attention to the appearance of constant hybrid forms, capable of propagating themselves unchanged as new species. Later, M. Wichura (1854, 1865) published the results of crossing experiments with various species of willow, which Mendel was later mistakenly to assign to the category of constant hybrids.

In 1861 the French academy of sciences offered a prize for an explanation of the fertility of hybrids and the constancy of their traits. Two essays were later submitted. In the first A.A. Godron (1863) argued the fertility of hybrids within the species and the infertility of those between species. In the other, C. Naudin (1863), who won the first prize, offered an explanation of the uniformity of hybrid plants, and the fact that the same results are obtained from reciprocal crossings of parental forms. He supposed that hybrids display either a preponderance of the traits of one or other of the parents, or an average of the parental traits, and also observed segregation of parental traits in the offspring of hybrids, offering the explanation that it was due to the action of a 'specific essence.'

At the time that Wolf was active the theories of preformation and epigenesis were still competing. The subsequent dispute was heavily influenced by Blumenbach (1752-1840), a representative of German Naturphilosophie and professor at the University of Göttingen. In his essay On the formation force and generation affair (Über den Bildungstrieb und das Zeugungsgeschõft), published in three editions in 1771-91, Blumenbach rejected any form of preformation, and as an experienced anatomist and anthropologist emphasized that the embryo formed from the very start by the action of a special 'formation force.' His natural history textbook (Blumenbach 1830), published in twelve editions between 1780 and 1830, had a profound influence on his contemporaries. Among these was the Czech physiologist Jan Evangelista Purkyne (1787-1869). (In German and English papers he spelled his name Purkinje.) In 1825 he dedicated one of his first papers to Blumenbach: his remarkable study on the origin of the avian egg, demonstrating a 'germinal vesicle' in the yolk, later shown to be the nucleus of the cell. Purkyne (1834), in his extensive speculations on generation, mentioned the transfer of traits from parents to offspring, though without using the term heredity (Orel et al. 1987). He supposed that a process of 'involution' reduced the parental traits to a mere quality in the germs of the parents and that, following their fusion, a process of evolution produced the embryo of a new individual, bearing the traits of the parents. Purkyne was also studying animal tissue under the microscope, and in 1837 he pointed to the analogy between plant cells and 'globules' in the tissue of animals. Two years later this analogy was generalized by Schwann (1810-82) as the cell theory. The idea of the cell as a common unit of structure and function in animals and plants became the starting-point for new efforts to explain the enigma of generation, and later that of fertilization.

In 1842-53, Professor R. Wagner, Blumenbach's successor at G÷ttingen university, edited in cooperation with leading European physiologists a Dictionary of physiology, comprising a series of monographs expounding the latest knowledge. The last of which, entitled Generation (Zeugung), was by Wagner's pupil R. Leuckart (1853), at the time professor of zoology at Giessen. He connected the enigma of generation with heredity, but could find no explanation for it, nor a method of investigating the problem experimentally. Dissatisfied, Wagner (1853) wrote an eighteen-page postscript dealing with the problem from an historical and methodological point of view, and recommending experimental research into heredity. He expected the explanation of the problem of heredity to resolve the enigma of generation. Shortly afterwards Wagner acquainted himself with the latest literature, demonstrating the penetration of sperm into the mammalian egg, and immediately added a second, four-page postscript. He inclined towards the view that the embryo came into being with the participation of both parents, attributing the idea to Purkyne, who had learnt it from research by Barry (1840). (Attention was drawn to his contact with Purkyne by Wood (1989-90).) Purkyne made a detailed exposition of his ideas in lectures entitled Physiological morphology, most probably written in Prague shortly after 1850 (Orel and Janko 1988). He had already been in correspondence with Wagner, and around this time received a visit from him. Purkyne set out from the assumption that in the process of fertilization a fusion occurred between the germ substances of the two parents. He supposed the participation of a 'living formative force and a creative endowment', which were 'involuted', and from which under certain conditions the evolution of an embryo began. KrÝzenecky (1987) drew attention to Purkyne's visit to the Augustinian monastery in Brno in 1850. He undertook an excursion in the surroundings of Brno with Mendel's Fr. Klßcel, discussing with him scientific ideas of the time relating to the phenomena of life, which interested them both. At that time Klßcel too had experimental knowledge of his own about the artificial fertilization of plants, and he was interested in the scientific concept of evolution.

Later. in an article on the animal cell in 1860, Purkyne distinguished in each organic part 'two manners of being. the external material, by which it persists physically and chemically in being and presents itself to the senses, and the internal, germinal, life-forming, involuted, through which in the course of time and according to the laws of life, it develops to maturity of propagation, and finally extinction.' Attention has recently been drawn to this by Janko and Orel (1989-90). Special germinal matter in the context of heredity was a theme later developed by Weismann.

Shortly after 1850, the physiologists Franz Unger (1800-70) and Carl Nõgeli (1817-91) began their physiological investigations into the problem of hybridization of plants at the Universities of Vienna and Munich respectively. They were seeking the basis of the variability of traits and the origin of new species. They set out from the enigma of fertilization, looking for an explanation in accordance with the cell theory as it was understood at the time. Their conception of research shows an attempt to make use of the methods of physics and chemistry, and hybridization is considered in quite a different light to that in which K÷lreuter and Gõrtner regarded it.

Since ancient times heredity had also been included in the observation of the varieties of the living world. The explanation was sought in the reflection of some large purpose in nature predestined by the will of God. In England scientists and theologians also saw God in the light of nature, and J. Ray (1627-1705), the father of British natural history, described the great variety of perfections and adaptations in animals and plants.

