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FORERUNNERS
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EDITED BY *BENTLEY GLASS*

OWSEI TEMKIN

WILLIAM L. STRAUS, JR.

under the auspices of

The Johns Hopkins History of Ideas Club

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THREE



AUPERTUIS, PIONEER OF GENETICS AND EVOLUTION *

BENTLEY GLASS

The mid-eighteenth century was a period almost unexampled in the vigor and advancement of science. Newton's physics had finished remaking the Heaven and the Earth. In biology, the new classification of plants and animals, introduced in 1735 by Linnaeus and developed into the binomial system in 1753, gave a vast stimulus to the discovery and description of new species. Louis Leclerc, Comte de Buffon, was beginning his tremendous *Natural History*, which ran to 36 volumes, yet was a best-seller to be found in the library of every European with any pretension to culture. Réaumur was engaged in detailed and fascinating studies of the life of insects. The Abbé Spallanzani had performed the first artificial fertilization of eggs by collecting semen from a male frog and applying it to freshly laid frog eggs. In Switzerland, Charles Bonnet had discovered parthenogenesis in plant-lice and thus had lent to the Virgin Birth an aura of scientific credibility; and while serving as a tutor in Holland, Bonnet's young relative, Abraham Trembley, had described the little Hydra and its powers of budding and regeneration, which awakened the greatest amazement. Was this supposed plant-animal not a living witness to the fact that, as Leibniz had asserted, "all advances by degrees in Nature, and nothing by leaps"? Here indeed was substantiation for the rightness of the concept of "The Great Chain of Being," which according to Arthur

* A revision of the two articles, "Maupertuis and the Beginning of Genetics" (*Quart. Rev. Biol.*, 22:196-210, 1947) and "Maupertuis, a Forgotten Genius" (*Scientific American*, 193:100-110, 1955).

O. Lovejoy was as much of a key to the thinking of the 18th century as the word "evolution" was to that of the 19th.¹

Preeminent among natural philosophers of the time was Pierre Louis Moreau de Maupertuis, President of Frederick the Great's Academy of Sciences in Berlin. As a young man, Maupertuis was the first person on the Continent to understand and appreciate Newton's laws of gravitation; and indeed, it was through Maupertuis that Voltaire first became convinced of their truth. When thirty years of age, in 1728, Maupertuis had visited London. It was the year of Newton's death. Here Maupertuis became a member of the Royal Society and a disciple of Newton. Upon his return to France, at a time when Newton's theory of gravitation was still violently opposed by the generality of believers in Cartesian vortices, Maupertuis became the open defender and expounder of the new scientific doctrines, just as Huxley over a century later sprang to the defense of Darwinism. D'Alembert, in his introduction to the *Encyclopedia* (1778),² praised Maupertuis' courage in being the first to declare himself openly (in the *Discours sur la figure des astres*, 1732) an adherent of Newton.³ In that same year Voltaire, more and more interested in scientific pursuits by the fascinating Mme. du Châtelet, who was undertaking to translate Newton's work into French, wrote to Maupertuis, asking him in flattering terms for his judgment upon Newton's theory. Voltaire's conversion followed, and later, his own work on the subject, which was by far his most serious scientific production.

Four years later, in 1736, Maupertuis headed one of two expeditions sent out to test the flattening of the earth toward the poles, by accurately measuring a degree along a meridian of longitude in two places, in the one instance at the equator, and in the other, just as far to the north as feasible. Maupertuis directed the expedition into Lapland, La Condamine the expedition to Peru; and between them they provided the first convincing proof to the world that Newton was correct, just as the expeditions to measure the gravitational deflection of light rays around the sun during an

¹ A. O. Lovejoy, *The Great Chain of Being*, p. 184. Harvard University Press, Cambridge, 1936.

² J. LeR. d'Alembert, *Discours préliminaire des éditeurs*. [In the *Encyclopédie*, Diderot and d'Alembert, editors, v. 1, i-lxxviii] Soc. Typographiques, Berne et Lausanne, 1778.

³ P. L. M. de Maupertuis, *Oeuvres*, nouvelle édition, corrigée et augmentée. 4 vol. J.-M. Bruyset, Lyon, 1756.

eclipse were in a later day and age to confirm the relativity theory of Einstein. There was no Nobel prize in those days, or surely Maupertuis would have earned one, at the age of 38.

Upon his return from Lapland, Maupertuis was addressed by Voltaire in these flattering words (letter of 19th Jan., 1741): "M. Algarotti is count; but you—you are marquis of the arctic circle, and you have won for yourself one degree of the meridian in France and one in Lapland. Your name covers a good part of the globe. I find you really a very great seigneur. Remember me in your glory." It was, in fact, on Voltaire's recommendation that, in 1740, Maupertuis was invited by Frederick the Great to come to Berlin as head of the reorganized Academy of Sciences.⁴ [Fig. 1].

Maupertuis, however, came to consider that his work as a champion of Newton on the Continent afforded him no great personal glory, and therefore in later years he laid great weight on his discovery in 1746 of the Principle of Least Action, which is all too commonly credited to one of the three great mathematicians, Euler, Lagrange, and Hamilton, who further developed it. This Principle is indeed one of the greatest generalizations in all physical science, although not fully appreciated until the advent of quantum mechanics in the present century.⁵ Maupertuis arrived at this principle from a feeling that the very perfection of the universe demands a certain economy in nature and is opposed to any needless expenditure of energy. Natural motions must be such as to make some quantity a minimum. It was only necessary to find that quantity, and this he proceeded to do. It was the product of the duration (time) of movement within a system by the "vis viva," or twice what we now call the kinetic energy of the system. Having found the quantity that tends to a minimum, Maupertuis regarded the principle as all-inclusive: "The laws of movement and of rest deduced from this principle being found to be precisely the same as those observed in nature, we can admire the application of it to all phenomena. The movement of animals, the vegetative growth of plants . . . are only its consequences; and the spectacle of the uni-

⁴ P. Brunet, *Maupertuis*. Vol. i. *Étude biographique*. Vol. ii. *L'œuvre et sa place dans la pensée scientifique et philosophique du XVIII^e siècle*. A. Blanchard, Paris, 1929. Cf. also *Les physiciens hollandais et la méthode expérimentale en France au XVIII^e siècle*, A. Blanchard, Paris, 1926; and *L'introduction des théories de Newton en France au XVIII^e siècle*, 2 vols., A. Blanchard, Paris, 1931.

⁵ J. Fee, Maupertuis, and the principle of least action, *Sci. Monthly*, 52: 496-503, 1941.

verse becomes so much the grander, so much the more beautiful, the worthier of its Author, when one knows that a small number of laws, most wisely established, suffice for all movements." This sort of talk aroused vigorous opposition. Translated into recent biological terminology, however, what is it other than Claude Bernard's principle of the maintenance of the internal environment, W. B. Cannon's principle of homeostasis, or the principle of Le Chatelier: "In a system in equilibrium, when one of the factors which determine the equilibrium is made to vary, the system reacts in such a way as to oppose the variation of the factor, and partially to annul it"? In these days when homeostasis has spread from physiology into embryology and genetics, and when social scientists, emulating ecologists who talk about the balance of nature, themselves talk about the balance of economic forces or social equilibria, the confidence of Maupertuis in the universality of his principle seems justified.

In any event, it seems unfair to say, as Sir James Jeans does, that Maupertuis arrived at his principle from reasons "theological and metaphysical rather than scientific."⁶ That is to decry the theoretical approach which has proved so fruitful in modern science, and which, to cite only one example, led Einstein first to the General Theory of Relativity and in after years to a search for its union with electromagnetic phenomena, in a single, magnificently simple, Unified Field Theory. Of the validity of the latter we are still uncertain, although Heisenberg now claims to have reached the goal; but that this is one valid type of scientific approach to nature who can doubt, when the evidence that $E = mc^2$ is so perpetually before us?

The magnificent irony is that it was through this very discovery of the Principle of Least Action that Maupertuis, so eminent and so highly respected in his own day, became a forgotten scientist, for whose name one must hunt assiduously to find more than a mention in the histories of scientific thought and achievement. The villain in this history was none other than Voltaire. It happened in the following way. A young scientist named Samuel Koenig, a friend and former fellow student of Maupertuis, moved by unknown motives, charged that Maupertuis' Principle of Least Action was in the first place erroneous, and in the second had been proposed by

⁶ Sir J. Jeans, *The Growth of Physical Science*, p. 233. Cambridge, at the University Press, 1948.