Ideas on heredity had also appeared in the first speculations regarding evolution. G.L.L. Buffon (1707-88), a contemporary of Linnaeus, placed the variability of traits of animals and plants in the same context as his speculations regarding the evolution of living things. He rejected the idea of constancy of species and pointed to their temporary existence. and the influence of external environment on heredity. It was on his teaching that Lamarck based his theory of transformation of organisms and of evolution from the lowest forms through to man himself. Lamarck (1809) attributed to living matter a tendency to grow in complexity, thus explaining the continual improvement of organisms. His name is associated with the idea of the inheritance of traits acquired through the action on organisms of the environment (as elucidated by R.W. Burkhardt 1977). Larmarck's ideas had a major impact on natural science not only in the nineteenth century, but also throughout the first half of the twentieth. German naturalists, under the influence of Naturphilosophie, conceived the idea of the evolution of the whole of living nature, including the evolution of individual organisms, whose investigation was to be treated as Entwicklungsgeschichte, translated into English as 'developmental history.' Orel et al. (1987) published the manuscript of Purkyne's lecture. explaining his understanding of he concept (this is dealt with in Chapter 5, p. 167). On Purkyne's suggestion, his pupil Valentin (1835) published a book on the topic. It was in connection with this attempt to clear up the enigma of generation and Entwicklungsgeschichte that the issue of heredity emerged as an independent problem.

The mysterious teleology in the evolution of living nature was explained without resort to divine intervention by Charles Darwin (1859) in his masterpiece The origin of species. His theory states that the progeny of parents includes individuals with random modifications of traits, which may by a process of natural selection become the basis not only of new traits, but ven of new species. In his preoccupation with the concept of natural selec~on Darwin failed to explain the basis of heredity, admitting that 'the laws governing inheritance are for the most part unknown.' Following the publication of Darwin's theory natural scientists began to consider the problem of heredity, and did so in connection with the latest findings regarding the structure of the cell and cell nucleus. By the end of the 1860s the issue of heredity was making its appearance alongside that of evolution itself, and the preceding speculation about the hybridization of plants and the crossing of animals was fading into the background.

HEREDITY IN BREEDING PRACTICE

We shall never know when it was that a farmer first began selecting and crossing animals and plants in order to obtain higher-yielding forms. There is just the occasional mention in the literature of isolated efforts to select deliberately individual specimens for agriculture. or of a combination of selection and crossing to produce new plant varieties. An example is the letter written by the noted chemist J. Priestley (1797) to Sir John Sinclair, where he draws the latter's attention to a remarkable improvement achieved in plants by the American breeder Joseph Cooper (1759-1840). whose practice was 'the same as that adopted by Mr. Bakewell in England with respect to animals.'

The pioneers of plant breeding through hybridization knew nothing of the arguments over the sexuality of plants which were raging among botanists, and did not consider questions of the constancy of species or theories of generation. They based their practices on the observed variability of plant traits and their combining by crossing. A natural curiosity led them to carry out field experiments. At that time few pure naturalists took into account the empirical knowledge acquired in agriculture. Francis Bacon. the intellectual founder of scientific philosophy. had already considered the possibility of changing plant and animal 'kinds' through the accumulation of variation during domestication and in agricultural plant and animal production. In his essay A new Atlantis he gave free reign to his imagination on the subject of the creation of totally new forms of animals and plants in agricultural practice; but his views seem to have had little influence, if any, on animal and plant breeders.

Isolated reports of breeding new varieties by means of crossing are to be found even in the seventeenth century. One facet of travel to newly-discovered regions in the sixteenth and seventeenth centuries was that natural scientists were sent out to investigate exotic flora and fauna. New plant species and varieties were found. and some of them were introduced to European countries. In newly established botanical gardens investigations were carried out into methods of plant propagation, allowing the dissemination of more attractive or more productive forms. The German naturalist G.A. Agricola (1716) published a remarkable book dealing with plant propagation. It is well illustrated with copperplate engravings to explain the various techniques of plant propagation. According to Agricola 'The plant soul is material and divisible, and as such can be divided into innumerable particles, so that it is preserved in the smallest particles in its function, which can be proved a posteriori through its effect.' Agricola's deliberations led him to the conclusion that 'vegetabilia or trees and shrubs' could be 'mutually transmuted and changed.' He therefore drew attention to the propagation of fruit trees and vine varieties from seed.

The French naturalist M. Duhamel (1700-82) was most probably the first to apply natural science systematically to growing plants. In his book La physique des arbres Duhamel (1758) tried to explain the variability of cultivated plants. In catalogues of seeds and plants he found descriptions of the traits of previous varieties not referred to at a later date. His conclusion was that most of the fruits which gardeners called new were nothing more than composites of previous varieties. The explanation he offered was that this occurred 'through a mixture of the pollen powder, through mutual fertilization.' On that occasion Duhamel referred to a similar process in crossing different races of animals, using for plant hybrids the term 'metis', formerly reserved for crossed animals.

A contemporary of Duhamel's in England was P. Miller (1692-1771), regarded as a leading expert on the question of raising cultivated plants. From 1722 to 1770 he was head of an apothecaries' company near Chelsea Gardens in London. His book The gardener's and florist's dictionary or complete system of horticulture was published in eight English-language editions during that period. Before its publication not more than a thousand species of cultivated plants were known. By the time he died more than 5000 plant species had been described. Miller also wrote about the process of plant fertilization and hybridization. stating that female plants could not bear fruit before being fertilized by the flower of the male plant. Miller (1751) called pollen grains flour or dust. He considered the discussion which was under way at that time on whether 'the impregnation process from farina fecundans, or male dust' entered the uterus 'in substance or effluvia' to be irrelevant, since Robert Boyle had shown that 'all effluvia are subtle particles of matter.' The mixture of traits in the progeny of hybrids Miller ascribed to the effluvium of particles from the dust into the fertilized egg. This was Miller's understanding of the origin of new varieties arising from hybridization. The German version of Miller's dictionary (1751) is preserved in the university library in Brno.

K÷lreuter was the first pure naturalist to carry out systematic experiments with plant hybridization. Attention has recently been drawn to his interest in the application of hybridization in plant breeding by Mayr (1986). In the third part of his essay on sex in plants K÷lreuter (1763, p. 176) wrote: 'I could wish that I, or someone else, might one day be lucky enough to produce hybrids of trees, the use of whose timber might have great economic effect. Among other good properties such trees might have one would be that if the original trees needed, for example, a hundred years of full growth, the hybrid would achieve the same in half that time. At least. I do not see why they should behave differently from other hybrid plants.'

Towards the end of the eighteenth century in the newly founded parks and botanical gardens in different European countries. introduced plants were grown and their economic traits were compared with those grown traditionally in fields and forests. In that period a unique park was organized in the agricultural economy of the large estates of the Duke of Liechtenstein's family in Lednice, south Moravia. After studying the organization of parks in France and in The Netherlands, T. Walashek (1753-1834), also known later by his title von Wahlberg, founded an extensive park where he grew a great collection of field and forest plant species and varieties. This collection was known in his lifetime as herbarium vivuni. In the view of Wahlberg, the comparison of different plant varieties in certain soil and climatic conditions was the best way to find more productive forms to be cultivated. Wahlberg published the results of his investigation in an extensive book in Vienna in 1810. It was the first book to critically evaluate. in detail, the economic traits of a great collection of cultivated plants, in the modern spirit of the gene reservoir.

By the end of the eighteenth century progressive plant cultivators in England had begun a systematic investigation into the hybridization of cultivated plants to obtain increased plant production. But it was Thomas Andrew Knight (1759-1838) who began to publish information on this new trend in plant growing, on the basis of his own experiments. Setting out from the idea of the limited duration of plant varieties, Knight (1797) recommended constant selection of new varieties. and also considered the possibility of using artificial pollination. His most influential paper was published under the title 'An account of some experiments of the fecundation of vegetables' (Knight, 1799). In the introduction attention is drawn to the analogy between animal and plant breeding, and it is also emphasized that the same means would produce the same consequences. His experiments soon confirmed his expectations. He set out from the animal breeders' idea of superfetation. According to this idea, the situation in plants was that in the fertilization process 'the explosion of the two vesicles of farina (taken from different plants) at the same moment may afford seeds (as I have supposed) of common parentage.' Ten years later Knight (1809) returned to the analogy that subsists between plants and animals, and considered the animal breeder's idea of superfetation for the purpose of explaining the role of parents in the transmission of traits.

In his deliberations on creating new varieties of fruit trees with the application of artificial pollination, Knight was aware that 'several years must elapse before the success or failure of this process could possibly be ascertained.' He therefore came upon the idea of carrying out hybridizing experiments with annual plants, in order to obtain experience of his new breeding system more quickly. Among these plants 'none appeared so well calculated to answer my purpose as the common pea, not only because 1 could obtain many varieties of this plant, of different forms, sizes, and colours, but because the structure of its blossom, by preventing the ingress of adventitious farina, has rendered its varieties remarkably permanent.' In his experiments, which Knight had begun as early as 1787, he examined the transmission of individual traits of seeds and observed a uniform appearance of the first hybrids and a greater variation of the trait in the next generation. The crucial problem here was whether the largest and smallest quantities of farina produced any difference in effect. Knight's publication stimulated other scientists to carry out experiments in plant-crossing. The publications most often cited are those of J. Goss (1824) and A. Seton (1824), relating to experiments with Pisum. Along with the dominance of seed traits they also described the segregation of parental traits in the hybrid progeny.

Being acquainted with the experiments of Goss and Seton, Knight (1823) returned to his motivation for experiments in plant hybridization, stressing that in his experiments with peas he wished to obtain such information as would enable him to 'calculate the probable effects of similar operations upon other species of plants.' In this context he believed that it would not be easy to suggest an experiment of cross-breeding upon this plant, of which one has not seen the result, 'through many generation.'

Knight's most influential paper on hybridization. published in 1799, did not escape the attention of plant breeders on the Continent. In the following year a German translation appeared in Leipzig (Knight 1800), bearing a remarkable footnote in which the anonymous translator states that 'The art of forming new varieties from two plants through blending of seeds is already known to Germans from the discoveries of K÷lreuter, and later from various writings and observations of I. Hedwig in the years 1793-97. The latter experimented with the crossing of different varieties of cucumbers, though his work was interrupted by his premature death (Hedwig 1797). In the footnote to the German paper it is stressed that Knight's paper has been written for the benefit of agriculturalists, and therefore the results of further experiments were anticipated. The journal in which the paper was published is deposited in the university library in Brno, with the stamp of the Agricultural Society. It was thus available to those who were interested in breeding plants in Brno (Orel 1978a).

Knight also influenced the respected French pomologist A. Sageret (1763-1851) who after 1800 began experimenting on the crossing of melons and studying the transfer of individual traits to the hybrids and their progeny. Sageret (1826) showed the dominance of traits in hybrids and the segregation of the parental traits in the hybrid progeny, and also the combination of parental traits. Like Knight, he gave as his motivation the goal of verifying in a few months what would in fruit trees be the work of many years.

Knight's interest in breeding new plant varieties came from his previous experience with sheep and cattle breeding for meat production according to the methods of Robert Bakewell (1725-95), whose achievements encouraged both animal and plant breeders at the end of the eighteenth century (Mylechreest 1988).

Bakewell's fame was founded chiefly on the creation of a new breed of meat-producing Dishley sheep (Wood 1973). Continental farmers, however. were more interested in keeping sheep for wool. Even in the seventeenth century it was known that the best-quality wool was that obtained from Spanish sheep, and in the course of the eighteenth century they came to be exported to various European countries. Because of the new conditions under which these animals were bred, their owners had to provide fodder all the year round and sheds for the winter, and there was also the new problem of reproduction within the relatively small flock of imported animals. Experts began to publish manuals and handbooks on the breeding of imported sheep; mention was made of the crossing of imported rams with local ewes and of consanguineous mating, at the time publicly regarded as violating the prohibitions of religious dogma.

The noted French naturalist L.G.M. Daubenton (1716-1800), on the instigation of government authorities, began in 1767 to experiment with the crossing of sheep breeds in order to improve the quality of wool produced. Ten years later he read to the Academy of Science a paper reporting the results he had achieved. In it he evaluated methods of crossing and the wool quality of the parental animals and of the progeny. This lecture was included in his book on sheep husbandry (Daubenton 1782).