Fig. 1. Pierre Louis Moreau de Maupertuis

Leibniz before his death in a letter, of which Maupertuis was supposed to have had knowledge. Koenig sent the Berlin Academy a fragment of the letter, and later transmitted to Maupertuis, upon his insistence, a complete copy of it. The two did not agree, and the original could not be found, for its reputed owner had literally lost his head some time previously, having been executed by the ministers of justice. After considering the charges, the Berlin Academy by unanimous vote, with Maupertuis abstaining, declared Koenig's letter to be a fabrication, and he was expelled from the Academy.

Voltaire reacted in characteristic fashion, whether because he was always eager to defend the injured against the tyranny of those in high places, or because, as some said, Maupertuis had refused him a requested favor. The world has heard largely Voltaire's side of this famous dispute, and a sober reappraisal, such as Fee has made, had long been overdue. Koenig seems to have been a sincere, well-meaning man; but one cannot credit him with very good judgment in attacking Maupertuis upon such flimsy evidence; and nothing but a smile seems appropriate for the logic that led him in one breath to claim first that the discovery was based on error and was without worth and then that it had already been made by another person. It seems quite probable that Leibniz did arrive at the Principle of Least Action, and he may have written such a letter as Koenig claimed. But at any rate he did not publish it, and Maupertuis was well within his rights in demanding that the original letter be produced. No unpublished discovery can take from Maupertuis that recognition due his priority on publication. Nor was his clear formulation of the law at all, as some have claimed, "a generalization vaguely conceived and ill formulated"⁷ or "proposed in metaphysical shape."⁸ It was far in advance of the understanding it was to receive during the next century and a half, and Maupertuis had worked out specifically its applications to both inelastic and elastic impact and to the principle of the lever (cf. Fee, 1941). To Voltaire, however, the Principle of Least Action seemed so much nonsense, and Maupertuis a vain man using his prestige and position to suppress criticism and to salve his injured pride. So he took up his pen to write against Maupertuis some of his finest invective, of which

⁷ A. O. Lovejoy, Some eighteenth century evolutionists, *Pop. Sci. Monthly*, 65: 238-251; 323-340, 1904. Reprinted, *Sci. Monthly*, 71: 162-178, 1950.

⁸ H. T. Pledge, *Science Since 1500*, p. 81. Philosophical Library, New York, 1947.

Macaulay was to say: "Of all the intellectual weapons which have ever been wielded by man, the most terrible was the mockery of Voltaire."

In the *Diatribes du Docteur Akakia*,⁹ Voltaire showered his ridicule on the proposals for the advancement of the sciences which Maupertuis had published in 1752 in his *Lettres*¹⁰ and in the *Lettre sur le progrès des sciences*.¹¹ Those ideas, looked at from the standpoint of today, strike us as mostly extraordinarily well-conceived suggestions for systematic experimentation and investigation, only too far ahead of the times. Maupertuis' comments on the nature of the chemical elements, for example, and the possibility yet impracticability of their transmutation, might have been written today. But to Voltaire the *lettres* were further evidence of Maupertuis' vanity and incompetence. Maupertuis had suggested, among other things, that it might be a good idea not to pay doctors when they failed to heal, so Voltaire chose a physician as the mouthpiece of his sarcasm, to ask:

What you think a man would say, I pray you, who had, for example, 1200 ducats pension for having talked of mathematics and metaphysics, for having dissected a couple of toads, and for having had himself painted in a fur bonnet [see Fig. 1], if the treasurer should come to him with this language: "Monsieur, there is a deduction of 100 ducats for your having written that stars are made like windmills; 100 ducats more for having written that a comet will come to steal away our moon and carry its attacks to the sun itself; 100 ducats more for having imagined that comets all of gold and diamond will fall on the earth; you are taxed 300 ducats for having affirmed that babes are formed by attraction in the abdomen of the mother, that the left eye attracts the right leg, etc.? One cannot deduct less than 400 ducats for having imagined understanding the nature of the soul by means of opium and by dissecting the heads of giants, etc., etc."¹²

What of this is not gross misinterpretation merely shows that Voltaire was not gifted with scientific prevision; but it had its effect. Frederick, supporting Maupertuis at least in public, although snick-

⁹ F. M. A. de Voltaire, *Diatribes du Docteur Akakia*, 1752. [In *Oeuvres complètes* (Mélanges II, v. 23).] Garnier Fr., Paris, 1879.

¹⁰ Maupertuis, *Lettres*, 1752. [In *Oeuvres*, v. 2, pp. 185-340.]

¹¹ Maupertuis, *Lettre sur le progrès des sciences*, 1752. [In *Oeuvres*, v. 2, pp. 341-400.]

¹² Voltaire, op. cit.

ering in private, made Voltaire leave Potsdam and retire temporarily to France; but the reputation of Maupertuis never recovered, particularly since from that time until Maupertuis' death in 1759 Voltaire did not relent in his flood of unmerciful, unscrupulous, and myopic ridicule. Particularly interesting is the relation of this quarrel to the allegories of *Micromégas*, which Voltaire also published in 1752.¹³ Literary critics seem not to have observed that it was unquestionably Maupertuis' expedition to Lapland that the giant Saturnian and the super-giant from Sirius were supposed to have discovered and conversed with—Voltaire's effective way of putting Maupertuis' philosophy and science in a Lilliputian scale. Maupertuis had fallen in love while in Lapland, and brought the young girl back with him to the South. On the way the expedition met with a shipwreck, which Voltaire introduces into the story, while making of Maupertuis and his little "Lapp" maiden the butt of some of his nastiest witticisms. These are hardly relieved by more favorable comments on the "follower of Locke," who might possibly be identified as Maupertuis also, since in a letter of 1734, Voltaire had addressed Maupertuis as a "disciple of Locke and Newton." But it is more probable that Voltaire was simply thinking of himself! Clearly, the significance of *Micromégas* and its attack upon pseudo-scientists and false philosophers is entirely missed if its connection with Voltaire's quarrel with Maupertuis is overlooked.

Actually, in philosophy as in physical science, Maupertuis proved himself a powerful and original thinker, reproached by Voltaire for views the latter was himself later to embrace. As Lovejoy has pointed out, Maupertuis anticipated Beccaria and Bentham, and along with Helvetius represents "the head-waters of the important stream of utilitarian influence which became so broad and sweeping a current through the work of the Benthamites."¹⁴ Maupertuis also considered anew the favorite argument of the eighteenth century for the existence of God—the argument from the apparent Design of Nature—and formulated in terms very like those of Romanes well over a century later a beautifully clear statement of the survival of the fittest:

May we not say that, in the fortuitous combination of the productions of Nature, since only those creatures *could* survive in

¹³ Voltaire, *Micromégas*, 1752. [In *Oeuvres complètes* (Romans), v. 21, Garnier Fr., Paris, 1879.]

¹⁴ Lovejoy, *op. cit.*

whose organization a certain degree of adaptation was present, there is nothing extraordinary in the fact that such adaptation is actually found in all those species which now exist? Chance, one might say, turned out a vast number of individuals; a small proportion of these were organized in such a manner that the animals' organs could satisfy their needs. A much greater number showed neither adaptation nor order; these last have all perished. . . . Thus the species which we see today are but a small part of all those that a blind destiny has produced.¹⁵

While he did not deny the possibility of ultimate purpose in the universe, Maupertuis thus pointed out that biology has no need of teleological explanations. In this he reminds us of David Hume, his Scotch contemporary, who argued, in similar fashion: "It is in vain . . . to insist upon the uses of the parts of animals or vegetables and their curious adjustment to each other. I would fain know how an animal could subsist, unless its parts were so adjusted."¹⁶

Maupertuis soon came to realize that Newton's principle of gravitation affords an insufficient basis for explaining the phenomena of chemistry, and especially the behavior of living organization. Here he turned to the ideas of Leibniz, who saw at the basis of life properties of consciousness as well as mass. Hence arose the fact that, as Cassirer says, "It was especially Maupertuis who brought Leibniz to France. His personal relation to Leibniz is not indeed free from contradictions, but the objective kinship of his metaphysics, his philosophy of nature, and his theory of knowledge with Leibniz's basic ideals is undeniable."¹⁷ In fact, Maupertuis' great work, the *Système de la Nature*, regarding which more will be said later, may properly be considered an attempt to "reconcile the two great opponents in the philosophy of nature of the seventeenth century," Newton and Leibniz. It would be a mistake, however, not to regard this work as one of the highest order, which goes far beyond either of the great originals; and Cassirer's evaluation of Maupertuis' ideas suffers fatally from a failure to understand the genesis of those ideas not solely in the philosophers named, but equally in Maupertuis' investigations of heredity.