After 1800 most of the books published on agriculture on the Continent dealt with the breeding of wool-producing sheep. The high prices commanded by wool from Spanish sheep aroused interest in improving the quality of that produced by local breeds by crossing them with imported Spanish rams. The finest wool, which was the type that fetched the highest prices, was then produced by imported Spanish sheep in Saxony. After 1800, however, greater and longer-lasting success was achieved in the Habsbury provinces of Moravia and Austria. The best known breeder in the early nineteenth century was Ferdinand Geisslern (1751-1824), who came to be known as the 'Moravian Bakewell.' The economic advantages of his breeding practices, as in England. stimulated interest among farmers in applying hybridization to plant-breeding practices in Mendel's homeland, Moravia (Orel and Wood 1981).

At the start of the nineteenth century Brno, capital of the province of Moravia. became the centre of the textile industry of the Habsburg monarchy (Freudenberger 1977) (Fig. 2.1). With an eye to this, those who were chiefly concerned with textile development tried to organize the furtherance of natural science on the basis of learned societies. The learned naturalist Christian Carl AndrÚ (1763-1831) was soon to be one of the foremost figures. In 1806, the Moravian Society for the Improvement of Agriculture, Natural Science, and Knowledge of the Country (henceforth referred to as the Agricultural Society) was inaugurated, combining the stagnating Moravian Agricultural Society, established in 1770, with very active private societies of naturalists. AndrÚ (1815) drew up a programme of scientific development, emphasizing the importance of developing basic and applied research in the natural sciences, and in this connection pointed out the significance of great scientific discoveries. The examples he gave were of the discoverers Copernicus and Newton, and he expressed a conviction that the members of the new society might, by dint of carefully conceived research work, lay the foundations for some similarly great achievement, though it might not see the light of day until a much later date, when the whole of civilization would be indebted to Moravia. At the time his choice of words seemed extravagant. Soon afterwards Andre' was to devote more and more time and attention to the question of sheep breeding, considering it a scientific activity, and in this connection he came into contact with the question of heredity. Later H.F. Salm and C.C. AndrÚ (1814) founded in Brno, in affiliation with the Agricultural Society, an 'Association of Friends of, Experts on, and Supporters of Sheep Breeding, for the achievement of the further well-founded advancement of this branch of the economy, and the manufacturing and commercial aspects of the important woollen industry which are based upon it.' (Throughout this essay this association is referred to as the

Sheep Breeders' Society.) This was the first animal-breeding association to he set up in continental Europe, and every year it held meetings of sheep breeders from throughout central Europe and also from as far afield as Mecklenburg in Prussia. The agenda included methods of artificial selection and the transmission of traits of wool from parents to offspring -- in other words, heredity (Orel 1974a).

Before coming to Brno, André, a former student of the University of Jena, had worked in Saxony as an educationist and author of natural scientific and economic publications. He also became a founder member of the first mineralogical society, established in Jena in 1798, and was an enthusiastic student of this nascent branch of science. In developing methods of sheep breeding, AndrÚ emphasized that this was the start of a new science, for which a new terminology would have to he created (Franke and Orel 1983). AndrÚ had been prepared for his understanding of the enigma of reproduction before coming to Brno through writing his textbook on zoology. In his extensive introduction to that work AndrÚ (1795), on the basis of his experience in animal breeding, explained the participation of both parents in the origin of the new individual, rejecting the old notion of preformation. In journals published in German in thousands of copies, AndrÚ reported the discussions of the society regarding methods of scientific breeding and heredity, though he used the latter term only exceptionally. He regularly published reviews of publications on agriculture and the natural sciences associated with it, paying special attention to animal and plant breeding.

Economic achievements in England and Moravia aroused interest among plant breeders in using methods of artificial pollination in order to achieve new and higher-yielding varieties of fruit trees. In 1816 AndrÚ drew attention to the success of Knight in breeding new varieties of vine and fruit trees, and recommended that his method should be used for creating new varieties of fruit trees. In the same year he founded in Brno a Pomological and Oenological Association, which later

Fig. 2.1 Map of the Habsburg monarchy, 1870, showing places connected with Mendel.

became known simply as the Pomological Association. Shortly afterwards the committee established a stock nursery for the creation of new varieties, combining useful traits from existing ones (Orel 1978b). AndrÚ repeatedly published reports on the activities of the Horticultural Society of London, established in 1804, of which Knight was president. Their author was AndrÚ's friend G.C.L. Hempel, secretary of the pomological Association at Altenburg, near Leipzig, founded in 1803. who was also an overseas member of the London Horticultural Society. In l818 it was even suggested that permanent cooperation should be initiated between London, Brno, and Altenburg.

A most remarkable article appeared in 1820. AndrÚ had asked Hempel whom he considered an expert in plant breeding, to explain the possibility of applying the methods of artificial fertilization to breeding new varieties of cereal. In an extensive paper Hempel (1820) described the experience of Knight in selecting new varieties of fruit trees. He was sure that 'higher scientific pomology' was moving towards the point where the breeder would be able to create a new variety according to a previously conceived ideal type, combining traits of fruit size, shape, colour, and flavour. But he emphasized that it would first be necessary to explain the laws of hybridization which applied to sexually reproducing plants such as grain crops. Only then, he thought, would hybridization in breeding practice open up the way to the creation of entirely new varieties of all species of cultivated plants, with much higher yields than farmers could at present imagine. He did not expect this problem to be solved in the near future, stating that a new type of natural scientist would have to emerge, able to perform demanding experiments in plant hybridization. He even tried to characterize him: he would be 'a researcher with a profound knowledge of botany and sharply defined powers of observation, who might, with untiring and stubborn patience, grasp the subtleties of these experiments, take a firm command of them, and provide a clear explanation.' This was a pretty fair description of Mendel, born two years later in Moravia (Orel 1974b).

At the time Hempel's predictions were published, the president of the Brno Pomological Association was AndrÚ's friend Jan Sedlßcek von Harkenfeld (1760-1827), who was then beginning to use methods of hybridization in breeding new varieties of fruit trees and vines. Shortly before he died he outlined a plan for breeding vines in order to achieve new varieties which would not only be 'constant in vegetation and suitable for our climate,' but whose grapes would also 'unite in themselves many superior characteristics, so that the wine pressed from them would be of higher quality.' Perhaps, he adds, they would also 'be such noble varieties as until now we do not have even from abroad' (von Harkenfeld 1826).

After Sedlßcek's death his place at the association's helm was taken by C.F. Napp (1792-1867), newly elected abbot of the Augustinian monastery in Brno (Orel 1975a). It was supposed that he would continue to 'promote pomology and wine-growing through experiments, observation and instruction, enrich science, and propagate useful findings.' He was the right choice for the job. Before being elected abbot, Napp had organized a nursery garden on the previously neglected monastery farm at the village of Sardice, about 80 km south-east of Brno. By 1829 it had 3400 seedlings, of which 700 were characterized as improved. According to the report of the Pomological Association. Napp also wrote a handbook to instruct village people on how to improve fruit trees in that neglected part of the province. The stock nursery for breeding and disseminating new varieties of fruit and grapes established by Sedlßcek inside the association soon became unsatisfactory, so in the 1830s Napp created another one in the monastery, later described by Hungarian expert F. Schams (1836) as 'an institute created for practical experiments' and 'a jewel among nurseries.' Over a hundred varieties were investigated there (Weiling 1991) from the view-point of yield. Keller, the head of the institute, wished to examine individual grape varieties in separately produced wines.

After 1820 the method of artificial pollination began to be used in many European countries for breeding new varieties of fruit trees and ornamental plants, and later also for other plant species. Much attention was paid to the breeding of plants by the members of the Horticultural Society in Bavaria, based in Frauendorf. The society published a journal which was subscribed to by some of the members of the Brno Pomological Association. Its president, Napp, used a report on the contents of this journal during meetings. A German translation of the English papers by I. Goss and A. Seton (Anon. 1837) appeared in the journal, describing the experiments on crossing of peas which they had performed at the suggestion of Knight. The German translation did not mention the English authors. The text also falsely gave the year of the start of the experiments as 1833 instead of 1821. The reader was certain to get the impression that the experiments had been carried out in Bavaria.

At the time much attention was also being devoted to the application of hybridization in plant breeding in The Netherlands and in Prussia, and prizes were being offered for elucidating the effect of hybridization.

The chief organizer of the development of methods of scientific breeding of sheep and plants in Moravia was C.C. AndrÚ, who laid the foundations for an exchange of experience with experts from abroad (d'Elvert 1870, II pp. 119-20). In 1820 he was forced to leave the territory of the Habsburg monarchy because of his liberal views, and moved to Stuttgart, where he no longer had the opportunity to devote his attention to questions of breeding animals and plants. But he had set off a chain reaction in Moravia, and his former colleagues continued to support the development of methods of breeding practice.

HEREDITY IN UNIVERSITY TEACHING

The introduction of rational methods in agriculture called for a knowledge of the natural sciences and its application to the production process. So in the late eighteenth and early nineteenth centuries the subject of agricultural science appeared on university curricula. One of the first universities to introduce this branch of study was Edinburgh. Later an enthusiastic propagator of the rational methods of British agriculture was A. Thaer (1752-1826), professor of agricultural science at the University of Berlin from 1810. His meritorious activities were reported by AndrÚ in his journal, one of whose readers was Thaer himself. AndrÚ had suggested setting up a professorship of agricultural science in Moravia as far back as 1808. He himself was the most suitable candidate, but he was not accepted, most probably because of his liberal views. The first professor of agriculture in Moravia was established at Olomouc in 1811, the second in Brno in 1816. But progress in methods of sheep and plant breeding was not affected by university teaching until the next generation of professors. In 1823 a former colleague of AndrÚ's, J.K. Nestler (1783-1841), began teaching the subject in Olomouc, and the Brno chair of agriculture was taken by F. Diebl (1770-1859), an associate of Napp's, in 1825. Nestler paid greater attention to sheep breeding, Diebl to plant breeding (d'Elvert 1870, II, pp. 203-15, 280-9. 315-31; Orel 1975a, 1977; Weiling 1976, 1982). Both professors took an active part in the activities of breeding societies, and published articles dealing, inter alia, with hybridization and heredity. At other schools in the Habsburg monarchy, teachers of agriculture dealt with questions of animal and plant breeding only marginally.

Nestler (1829) published his lectures on breeding under the title 'The influence of generation on the characteristics of the progeny.' An editor's note pointed out that this was 'part of the model lectures on agricultural science and natural history in which that worthy author develops the most important aspects of rational animal breeding, motivated by their various relations even in 1827.' The title does not mention the word inheritance, but the reader knew that this was a study of the principles according to which traits were transferred from parents to offspring. Right at the beginning of his text Nestler stated that 'fruitful generation with heredity of all the substantial traits in the progeny is possible only between two kinds (in the natural historical sense) belonging to the same species.' The lectures describe empirical knowledge derived from selection practice, but treated from a wider natural scientific understanding of the phenomena of variation, crossing, and hybridization. Attention is also paid to the hybridizing experiments of K÷lreuter. Examples are given from the animal and plant kingdoms, and man is also mentioned. Finally the influence of consanguineous crossing on hereditary diseases is considered, and in this connection the author points to the significance of progeny testing in animal breeding.

Nestler described the animal and plant traits determining production in agriculture, and mentioned the endowment (Anlage) of traits, but did not get as far as distinguishing the determinants governing heredity. The lectures deal with the concept of blending inheritance, but on the other hand mention is made of the observed inheritance of alternative traits, such as the presence of horns in cattle. Nestler refers to the sudden appearance of new traits as sports, or freaks, of nature, which he considered inexplicable at that time. He also tries to differentiate between the influence of the environment and that of heredity in the manifestation of the production traits. The heredity of acquired characteristics is described as problematical. In describing the application of consanguineous crossing in breeding practice. Nestler defends this method against its opponents, who were still in the majority.