Another significant aspect of Maupertuis' philosophy was his

¹⁵ Maupertuis, *Essaie de cosmologie*, 1750. [In *Oeuvres*, v. 1, pp. i-xxviii, 1-78.]

¹⁶ D. Hume, Dialogues concerning natural religion (posthumous). [In *Essays and Treatises on Various Subjects*, v. 2.] Edinburgh, 1793.

¹⁷ E. Cassirer, *The Philosophy of the Enlightenment*, trans. by F. C. A. Koelln and J. P. Pettegrove, p. 86. Princeton University Press, Princeton, 1951.

attempt to introduce a calculus of pleasure and pain in order to evaluate the "good life" and to measure happiness. Here again his effort to quantify and to apply mathematical methods was characteristic of his whole approach to nature, for he proposed that the amount of pleasure or pain was a product of intensity and duration, a formulation strongly reminiscent of his Principle of Least Action. Maupertuis concluded pessimistically that in general the sum of the evils in life always exceeds the sum of the goods. In this philosophy his thinking leads straight to Kant, who spent much effort in fruitless argument against Maupertuis' ideas, ultimately to set aside the whole problem of objective measurement when developing his own ethical theory in which "there is evidently nothing left but the value which we ourselves place upon our lives, not only through what we ourselves do, but through what we perform independently of nature in a purposive manner. . . ." ¹⁸ In so doing, Kant places the aims of human life within a subjective area forever barred to science. But his solution ignores the later development of the theory of evolution, including the origin of man from lower forms of life, a theory which has inescapable implications for the sources of mental, emotional, and behavioral phenomena. To Maupertuis, these implications could not be set aside. His theory of human evolution was consistent with his philosophy, and only too far ahead of his time.

Maupertuis as Epigenesist

Eminent as were these contributions to physical science and to philosophy, it is in his biological ideas that Maupertuis was most clearly gifted with prevision. Here he must be reckoned as fully a century or a century and a half before his time. His biological ideas may be considered under the three heads of the formation of the individual, the nature of heredity, and the evolution of species, although obviously these are so closely interrelated that the division is largely artificial.

He began with an interest in the formation of the embryo, and quickly put his finger on the soundest argument against the preformationists, who believed the embryo to be fully preformed be-

¹⁸ Kant, *Werke*, ed. by Cassirer, v. 5, p. 514n, *Critique of Judgment*, sect. 83. [Quoted from Cassirer, op. cit., p. 151.]

fore conception, and present either in the sperm or the egg. This argument led him to a study of heredity, and he may be justly claimed as the first person to record and interpret the inheritance of a human trait through several generations. He was also the first to apply the laws of probability to the study of heredity. He was led by the facts he had uncovered to develop a theory of heredity that astonishingly forecast the theory of the genes. He believed that heredity must be due to particles derived both from the mother and from the father, that similar particles have an affinity for each other that makes them pair, and that for each such pair either the particle from the mother or the one from the father may dominate over the other, so that a trait may seemingly be inherited from distant ancestors by passing through parents who are unaffected. From an accidental deficiency of certain particles there might arise embryos with certain parts missing, and from an excess of certain particles could come embryos with extra parts, like the six-fingered persons or the giant with an extra lumbar vertebra whom Maupertuis studied. There might even be complete alterations of particles—what today we would call “mutations”—and these fortuitous changes might be the beginning of new species, if acted upon by a survival of the fittest and if geographically isolated so as to prevent their intermingling with the original forms. In short, virtually every idea of the Mendelian mechanism of heredity and the classical Darwinian reasoning from natural selection and geographic isolation is here combined, together with De Vries’ theory of mutations as the origin of species, in a synthesis of such genius that it is not surprising that no contemporary of its author had a true appreciation of it.¹⁹

Even in his earliest biological essays, “Observations et expériences sur une des espèces de salamandre” (1727),²⁰ and “Expériences sur les scorpions” (1731),²¹ Maupertuis evinced an absorbing interest in reproduction and those problems that it inevitably generates. Having observed both eggs in the ovaries and live young to the number of 54 in the oviducts of single female salamanders, Maupertuis remarked that “these animals appear very suitable for enlightening the mystery of generation.” In the study of scorpions

¹⁹ Buffon, it is true, seems to have derived his own ideas of the seminal particles at least in part from Maupertuis (see pp. 77, 81).

²⁰ Maupertuis, *Mémoires de l'Académie des Sciences*, 1727, 27-32. [Published, 1729.]

²¹ Maupertuis, *Mémoires de l'Académie des Sciences*, 1731, 223-229. [Published, 1733.]

it was again the presence of living young (up to 65 in number) within the female, and the fantastic courtship of the sexes which excited his interest, as it did that of Fabre a century and a half later.

The prevailing ideas regarding the origin of the individual in Maupertuis' time were those of preformation. William Harvey, in 1651, had plainly declared his conviction, based on the study of the development of the embryo chick, in favor of epigenesis, that is, of the view that the parts of the embryo are formed in succession out of unorganized material; but the application of the microscope to the reinvestigation of the matter, by Malpighi, led to the common opinion that Harvey had been wrong. Malpighi was perhaps led astray by his inability to find any but a fairly well-developed embryo in freshly laid eggs, not recognizing that the embryo might have begun its development while the egg was descending the oviduct. Swammerdam's investigations of insect metamorphosis—in particular, his demonstration that a perfectly formed butterfly is to be found within the chrysalis—seemed convincing demonstrations of a like sort, although the idea was pushed far beyond demonstrable limits. The caterpillar must mask a perfect butterfly, within which there would be eggs containing, *multum in parvo*, caterpillars, chrysalids, and butterflies of a generation still to come; and so on (see chap. II, pp. 43-46).

Another notable scientific doctrine was involved in the common acceptance of the preformation theory in the seventeenth and eighteenth centuries. This was the belief in spontaneous generation. As long as it was believed that living creatures could arise spontaneously from mud, filth, and putrescent matter, either epigenesis or some preformation of germs disseminated throughout nature seemed inescapable, at least for such organisms. The demonstration by Redi, in 1668, that maggots hatch only from flies' eggs, and do not appear in putrefying meat except when the flies have access to it, cleared the way for the encasement ("*emboîtement*") theory of preformation.

The predominance of the preformationist doctrine led to heated claims in behalf of the ovum by the followers of Malpighi and Swammerdam, on the one hand, and of the spermatozoa by the disciples of Leeuwenhoek, on the other; since, if the embryo is preformed, it could not logically be preformed in both parents alike. The discovery of the mammalian egg (or, in reality, of the ovarian follicle) by Regnier de Graaf, in 1672, was a great victory

for the ovists, who claimed that the spermatie animalcules possessed only the function of stirring and mixing the two seminal fluids. The animalculists countered with purported observations of homunculi within the heads of the spermatozoa. But this is not the place to trace the exaggerated and frequently ridiculous claims and counter-claims of these two schools of thought. Suffice it to say that by 1740 there remained very few epigenesists indeed, and the encasement theory of preformation prevailed almost universally.

In 1745 a small anonymous volume appeared from the press entitled *Vénus Physique, contenant deux dissertations, l'une sur l'origine des hommes et des animaux: et l'autre sur l'origine des noirs*.²³ (The second part had already been printed in the preceding year, with the interesting title *Dissertation Physique à l'Occasion du Negre Blanc*.)²⁴ This book was written in a popular style for gentlemen and ladies of the court. The author, who later turned out to be Maupertuis, dared to adopt the discredited epigenetic theory of development. He was led to this by a consideration of the plain facts of biparental heredity, which had been pointed out by Aristotle and again by Harvey, but which the ovists and animalculists attempted to explain away. According to them, heredity might be regarded as a spiritual essence, transferrable in the seminal fluids, and impressing itself upon the preformed embryo provided by one or the other of the parents. This essentially vitalistic idea was abhorrent to Maupertuis. A mathematician trained in Cartesian views, an early convert to Newton's teachings, Maupertuis belies the remark made by Driesch that all epigenesists were vitalists, for Maupertuis was a consistent mechanist. In criticizing the views of the preformationists, Maupertuis would have nothing to do with essences and spiritual "virtues." He argued against the possibility that maternal impressions can affect the foetus, and to him biparental heredity necessarily implied *corporeal* contributions from each of the two parents.

Maupertuis' Investigation of Polydactyly

One may well wonder what led Maupertuis to these views. The

²³ Maupertuis, *Vénus Physique, contenant deux dissertations, l'une sur l'origine des hommes et des animaux; et l'autre sur l'origine des noirs*. La Haye, 1745. [Also in *Oeuvres*, v. 2, pp. 1-134.] Hereafter abbreviated as *V.P.*

²⁴ Maupertuis, *Dissertation Physique à l'Occasion du Negre Blanc*. Leyde, 1744.

answer is sufficiently clear. He had already, ~~prior to~~ 1745, conducted a careful study in human genetics that is matched by only one other of its time. It seems that a young albino negro had been brought to Paris and naturally enough created a great stir. This started Maupertuis to thinking about heredity. Surely the albino condition must be hereditary, for although it seemed to appear sporadically among Negroes, it was reportedly not rare in Senegal, where whole families were said to be "white." Of the famous albino Indians of Panama he had also heard, and discoursed about them with no little sentimentality. "The black color," he said, "is just as hereditary in crows and blackbirds, as it is in Negroes: I have nevertheless seen white blackbirds and white crows a number of times." ²⁵

Shortly after coming to Berlin, Maupertuis began to hunt for a case he could study at first-hand. He was fortunate in his search: he ran across the polydactylous Ruhe family. The investigation had been completed some time before the *Vénus Physique* was written, and from the internal evidence seems to have been the main directive to the thoughts and arguments presented in that book. When it is remembered that this was Maupertuis' first extensive venture into biological investigation, that the collection of human pedigrees was a novel enterprise, and that even in the present century the necessity of making a complete record of all normal as well as all abnormal members of a family has frequently been neglected, one can only marvel at his perspicacity. Maupertuis described his study of this hereditary trait no less than three separate times, in the *Vénus Physique*, in the *Système de la Nature*, and in the *Lettres*. It is in the latter (Letter XIV) that we find the fullest account, which follows:

A great physician proposes in a useful and inquiring work (*L'art de faire éclore des oiseaux domestique*, par M. de Réaumur, t. II, mém. 4) to perform some experiments on this question [of biparental inheritance]. In the race (*genre*) of fowls it is not rare to see types (*races*) which bear five toes on each foot; it is hardly more to see those which are born without rumps. M. de Réaumur proposes to mate a hen with five toes with a four-toed cock, a four-toed hen with a five-toed cock; to do the same experiment with the rumpless cocks and hens: and [he] regards these experiments as able to decide whether the foetus is the

²⁵ *V. P.*, Part II, Chap. IV.

product solely of the father, solely of the mother, or of the one and the other together.

I am surprised that that skilful naturalist, who has without doubt carried out these experiments, does not inform us of the result. But an experiment surer and more decisive has already been entirely completed. That peculiarity of the supernumerary digits is found in the human species, extends to entire breeds (*racés*); and there one sees that it is equally transmitted by the fathers and by the mothers.

Jacob Ruhe, surgeon of Berlin, is one of these types. Born with six digits on each hand and each foot, he inherited this peculiarity from his mother *Elisabeth Ruben*, who inherited it from her mother *Elisabeth Horstmann*, of Rostock. *Elisabeth Ruben* transmitted it to four children of eight she had by *Jean Christian Ruhe*, who had nothing extraordinary about his feet or hands. *Jacob Ruhe*, one of these six-digitated children, espoused, at Dantzic in 1733, *Sophie Louise de Thüngen*, who had no extraordinary trait: he had by her six children; two boys were six-digitated. One of them, *Jacob Ernest*, had six digits on the left foot and five on the right: he had on the right hand a sixth finger, which was amputated; on the left he had in the place of the sixth digit only a stump.

One sees from this genealogy, which I have followed with exactitude, that polydactyly (*sex-digitisme*) is transmitted equally by the father and by the mother: one sees that it is altered through the mating with five-digitated persons. Through these repeated matings it must probably disappear (*s'éteindre*); and must be perpetuated through matings in which it is carried in common by both sexes.

The pedigree is diagrammed conventionally in Fig. 2.

Maupertuis was quite struck by this apparent weakening of the trait with time, and it led him to the conclusion that through repeated matings with normal individuals the trait might in time disappear. In other words, the deviations of nature tend to fade out, and "her *works* always tend to resume the upper hand."²⁶ Maupertuis had evidently a clear idea that most if not all abnormalities are disadvantageous, and as we shall see later, this became an important part of his evolutionary thought.

It is truly astonishing to discover that in the second edition of that very book by Réaumur which served as inspiration to Mau-

²⁶ *V.P.*, Part II, Chap. v, italics added.

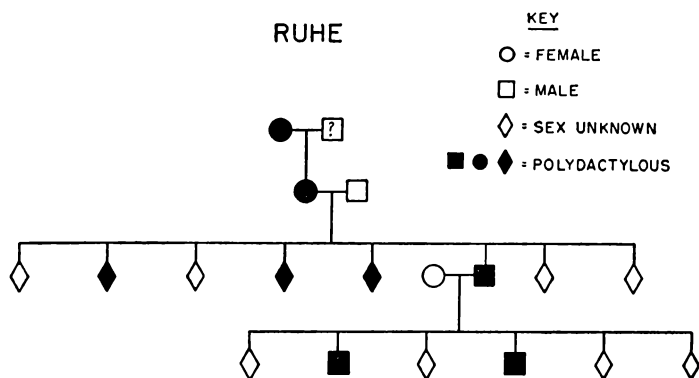


Fig. 2. Polydactyly in the Ruhe family, according to Maupertuis

pertuis (*L'art de faire éclore les oiseaux domestiques*),²⁷ there is a celebrated account of the inheritance of human polydactyly that is as circumstantial and complete as that of the Ruhe family. Charles Bonnet, in 1762, struggled vainly to deal with its implications, so embarrassing to the theory of preformation and to ovists in particular.²⁸ A Maltese couple, named Kelleia, whose hands and feet were constructed upon the ordinary human model, had a son, Gratio, who possessed six perfectly moveable fingers on each hand and six toes, deformed and crownlike, on each foot. This man married a normal woman and had by her four children. The eldest, Salvator, a boy, had six fingers and six toes; the second, George, had five fingers and toes, but his hands and feet were slightly deformed; the third, André, was normal; the fourth, a girl, Marie, had five fingers and toes, but her thumbs were slightly deformed. All of these children grew up and married normal persons. The eldest had four children, two boys and a girl polydactylous, and one normal boy. The second, George, had three girls, all polydactylous, and a normal son. Two of these girls had six fingers and six toes on each side, but one had only five toes on his left foot. The fourth of Gratio Kelleia's children, his daughter Marie, had one boy with six toes and three normal children (one boy; two girls). The normal son of Gratio had only normal children. This pedigree is represented in Fig. 3.

How did Maupertuis come to overlook this account by Réaumur,

²⁷ R. A. F. de Réaumur, *L'art de faire éclore et d'enlever en toute saison des oiseaux domestiques des toutes espèces*, 2 vol. Impr. Royale, Paris, 1749. Second edition, 1751.

²⁸ C. Bonnet, *Considérations sur les corps organisés*, Part II, Chap. VIII, CCCLV. In *Collection complète des Oeuvres*, T. III, pp. 518 ff. Neuchatel, 1779.

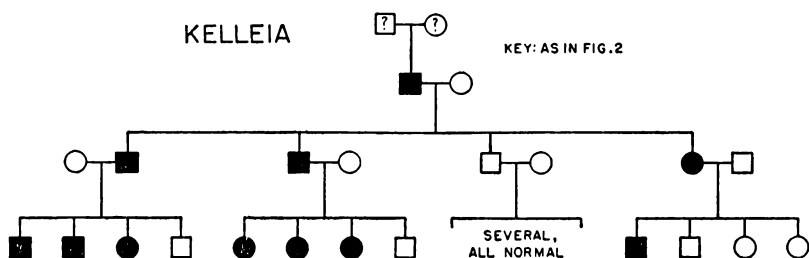


Fig. 3. Polydactyly in the Kelleia family, according to Réaumur

which so closely resembles his own investigation? An examination of Réaumur's rather rare book shows that the edition of 1749 does not contain the account. It was first added in the second edition, of 1751, in an appended section in square brackets at the very end of the book. It must be presumed that Maupertuis never saw it.