The publication of Nestler's lectures on animal and plant breeding evoked a renewed discussion among sheep breeders regarding the theoretical bases of the process of scientific breeding, which had been a subject of discussion in the new journal Mittheilungen, published by the Agricultural Society since 1821. Studying natural scientific literature, Ehrenfels (1831) tried to explain the origin of life from 'the lifeless chaos of matter' by means of a 'generation force.' He also referred to it as a 'genetic force', which in interaction with climate and nutrition was considered 'the main lever of nature in the formation of matter.' From this the sheep breeders deduced that it was possible to modify the traits of animals in order to form organisms with a higher production-capacity. These speculations based on empirical findings from breeding practice encouraged them to elucidate the theory of breeding and to seek a new breeding method in order to improve production.

The discussions among breeders in Brno regarding generation and artificial selection reached a climax in 1836 and 1837. The president of the Sheep Breeders' Association, E.. Bartenstein, asked Professor Nestler to choose the topic which would be most benefit to and most desirable for sheep breeders. According to Nestler 'the most essential thing of all for improved sheep breeding, as well as being an urgent question of our time' was 'the ability to inherit.' He thus provoked a discussion among the participants in the annual meeting on a crucial problem in breeding practice, heredity. The participants expected a solution to the problem to come from an analysis of pedigree records and the data from progeny testing of traits determining production capacity (Orel 1978c).

The two professors of agricultural science and natural history in Moravia worked together with fruit and plant breeders, and every year they published numerous specialized articles explaining the latest scientific findings and their application to agricultural practice. The agricultural schools in the monarchy used the textbook by L. Trautmann (1814), a professor at the University of Vienna. It came out in four editions. Another widely diffused book was that written by agriculturalist I. Burger (1819), which was translated into Swedish and Polish. There is no mention in either of these books of the breeding of new plant varieties through hybridization. The number of students studying agricultural science in Moravia increased rapidly, a trend which was reflected in the publication of a five-volume book by F. Diebl (1835) under the appropriate title On the science of agriculture for agriculturalists, especially those devoting themselves to a study of this science. The second volume, on plant production, describes the anatomy of flowers and the technique of artificial pollination as a method of obtaining new, more productive varieties. Both Nestler and Diebl taught agricultural science and natural history. This led to a textbook on which they cooperated, called General natural history (Nestler and Diebl 1836).

In the journal of the Agricultural Society there appeared an article by Baron von Witten (1828) called 'On wheat varieties,' which had previously been published in the journal of the Prussian Horticultural Society. It was considered interesting, and in the next year Diebl (1829) published a critique of it explaining his own view on the classification of cultivated plants. This was based on a knowledge of agriculture and of natural scientific literature, especially concerning the practice of selecting cereals. According to him the naturalist considers only constant traits which are inherited. Under special conditions these traits do not appear, but they may reappear. Their origin cannot be explained from the viewpoint of contemporary natural history. Plant physiology, however, allows us to accept the view that such traits arise through hybrid fertilization under certain conditions, through a force still unknown to us. Most cultivated plants have their subspecies, and investigation shows that their distinctive traits are not constant, and undergo changes attributable to the factors mentioned above. Natural historians only establish the existence of varieties, but the plant breeder investigates them scientifically with the goal of creating new, more productive forms.

Another remarkable article appeared in Brno some time later. The author (Anon 1834) pointed out the possibility of prudent pairing of individual plants with different traits. He emphasized that by using artificial selection it was possible to obtain a combination of selected traits and reproduce them permanently in new varieties. At the end of the article there is a reference to a different technique of pollination in beans and peas. The author may again have been Diebl. This self-taught man had, through tremendous hard work, attained a broad knowledge, and was acknowledged not only as a skillful farm manager, but also as a breeder and later as a teacher. Diebl (1839) considered the development of agricultural production in an article called 'The necessary struggle of a farmer for the improvement and preservation of agricultural products.' In his view 'man raised himself from his original animal position in nature and placed himself over the animal kingdom.' His needs began to increase, and their satisfaction began to refine his existence. He considerably improved the products of nature for his own purposes. But improved plants and animals still had a tendency to revert to their original state. Man found that the improvement of forms had its limitations. But now natural science was offering new possibilities of pushing back the barriers to further improvement, and a new process of plant and animal breeding was leading to the gradual overcoming of nature. In this progressive spread of new knowledge Diebl gave pride of place to the local grass-roots gatherings of learned societies, where agriculturalists met natural scientists, which led to the diffusion of more and more new knowledge, and also encouraged new discoveries in natural science.

In the 1830s Professor Diebl worked in close conjunction with Abbot Napp on the committee of the Agricultural Society, and in particular in the Pomological Association, of which Napp was president. Napp and Diebl (1838) announced a prize essay sponsored by the Pomological Association on the subject of a new, improved variety of currant bush. They expected a presentation of the improved fruit and an essay describing the manner in which the variety was obtained. In 1839 the essays of the gardeners M. Frey (1839) and J. Twrdy (1839) were published in the journal of the Agricultural Society. There is a footnote to Frey's paper describing the method of artificial fertilization. Its author can only have been Professor Diebl, who had already published his ideas on the breeding of cereal varieties using artificial selection.

In 1840 the Agricultural Society, on whose committee Abbot Napp occupied a position of great influence, decided to offer an extraordinary prize of 1000 guilders, and to award the gold medal of the society, to the author of a chronicle of the development of natural science over the preceding hundred years in connection with the improvement of agriculture. The anonymously published announcement stated that many of the findings of natural science had still to be exploited in practice, and that the work was intended to evoke interest in a more detailed study of the subject and in particular of ways in which its findings could be used by farmers. Suggested models for the work were the history of the natural sciences published by the Frenchman G. Cuvier (1769-1832) or the history of natural science by the Englishman H. Davy (1778-1829). The author was expected to deal with agricultural production in its entirety, but without going into detail.

Not until 1850 was a manuscript submitted anonymously by N.K. Fraas (1810-75), professor of agricultural botany at the University of Munich. A commission of ten experts appointed by the committee of the Agricultural Society studied the work at daily sessions over a period of two months. Their report to the committee stated that it represented a summary of knowledge acquired in the course of progress in natural and agricultural science, with an extensive bibliography of literature published in Germany, France, England, Italy, Holland, Sweden, and elsewhere. It was thus of enduring value and a tribute to both the author and the society which had given the stimulus for its creation (Hackler 1851). Fraas (1852) published his work in Prague, in two volumes. The introduction to the commission's report highlights the author's pointing to inconsistencies between the way in which certain problems are understood by 'pure' natural scientists and by agricultural experts. Fraas emphasizes that naturalists have failed to grasp that agriculture is a synthesis of the application of natural science with that of economic principles. Though knowing nothing of research into the cell and the penetration of the pollen tube in the fertilization of a plant, or of the systematics of plants, farmers have for centuries made use of the sexuality of plants in the artificial pollination of various varieties. New varieties, even species, of agricultural crops are created, and no-one can now say where they originated from. Agriculturalists have thus refuted the mistaken view of natural scientists that species are constant, and have shown that hybrids are fertile.

The report on Fraas' work was presented to the committee of the Agricultural Society, where the views on artificial pollination and the breeding of new plant varieties cannot have escaped the attention of Abbot Napp. The report was published in Brno at the time Napp sent Mendel to study at Vienna University.

HEREDITY AS A RESEARCH PROJECT

Research into heredity received its first substantial impetus from sheep breeding. C.C. AndrÚ (1812) (Fig. 2.2), dealing with the scientific concept of breeding, had described artificial selection as a method of increasing the production capacity of wool sheep. Four years later his son Rudolf AndrÚ (1816) published an important manual on scientific methods of sheep breeding, emphasizing that this was a new method. Two years after this, the elder AndrÚ (see Note published with Anon. 1818) reached the conclusion that if animal propagation in the closest kinship was continued unrestricted it would lead to a weakening of the breed. Here he saw the operation of 'a natural physiological law,' which he wished to investigate in more detail, adding: 'To do justice to this problem I should have to write a book on it.'

Fig. 2.2 Christian Carl André (1763-1831). who gave the main impulse for the promotion of science in Moravia after 1800. He also began to organize animal and plant breeding on a new scientific level.

In the same year André the elder asked Count E. Festetics (1764-1847) to formulate the main principles of the use of interbreeding in breeding practice. In the following year Festetics (1819) published the first rough formulation of 'genetic laws,' already explicitly using a terminology (in German genetische Gesetze) that was to be more generally introduced into genetics in 1906. He states: (1) the characteristic traits of healthy parents are inherited by the progeny; (2) sometimes the traits of one of the grandparents appear in the progeny; (3) on other occasions the progeny exhibit traits which are quite different, and, if they do not correspond to the aims of the breeder and are heritable, are undesirable; (4) the main requirement for the use of inbreeding is scrupulous selection of the stock animals. In conclusion Festetics recommends the circumspect use of consanguineous mating to maintain the required production traits of animals (Orel 1989, 1994).

Count Festetics was an acknowledged expert on sheep breeding in Hungary, and as a participant in the annual meetings of breeders held in Brno he returned to Rudolf AndrÚ's proposal for the testing of wool quality: 'It will be judged as marking the beginning of a new epoch in the science of breeding, that in 1819 grades of wool fineness were established and defined with mathematical precision (Festetics 1820).'

An important milestone along the road to understanding the principles of scientific sheep breeding was the annual meeting in 1836. The president of the Sheep Breeders Association at that time, Bartenstein (1837), reached the conclusion that even if sheep breeders knew much more of the principles of selection since the founding of the society than they had before that, they realized that there was 'much more to be investigated'; indeed, they were only just arriving at the stage of rethinking their ideas. According to him it was necessary to take 'a deep look at the great and mysterious works of nature.' Given such a bold start, one might 'through the weakness of mortals' easily and understandably be led astray. Thus the president of the society, Bartenstein, turned to university professor Nestler to suggest a new topic for discussion at the annual general meeting of the Association in 1836. Nestler pointed out the importance of clearing up the question of which traits were transmitted more readily to the offspring, which were transmitted with difficulty, and which were passed on predictably, and under what circumstances.

Sheep breeders, along with Nestler, supposed that they could contribute to new findings, and to the monitoring of heredity through a posteriori analysis of the pedigree and progeny testing records of animals. According to Teindl et al. (1836), the discussion was pursued by Abbot Napp, who asserted that 'heredity of the characteristics from the producer to the produced (seitens der Erzeuger auf die Erzeugten) consisted above all of mutual elective kinship of the paired animal.' As a result a ram should be chosen for the ewe which corresponds to it in its inner and outer organism: this process must be the result of a substantive physiological study.

The meeting mentioned above also provoked a subsequent discussion on heredity in the pages of the Agricultural Society's journal. In the next year the prominent Austrian sheep breeder Ehrenfels (1837) called the discussion on heredity which arose very important, and said that the result was that it was carried on at the annual general meeting the next year. Its notable conclusions were summarized by Napp with rigorous brevity. He emphasized that it was not only a question of the breeding process, but that the question to be answered was 'what is inherited, and how?' Professor Nestler (1837) reviewed the debate, and in an article entitled 'Heredity in sheep breeding' expressed his satisfaction over the progress which had been achieved, though he was unable to add anything new to the discussion. But a volte-face had occurred in his conception of the matter. Whereas in 1829 he had published his lectures on scientific breeding without using the term heredity in the title, by 1837 he considered heredity to be a new scientific problem with serious economic implications that was crying out for experimental investigation. At this latter date he also explained how he had arrived at a definition of the problem of heredity. At an exhibition of pedigree sheep a prize-winning ram from the breeding farm of Count R.E. Wrbna provoked the question of what price to put on such an animal, and concluded: 'It cannot be sold at any price if its advantages are inherited by its offspring; if they are not, then its price is no more than that of its wool. meat. and skin.' Nestler went on: 'Thus Count Wrbna has posed the question of heredity to me, and through me to the Sheep Breeders' Association.' At that time the question seemed to many participants, according to Nestler, a strange one. Some even declared it not worth discussing, which Nestler considered a great mistake. He was convinced that he had 'sown the seed of the question in the proper soil' and that it could 'gradually be developed into the luxuriant fruit of science,' if the embryo was cared for.