This well-known pedigree was cited by T. H. Huxley in his essay of April, 1860, entitled "[Darwin on] the Origin of Species,"²⁰ but with one egregious addition to the original. Huxley stated: "A Maltese couple, named Kelleia, whose hands and feet were constructed upon the ordinary human model, had born to them a son, Gratio. . . ." Nowhere in Réaumur's account, however, is it said that both the parents of Gratio Kelleia definitely had normal hands and feet. I was consequently misled in my original essay on Maupertuis when I relied on Huxley's account for this point, which would instantly be recognized by a geneticist as highly significant. For if both parents had been carefully examined and had been found to have normal digits, one might suppose that a mutation had occurred in one of the germ cells from which Gratio issued, although the very mild expression of the deformity in his daughter Marie is sufficient warning of a highly variable manifestation of the condition and a possibly reduced penetrance, such that occasionally a seemingly normal person might transmit the deformity. It would be necessary, therefore, to establish that Gratio Kelleia's ancestry for more than one generation back had been free of the trait before the assumption of a mutation would be warranted. However, Maupertuis might well have seized upon the sudden

²⁰ T. H. Huxley, [Darwin on] the Origin of Species, April, 1860, *Westminster Review*. In *Darwiniana* (Collected Essays, II), pp. 22-79, Appleton, New York and London, 1912. Also in *Man's Place in Nature and Other Essays*, Everyman's Library, Dent, London, 1906.

appearance in the son of normal parents of a hereditary condition that thereafter descended in unbroken lineage as a striking example of one of those fortuitous and tenacious alterations of the hereditary particles which he thought might constitute the beginning of a new species (see below).

Maupertuis' Theory of Heredity and the Origin of the Foetus

This investigation of polydactyly was the work upon which Maupertuis founded his theory of the formation of the foetus and the nature of heredity, a theory that was more than a century before its time and that brilliantly anticipated the discoveries of Mendel and de Vries. Maupertuis started out with the idea of chemical attraction, that attraction between the particles of different elements which results in the formation of compounds between them. This new chemical concept of Geoffroy and other French chemists of the time was much discussed, and Maupertuis was pre-disposed to it on account of his early devotion to the concept of gravitational attraction, which seemed to him to be an analogous phenomenon. As Maupertuis conceived it, two substances possess a tendency to unite by virtue of their chemical affinity (*rapports*); but if a third appears on the scene with a greater affinity for one of the two, it "unites with it while making it take leave of the other."³⁰ Maupertuis boldly applies these laws of chemistry to living beings. "Why," he asks, "if this force exists in Nature, would it not operate in the formation of the body of animals? Let us suppose that there are in each of the semens particles destined to form the heart, the head, the intestines, the arms, the legs; and these particles may each have a greater uniting power (*rapport d'union*) with that one which, in order to form the animal, has to be its neighbor, than with any other; the foetus will form, and were it yet a thousand times more organized than it is, it would form."³¹ Several years later, when Maupertuis, under the pseudonym of Doctor Baumann, wrote the *Système de la Nature* (1751),³² his ideas regarding these hereditary particles had apparently been influenced both by Leibniz's famous monads and by Buffon's theory of organic particles disseminated throughout nature, the latter theory having appeared

³⁰ *V. P.*, Part I, Chap. xvii.

³¹ *Ibid.*

³² Maupertuis, *Système de la Nature*, 1751. In *Œuvres*, v. 2, pp. 135-184. Hereafter abbreviated as *S. N.*

in the meantime; and Maupertuis attributed to these postulated particles a property "akin to that which in us we term desire, aversion, memory."³³ Moreover, although in the *Vénus Physique* he proposed pangenesis with cautious reservation and only as a hypothesis worthy of investigation, in the *Système de la Nature*, no doubt encouraged in this direction by Buffon's embracement of the idea, he spoke without reserve. In the *Vénus Physique* the 1746 edition reads simply: "As to the manner whereby there form in the semen of each animal particles analogous to those of that animal, I do not at all examine it here." The same passage in the later version included in the *Oeuvres* (1756) is amplified as follows: "As to the matter of which, in the semen of each animal, particles like that animal are formed, it would be a very bold conjecture, but one perhaps not destitute of all truth, to think that each part furnishes its own germs. Experiment could perhaps clear up this point, if one tried over a long period to mutilate certain animals generation after generation; perhaps one would see the parts cut off diminish little by little; perhaps in the end one would see them annihilated."³⁴ In the *Système de la Nature* we find: "The elements suitable for forming the foetus swim in the semens of the father and mother animals; but each, extracted from the part like that which it is to form, retains a sort of recollection of its old situation; and will resume it whenever it can, to form in the foetus the same part."³⁵

This particulate theory of heredity and the formation of the foetus is logically analogous to Mendelian theory, and far in advance of those ideas that heredity is determined by indivisible entities, fluids or vapors, subject to irrevocable blending through intermating, that were current until late in the nineteenth century. If in one direction Maupertuis' hereditary particles therefore look back to the monads of Leibniz, in the other they look forward to the concept of the genes; and they have really much more in common with the latter than the former. Of course, Maupertuis confused the hereditary particles with the effects they produce and with the parts whose development they control, but that was hardly avoidable at the time. After all, this was nearly a century before the formulation of the Cell Theory. To see that at bottom heredity must depend on a sort of organic, chemical memory, and to attribute this to separable

³³ S. N., xxxi.

³⁴ V. P., Part II, Chap. v.

³⁵ S. N., xxxiii.

particles that maintain their nature in combination is extraordinary enough. And what can one say of the perspicacity that proposed, as a test of pangenesis, the very experiment that Weismann was to perform nearly 150 years later?

Next to the particulate nature of the hereditary material, the most important of Mendel's principles is that of segregation. The hereditary units, or genes, as we now call them, are present in pairs as a consequence of fertilization, and the members of each pair segregate from one another in the reproductive cells prior to the production of another generation of offspring. This principle, too, was foreshadowed by Maupertuis. However the particles might previously be combined in each one of the parents, the particles from the two semens, he supposed, would unite *separately* in accordance with their affinities and, since corresponding particles from the mother and the father would be most alike, they would unite two by two and exclude other combinations. "One ought not to believe," he says," that in the two semens there are only precisely the particles which are needful to form one foetus, or the number of foetuses that the female is to bear: each of the two sexes without doubt furnishes a great many more than are necessary. But the two particles which are to be adjacent once being united, any third, which could have made the same union, would no longer find its place, and would remain useless. It is this, it is by these repeated operations, that the child is formed from the particles of the father and the mother, and often bears visible marks that it partakes of the one and of the other."³⁶ "In the seminal fluid of each individual the particles suitable for forming traits like those of that individual are the ones which are ordinarily most numerous, and which have the greatest combining power (*affinité*); although there are a great many others for different traits. . . . The particles analogous to those of the father and the mother being the most numerous, and having the most combining power, will be those which most commonly unite; and they will ordinarily form animals like those from which they are come."³⁷

This is further clarified by Maupertuis' consideration of hybrids: ". . . For as soon as there is a mixing of species, experience teaches us that the child resembles both the one and the other."³⁸ "If the elements come from animals of different species, but in which there still remains sufficient affinity between the elements; these

³⁶ V. P., Part I, Chap. xvii.

³⁸ Ibid.

³⁷ V. P., Part II, Chap. v.

more attached to the form of the father, those to the form of the mother, [they] will produce hybrid animals.”³⁹ “Finally if the elements come from animals who no longer have between them sufficient analogy, the elements not being able to assume, or not being able to retain a suitable arrangement, generation becomes impossible.”⁴⁰ Thus, Maupertuis goes on, one can explain the sterility of hybrids such as the mule. “One of the most singular phenomena, and one of the most difficult to explain, is the sterility of hybrids. Experiment has shown that any animal born of the coupling of different species cannot reproduce. Could one not say that in the parts of the hinny and of the mule, the elements having taken a particular arrangement which was neither that which they had had in the ass, nor that which they had had in the mare; when these elements pass into the semens of the hinny and of the mule, the habitude of this last arrangement being most recent, and the habitude of the arrangement which they had had in the ancestors being stronger, because contracted over a greater number of generations, the elements remain in a certain equilibrium, and unite neither in one manner nor in the other?”⁴¹ To anyone familiar with the causes of hybrid sterility this last paragraph has a startlingly modern ring. For Maupertuis was essentially correct. A set of chromosomes is indeed an arrangement of hereditary elements, and very often in hybrids the chromosomes derived from the two pure species are incapable of normal segregation, because of differences in the arrangements of their genes. The sterile hybrid between the radish and the cabbage furnishes an example. Radish chromosomes cannot pair with cabbage chromosomes. Segregation produces no effective germ cells, for neither an array wholly of radish elements nor one wholly of cabbage elements is likely to recur, and random mixtures of radish and cabbage chromosomes are physiologically ill-assorted. In spite of the crudity of Maupertuis’ idea, it is impossible not to admire his insight.

Mendel is often credited with having discovered genetic dominance, although actually it was known long before his day, having been described by Knight in 1823. Maupertuis also arrived, though vaguely, at the idea of dominance. This came about from two considerations. In the first place, as we know today, polydactyly is a dominant trait. In the second place, the other genetic character in

³⁹ *S.N.*, XXXVIII.

⁴⁰ *S.N.*, XXXIX.

⁴¹ *S.N.*, XLIII.

which Maupertuis became interested, and to which he devoted the second part of the *Vénus Physique*, was albinism in negroes, and this is a recessive. Maupertuis was therefore aware that whereas polydactyly descends regularly from affected persons, married to normals, to some but not all of their offspring, albinism, on the other hand, seemed to appear sporadically among negroes, albino negroes being born of parents both of whom were black. Yet Maupertuis was convinced that albinism was hereditary. Maupertuis was thus faced with the problem of accounting in his theory for the different modes of inheritance, and concluded: "There could be, on the other hand, arrangements so tenacious that from the first generation they dominate (*l'emporte*) over all the previous arrangements, and efface the habitude of these."⁴²

Had Maupertuis evolved a metaphysical system of heredity and embryogenesis, and done nothing more, he could hardly be ranked above his contemporary biologists. Metaphysical systems, in the eighteenth century, were "a dime a dozen." Georges Hervé, the first person to have considered the work of Maupertuis in the light of Mendelian genetics, has said: "His right to figure in a gallery of pre-Mendelian genetics would in that case have been disputable; if he holds a place there, it is because he knew enough to carry his researches into experimental realms."⁴³ He diligently pursued the collection of further evidence on polydactyly, and with some success, since he could write (later): "I have found in Berlin two six-digitated persons, and I have given the genealogy of one. I have not been able to follow with sufficient exactitude the genealogy of the other, who is a foreigner, and who has concealed himself from me: but he had six-digitated children, and I have been assured that this polydactyly has been hereditary in his family for a long time. A scientist illustrious in Germany and Minister to the Duke of Würtemberg, M. de Bulfinger, was of such a family, and born with a sixth finger that his parents had cut off as a monstrosity."⁴⁴

Like Mendel, Maupertuis applied mathematics to genetic investigation, by calculating the probability that the polydactyly observed might be only a sporadic accident and not really inherited. He wrote:

⁴² S. N., XLIV.

⁴³ G. Hervé, Maupertuis génétiste, *Rev. anthropol.*, 22: 217-230, 1912.

⁴⁴ *Lettres*, xiv.

But if one wished to regard the continuation of polydactyly as an effect of pure chance, it would be necessary to see what the probability is that this accidental variation in a first parent would be repeated in his descendants. After a search which I have made in a city which has one hundred thousand inhabitants, I have found two men who had this singularity. Let us suppose, which is difficult, that three others have escaped me; and that in 20,000 men one can reckon on one six-digit: the probability that his son or daughter will not be born with polydactyly at all is 20,000 to 1; and that his son and his grandson will not be six-digit at all is $20,000 \times 20,000$ or 400,000,000 to 1: finally the probability that this singularity will not continue during three generations would be 8,000,000,000,000 to 1; a number so great that the certainty of the best demonstrated things of physics does not approach these probabilities.⁴⁵

This is not only an excellent example of scientific caution, but also represents what is without doubt the first application to genetics of one of the most important of the principles of the mathematics of probability, that of the probability of coincidence of independent items. It was this very principle that Mendel applied so effectively in his analysis of segregation, random recombination, and independent assortment.

Breeding Experiments

But Maupertuis was not content to make only this analysis. He undertook actual breeding experiments with animals to test out his theories, although of the results of these he has unfortunately left us only the account of a single one. It is related that he "adored animals and lived surrounded by them." "You are more pleased with Mme. d'Aiguillon than with me," wrote Mme. du Deffand to him one day, "she sends you cats." And Frederick wrote, too: "I know that at Paris just as at Berlin you are enjoying the delights of good company. . . . I am only afraid that Mme. la duchesse d'Aiguillon is spoiling you. She loves parrots and cats, which is a prodigious merit in your eyes . . ." ⁴⁶ Maupertuis had established himself in the outskirts of Berlin, in a spacious house adjacent to the royal park, near the present Tiergarten; and this house he had con-

⁴⁵ Ibid.

⁴⁶ Letter of Frederick, Potsdam, 15 Nov., 1748. Quoted from Hervé, op. cit.

verted into a virtual Noah's ark. Samuel Formey, permanent secretary of the Berlin Academy, has left us the following description: "The house of M. de Maupertuis was a veritable menagerie, filled with animals of every species, who failed to maintain the proprieties. In the living-rooms troops of dogs and cats, parrots and parakeets, etc. In the fore-court all sorts of strange birds. He once had sent from Hamburg a shipment of rare hens with a cock. It was sometimes dangerous to pass by the run of these animals, by whom some had been attacked. I was especially afraid of the Iceland dogs. M. de Maupertuis amused himself above all by creating new species by mating different races together; and he showed with complaisance the products of these matings, who partook of the qualities of the males and of the females who had engendered them. I loved better to see the birds, and especially the parakeets, which were charming. . . ." ⁴⁷

It was of the Iceland dogs that Maupertuis has left us the account of his breeding experiment: "Chance led me to meet with a very singular bitch, of that breed (*espèce*) that is called in Berlin the Iceland Dogs: she had her whole body the color of slate, and her head entirely yellow; a singularity which those who observe the manner in which the colors are distributed in this sort (*genre*) of animals will find perhaps rarer than that of supernumerary digits. I wished to perpetuate it; and after three litters of dogs by different fathers which did not yield anything of the sort, at the fourth litter she gave birth to one who possessed it. The mother died; and from that dog, after several matings with different bitches, there was born another who was exactly like him. I actually have them both." ⁴⁸ His breeding of dogs led him to wonder particularly about the supernumerary fifth digit which is not uncommon on the hind foot: "There are no animals at all upon whom supernumerary digits appear more frequently than upon dogs. It is a remarkable thing that they ordinarily have one digit less on the hind feet than on those in front, where they have five. However, it is not at all rare to find dogs who have a fifth digit on the hind feet, although most often detached from the bone and without articulation. Is this fifth digit of the hind feet then a supernumerary? or is it, in the regular course, only a digit lost from breed (*race*) to breed throughout the entire species, and which tends from time to time

⁴⁷ Quoted from Hervé, *op. cit.*

⁴⁸ *Lettres*, xiv.

to reappear? For mutilations can become hereditary just as much as superfluities.”⁴⁹ Were all dogs, in other words, once five-toed on both front and back feet? Have we here a remnant, a vestige of a once functional structure? These observations might well have been made by Charles Darwin.

His Theory of Evolution

Maupertuis' studies thus led him to evolution. Here with certainty he must be ranked above all the precursors of Darwin. To begin with, he was faced with the problem of accounting for supernumerary digits, albinism, and other hereditary anomalies on the basis of his theory of generation. This he solved ingeniously. "If each particle is united to those that are to be its neighbors, and only to those, the child is born perfect. If some particles are too distant, or of a form too little suitable, or too weak in affinity to unite with those with which they should be united, there is born a monster with deficiency (*monstre par défaut*). But if it happens that superfluous particles nevertheless find their place, and unite with the particles whose union was already sufficient, there is a monster with extra parts (*monstre par excès*)."⁵⁰ Even Mendel did not foresee that deficiencies and duplications of the hereditary material might constitute a basis of abnormal development, a sort of mutation! Maupertuis comments on the remarkable fact that in monsters with extra parts, these are always to be found in the same locations as the corresponding normal parts: two heads are always on the neck, extra fingers are always on the hand, extra toes on the foot. This is very difficult to explain on the basis of the theory that monsters come from the union of two foetuses or eggs, which was the explanation forced upon the preformationists by the nature of their views; but it was not at all difficult to explain on the basis of Maupertuis' concepts. He described the skeleton of a giant man, preserved in the Hall of Anatomy of the Academy in Berlin, with an extra vertebra in the lumbar region, inserted in a regular fashion between the ordinary vertebrae. How could this be the remains of a second foetus fused with the first? he asked.

But on Maupertuis' particulate theory, "chance, or the scarcity of family traits, will sometimes make rarer assemblages; and one

⁴⁹ Ibid.