In 1840 the fourth congress of German-speaking farmers and foresters was held in Brno. with Abbot Napp chairing a discussion on fruit-tree breeding, where he defended the hypothesis that artificial fertilization was a method of creating new varieties, against the view of some other participants that hybridization was merely a random process. Nestler edited the proceedings. According to Napp: 'In the mean-time nothing certain can be said in advance as to why production through artificial fertilization remains a lengthy, troublesome and random affair' (Nestler 1841. p.337). In fact he was thus completing his formulation of the problem of heredity begun in 1837 with a third point-what was the role of chance in heredity?

In the 1830s the discussion of methods of sheep breeding in Brno was at its height. Before that the members of the Sheep Breeders' Association had exchanged their experience at the annual meetings and on the pages of journals. This gave rise to mutual cooperation, which J. Teindl (1822), described as follows: 'Through mutual endeavour a desire for the progressive improvement of domestic animals is being awakened in landlords as a matter of priority; instead of uncertain procedures, more correct principles derived from experience and exact observation are being established, and candid warnings against the false trails and blind alleys to be avoided are being disseminated, so that the general standard of oviculture is everywhere being simultaneously improved.' At the congress of farmers in Brno in 1840 mentioned above Nestler, at the instigation of Napp, noted (Nestler 1841, p.216) that: 'Moravia can claim special credit for having become. through Geisslern's school at Hostice and from 1814 through the stimulus provided by the meritorious activity of Sheep Breeding Society in Brno, a source of modern rational sheep breeding.' After AndrÚ left Moravia, his former colleague Nestler continued to develop the principles of scientific breeding. In 1841 he died suddenly; but by then the import of cheap wool from British colonies had begun to have an impact, and sheep breeding in Moravia had lost much of its economic significance. In the 1840s no one showed any further interest in performing experiments for the improvement of sheep-breeding methods. Increased attention was, however, being paid in Brno to the use of plant hybridization, mainly owing to the efforts of Professor Diebl and Abbot Napp.

The enigma of heredity in connection with sheep breeding reappeared in 1853 in the theoretical speculations of the pure naturalist Professor Wagner (1853, p. 1007) at G÷ttingen; he was seeking an explanation of what were then the key questions of generation and heredity. He mentioned the corporeal peculiarities of organisms which were passed on to the next generation and beyond, and perspicaceously called for a critical examination of the observed facts and a careful elucidation of the accumulated statistics (Zusammenstellungen). He believed that 'more exact ascertainment of the numerical data could furnish a reliable clue.' Wagner defined six areas of interest in research into heredity, some of which had already been explained by Professor Nestler in his published lectures on the basis of empirical knowledge arising from sheep breeding. Wagner was sure that research into heredity could be carried out, but he saw it as being both an expensive and time-consuming undertaking.

In 1851 he himself tried to experiment with crossing various amphibians with differing qualitative traits. In the end he chose frogs and fish. He was aware that experiments must be carried out on a large number of animals. But he did not manage to obtain specimens of the same age after artificial fertilization, and he abandoned his efforts, realizing that it was not feasible to carry out such experiments in the laboratory of his institute. He expressed the opinion that they could be performed on large stud- or sheep-breeding farms. He also admitted the possibility of doing experiments with crossing exotic animals at London Zoo. In connection with attempts to achieve artificial insemination in dogs he suggested that experiments might be carried out at veterinary schools. Professor Wagner had no idea that experiments had been carried out on a large scale in Moravia in connection with sheep breeding, and that on the basis of the results obtained Professor Nestler had, along with Abbot Napp, already defined a research task relating to the basis of heredity.

A noteworthy conclusion of Wagner's (1853, p.1018) was that 'teaching on plant hybridization rests on a similar, more enlightened basis.' He refers to the latest publications on plant fertilization. Thus Wagner was the first pure naturalist who explicitly drew attention to the possibility of independent research into heredity through plant-hybridizing experiments.

The variance of views on research into hybridization and the use of hybridization methods in breeding plants was clearly pointed out by learned forester R. Geschwind (1829-1910), who lived and worked in Bohemia, Slovakia, and Hungary. He first applied his knowledge of botany to the successful breeding of roses (Geschwind 1885). His achievements in this field led him to propose the founding of nurseries for breeding new varieties of forest trees. In a remarkable paper Geschwind (1864) describes his experience with breeding woody species. The introductory sentence emphasizes that the art of producing plant bastards by means of the artificial cross-fertilization of plants had become established in horticulture a hundred years previously, over a broad area, and would transform horticulture. Hence, it is no wonder that men of science have welcomed the progress of hybridization with open arms, because of the opportunity it provides of examining the mystery of its laws (Orel 1986; Weiling 1975a).

Geschwind's experiments were in fact applied research. He showed a familiarity with the literature on research by botanists, the methods of breeders, and the work of physiologists investigating hybridization and the fertilization enigma. He also knew that some naturalists were already engaged in theoretical research into the problem. Forty-four years previously, Hempel had foreseen a new type of researcher, who would explain the laws of hybridization in the distant future. By the time Geschwind's paper was published, just such a researcher was already writing up in Brno his theoretical conclusions drawn from experiments into plant hybridization.

The problem of hybridization as seen by botanists and plant breeders was treated in an extensive paper by Ch.F. Hornschuh (1848). Its citation in Gõrtner's monograph did not escape Mendel's attention. Hornschuh wrote that the problem of the transformation of species was the weakest link in plant science, and that no one had yet explained the transformation of species or refuted the idea. It was still claimed that many forms of vetch were derived from forms of peas and lentils. Hornschuh drew attention to the fact that the rigorous segregation of forms of plants came to the fore without the occurrence of any intermediate forms. In his view these questions were only just starting to become the subject of research by a few isolated scholars, whilst others considered them almost ridiculous. Mendel was among the scholars for whom the problem was ripe for scientific research.

What, then. was the milieu from which this 'new type of researcher' came, and what qualifications, what motivation, did he have for undertaking such research?