⁵⁰ *V.P.*, Part I, Chap. xvii.

will see born of black parents a white child, or perhaps even a black of white parents. . . ." ⁵¹ ". . . there are elements so susceptible of arrangement, or in which recollection is so confused, that they become arranged with the greatest facility . . . ;" ⁵² elements which represent the condition in an ancestor rather than that in the immediate parent may enter into union in forming the embryo, producing resemblance to the ancestor rather than to the parent, ⁵³ but also "a total forgetfulness of the previous situation" may occur. ⁵⁴

Maupertuis thus came to the conclusion that hereditary variants are sudden, accidental products—mutations, to use the modern term. Moreover, since negroes could by mutation produce "whites" (i. e., albinos), it was clear that racial, or species, differences—the distinction was not too clear in the eighteenth century—are produced by mutations. To Maupertuis, exactly as to Hugo de Vries a century and a half later, a species was merely a mutant form that had become established in nature. The evidence for this was clear from the artificial breeds of domestic animals. As in the case of Charles Darwin a century later, it was in particular the pigeons that clinched the argument. "Nature contains the basis of all these variations: but chance or art brings them out. It is thus that those whose industry is applied to satisfying the taste of the curious are, so to say, creators of new species. We see appearing races of dogs, pigeons, canaries, which did not at all exist in Nature before. These were to begin with only fortuitous individuals; art and the repeated generations have made species of them. The famous Lyonnés [Lyonnet] every year created some new species, and destroyed that which was no longer in fashion. He corrects the forms and varies the colors: he has invented the species of the harlequin, the mopse, etc." ⁵⁵ And then Maupertuis wonders seditiously why this art should be restricted to animals. Might sultans in their seraglios practise a similar art? Had not Frederick William of Prussia built an armed force of giant soldiers, and thereby, thought Maupertuis, singularly increased the stature of the Prussian people?

If the ingenuity of man can produce species, why not nature, either by "fortuitous combinations of the particles of the seminal fluids, or effects of combining powers too potent or too weak among the particles" ⁵⁶ or by the action of the environment, such

⁵¹ *V. P.*, Part II, Chap. v.

⁵² *S. N.*, XL.

⁵³ *S. N.*, XLI.

⁵⁴ *S. N.*, XLII.

⁵⁵ *V. P.*, Part II, Chap. III.

⁵⁶ *V. P.*, Part II, Chap. VII.

as the effect of climate or nutrition, on the hereditary particles. It is worth emphasizing, for it has been misunderstood, that Maupertuis raises the latter possibility only as one worthy of investigation; but clearly at this point he anticipated both Erasmus Darwin and Lamarck in suggesting the possibility of evolution through an inheritance of environmentally modified characters. Even so, it is the direct mutational action of heat or other factors on the hereditary material itself that Maupertuis seems most to have had in mind. "For the rest," he says, "although I suppose here that the basis of all these variations is to be found in the seminal fluids themselves, I do not exclude the influence that climate and foods might have. It seems that the heat of the torrid zone is more likely to foment the particles which render the skin black, than those which render it white: and I do not know to what point this influence of climate or of foods might extend, after long centuries of time."⁵⁷

It is likewise clear that Maupertuis understood that most mutant forms are deleterious and at a disadvantage in comparison with the normal or wild types. "What is certain is that all the varieties which can characterize new species of animals and plants, tend to become extinguished: they are the deviations of Nature, in which she perseveres only through art or system. Her *works* always tend to resume the upper hand."⁵⁸

How, then, account for the distribution of different races and species? The "thousands" of human varieties are insuperable difficulties for the preformationist; but by mutation, migration, and isolation they are readily accounted for by Maupertuis. Perhaps, he suggested, in the tropics all the peoples are dark of skin in spite of the interruptions caused by the sea, because of the heat of the torrid zone over a long period of time. The geographical isolation of Nature's deviations must play a part here, for "in travelling away from the equator, the color of the people grows lighter by shades. It is still very brown just outside the tropics; and one does not find complete whiteness until one has reached the temperate zone. It is at the limits of this zone that one finds the whitest peoples."⁵⁹ Well, "men of excessive stature, and others of excessive littleness, are species of monsters; but monsters which can become peoples, were one to apply himself to multiplying them."⁶⁰ Are there not

⁵⁷ V.P., Part II, Chap. v.

⁵⁸ Ibid. Italics added.

⁵⁹ V.P., Part II, Chap. I.

⁶⁰ V.P., Part II, Chap. VII.

racés of giants and dwarfs? These "have become established, either by the suitability of climates, or rather because, in the time when they commenced to appear, they would have been chased into these regions by other men, who would have been afraid of the Colossi, or disdain the Pygmies.

"However many giants, however many dwarfs, however many blacks, may have been born among other men; pride or fear would have armed against them the greater part of mankind; and the more numerous species would have relegated these deformed races to the least habitable climates of the Earth. The Dwarfs will have retired toward the arctic pole: the Giants will have inhabited the Magellanic lands: the Blacks will have peopled the torrid zone."⁶¹ However naïve these anthropological conceptions may be—and they were an easy target for the sharp gibes of Voltaire—there is nevertheless a groping here for a truth that was only to be captured fully by Charles Darwin and Alfred Russel Wallace in a later day.

There is no naïvety, only pure genius, in these final words: "Could one not explain by that means [mutation] how from two individuals alone the multiplication of the most dissimilar species could have followed? They could have owed their first origination only to certain fortuitous productions, in which the elementary particles failed to retain the order they possessed in the father and mother animals; each degree of error would have produced a new species; and by reason of repeated deviations would have arrived at the infinite diversity of animals that we see today; which will perhaps still increase with time, but to which perhaps the passage of centuries will bring only imperceptible increases."⁶²

Maupertuis and His Contemporaries

Among his contemporaries in biology, the work of Maupertuis was most highly regarded. With Buffon, in particular, Maupertuis had much in common. Maupertuis was the author who seemed to Buffon "to have reasoned better than all those who have written before him on this subject" (of the generation of the individual); and Buffon spoke of the *Vénus Physique* as a treatise which, "although very short, assembles more philosophical ideas than there are all told in several great volumes on generation. . . . This author,"

⁶¹ Ibid.

⁶² S. N., XLV.

he continued, "is the first to have commenced to draw near to the truth, from which we were farther than ever since eggs had been supposed to exist and the spermatic animals were discovered."⁶³

It is equally significant that Charles Bonnet, the great exponent of preformation, directed his main arguments against the "internal molds" (*moules intérieurs*) of Buffon and the "attractive forces" and the "memory of the seminal molecules" of Maupertuis fully as much as against the epigenetic *vis essentialis* of Kaspar Friedrich Wolff. What is often overlooked today is the fact that Bonnet was profoundly right in holding as senseless the view that "that unity, that organic whole one calls an animal" can arise from an *amorphous* semen, and in affirming that a gel (*glu*) which appears to become organized in development must possess some organization to start with. Years later, writing in the *Palingénésie* (1769), Bonnet arrived at a view of preformation that is as close to our modern understanding of heredity and development as was the epigenetic view of Maupertuis. It is not necessary, he said, to limit the significance of preformation "to express an organic corpuscle that actually encloses in extreme miniature all the parts which characterize the species." It may be extended to include "every organic preformation from which an animal can result as its immediate principle."⁶⁴ And again, in the *Contemplation de la Nature*, he wrote: "I do not affirm that the buds which produce separate young polyps (*les rejetons d'un Polype à bras*) were themselves miniature polyps, hidden under the skin of the mother, but I affirm that there are, under the skin certain particles which have been preorganized in such a manner that a little polyp results from their development."⁶⁵ Every genesis, in other words, must issue from a "predetermination," a "secret preorganization," a "primordial design." Seen in this light, there is a close rapprochement between the ideas of Maupertuis and Bonnet, such that the modern theory of the genetic organization of the fertilized egg covers them both. As so often in the history of scientific ideas, the ultimate truth includes those antithetical ideas over which earlier men were embroiled in controversy.

⁶³ Buffon, *Histoire naturelle générale et particulière*, nouvelle édition, III, p. 244, Paris, 1769. [Quoted in Brunet, op. cit., Vol. II, p. 329.]

⁶⁴ Bonnet, *Palingénésie* [Quoted from J. Rostand, *Esquisse d'une histoire de la biologie*, 12th edition, p. 77. Gallimard, Paris, 1945.]

⁶⁵ Bonnet, *Contemplation de la Nature*.

The Reputation of Maupertuis in the 19th and 20th Centuries

It remains to account for the reputation of Maupertuis to the present day. There is little indeed to say. Darwin, it would seem, never heard of him. Thomas Henry Huxley, who was the first to make a somewhat careful study of Darwin's predecessors, makes only a cursory reference to Maupertuis' "curious hypothesis as to the causes of variation, which he thinks may be sufficient to account for the origin of all animals from a single pair."⁶⁶ Quatrefages, Perrier, Clodd, Packard, Nordenskiöld, Radl, Singer, and other historians of the theory of evolution have ignored him completely. Henry Fairfield Osborn, in *From the Greeks to Darwin*, almost completely misunderstood Maupertuis, classifying him with those who made speculations without the support of observation or the least deference to inductive canons.⁶⁷ Osborn apparently read only the *Système de la Nature*, which is admittedly difficult to interpret without prior knowledge of the *Vénus Physique*. In 1904, Lovejoy published a scholarly study of Maupertuis and other early evolutionists.^{67a} Although Osborn knew of this study, he did not make the slightest use of it in preparing the revised edition of his book (1928), and he may consequently be regarded, after Voltaire, as the person chiefly responsible, at least in the English-speaking world, for the misapprehension of Maupertuis' significance as a scientist. Yves Delage, the great French historian of biological theories, was just to Maupertuis in discussing the latter's views in *L'hérédité et les grands problèmes de la biologie générale*. He considered Maupertuis' theories regarding ontogenesis, heredity, variation, and the formation of species in a spirit of admiration, and summed up by saying, "Geoffroy Saint-Hilaire could subscribe to his law of teratogenesis; Lamarck, to his ideas on variation; Darwin, to his system of representative germs. And all that had been said by him a century before them!"⁶⁸ And Delage compared Maupertuis with Buffon not en-

⁶⁶ Huxley, *Evolution in Biology*, 1876. In *Darwiniana* (Collected Essays, II), pp. 187-226. Appleton, New York and London, 1912.

⁶⁷ H. F. Osborn, *From the Greeks to Darwin*, Scribner's, New York, 1894. Second edition, 1928.

^{67a} See footnote 7, this essay. Lovejoy's essay was the first, at least in English, to do justice to Maupertuis' theory of organic evolution, and to show that it was based on an empirical study of the inheritance of polydactyly and upon a considered epigenetic view of the nature of development, in contradistinction to currently prevailing preformationist views.

⁶⁸ Y. Delage, *L'hérédité et les grands problèmes de la biologie générale*, Schleicher Fr., Paris, 1896. Second edition, 1903.

tirely to the latter's advantage. Nevertheless, it must be remembered that Delage's book was written before the rediscovery of Mendel's laws and before the mutation theory of de Vries was published. In many respects the criticisms of Delage therefore sound antiquated—in matter of fact, some of the imperfections with which he charged Maupertuis have turned out to be the imperfections of Delage. Nor was Delage always correct, as when, for instance, he charged Maupertuis with having been a purely theoretical critic of preformation, or with having believed in the inheritance of acquired characters in a Lamarckian sense. Delage also seems to have regarded Maupertuis' theories as succeeding those of Buffon instead of preceding them, an error due to his listing the *Vénus Physique* as first published in 1748, instead of 1744-45. As Lovejoy pointed out, it was more likely Buffon who was influenced by the theories of Maupertuis than the reverse; although the differences between the views expressed in the *Vénus Physique* and those in the *Système de la Nature* may very well represent a counter-influence.

In this period the common judgment of Maupertuis was that derived from Voltaire. It is enlightening, for example, to read, in the light of D'Alembert's praise of Maupertuis' clarity and literary style (1778), the dictum of such a critic as Leon Sagnet, writing in *La Grande Encyclopédie* (1896): "Certainly, Voltaire was unjust. Before covering Maupertuis with insults, moreover, he had praised him above measure. One is none the less obliged to state that the favorite of the king of Prussia was a very mediocre writer, with a style stiff and pretentious, and who, inflated with pride and with his spirit warped by vanity, produced as a scientist, outside of his measurement of the arc of Tornea, neither any work nor discovery of the first rank, that, consequently, the great celebrity which he enjoyed among his contemporaries and the honors with which he was overwhelmed were as little justified as the mockeries of Voltaire were themselves exaggerated."⁶⁹

In 1912 Georges Hervé wrote a brief paper entitled *Maupertuis génétiste*.⁷⁰ This is a very fine critique of Maupertuis' theories in the light of Mendelian genetics, paying tribute to his experimental approach. But it was by no means exhaustive, and, since it appeared in a journal little consulted by experimental biologists, it seems to

⁶⁹ L. Sagnet, Maupertuis. In *La Grande Encyclopédie*, v. 23, p. 241, 1896.

⁷⁰ Hervé, *op. cit.*

have been almost completely overlooked. The comments of Curtis⁷¹ on Maupertuis relied wholly upon the previous analysis by Lovejoy (1904).

Coming to a more recent period, we find a number of biologists referring to Maupertuis, but always in a partial light. Joseph Needham, in his *History of Embryology*,⁷² pays fitting tribute to Maupertuis as an epigenesist, but was not interested in his genetics or his evolutionary theories, F. J. Cole, in *Early Theories of Sexual Generation*,⁷³ besides an interest in the same subject, seems to have been struck chiefly by the fact that Maupertuis failed to appreciate the importance of the spermatozoa, and by other inadequacies in his views. But he does state that there can be no doubt that Buffon's famous system of organic particles, "his elaborate system of pangenesis . . . was inspired by that of Maupertuis, of which it is a development and extension." Conway Zirkle, in several papers investigating the history of the ideas of pangenesis and the inheritance of acquired characteristics,⁷⁴ has discussed the ideas of Maupertuis on these subjects; but his work is restricted in point of view, and somewhat confuses Maupertuis' arguments in favor of epigenesis and his position as to pangenesis. Emile Guyénot, alone among modern students of genetics and evolution, has been aware of the significance of Maupertuis. His masterly treatise, *Les sciences de la vie au XVII^e et XVIII^e siècles*,⁷⁵ estimates Maupertuis' evolutionary and genetic contributions at full worth. It is thus disappointing to find, after reading Guyénot's comment that "after these two precursors indulging in fantasy [Robinet and de Maillet], the work of Maupertuis can only appear to us more serious and more profound," that in a very recent and generally excellent account of the origins of Darwinism, the fantasies of Benoit de

⁷¹ W. C. Curtis, *Science and Human Affairs*, Harcourt, Brace, New York, 1922.

⁷² Needham, *A History of Embryology* (Part II of *Chemical Embryology*), Cambridge, at the University Press, 1931.

⁷³ F. J. Cole, *Early Theories of Sexual Generation*, Clarendon Press, Oxford, 1930.

⁷⁴ C. Zirkle, The inheritance of acquired characters and the provisional hypothesis of pangenesis, *Amer. Naturalist*, 69: 417-445, 1935; Further notes on pangenesis and the inheritance of acquired characters, *Amer. Naturalist*, 70: 529-546, 1936; The early history of the idea of the inheritance of acquired characters and of pangenesis, *Trans. Amer. Philos. Soc.*, n.s., 35(2): 91-152, 1946.

⁷⁵ E. Guyénot, *Les sciences de la vie aux XVII^e et XVIII^e siècles: l'idée d'évolution*, Albin Michel, Paris, 1941.

Maillet receive seven pages and Buffon a like amount, while Maupertuis, mentioned as rescued from undeserved obscurity, is dismissed in one brief paragraph.⁷⁶ Guyénot's summation is more just. He writes: "Geneticist from the very start, Maupertuis sketched, in all, an evolutionary conception that was based at once on heredity, on the fortuitous production of variations, on a prophetic vision of the phenomena of selection and of preadaptation. We feel him infinitely closer to us than the great theoreticians of Transformism. Already he was reasoning more on the basis of facts than of conceptions *a priori*. He was one of the founders of Evolution and appears to us, in addition, as the most remarkable precursor of contemporary Mutationism."⁷⁷ A paper, on the uncelebrated bicentennial of the publication of the *Vénus Physique*, by J. and M.-L. Dufrenoy hails Maupertuis not only as geneticist and evolutionist, but as also a brilliant precursor of comparative pathology.⁷⁸

Conclusion

Here was a man who argued on genetic grounds against preformation fifteen years before the work of Kaspar Friedrich Wolff which was eventually to dispose of the encasement theory of preformation; who investigated human heredity in a manner calculated to draw the admiration of any geneticist of the present day, and who applied the mathematical theory of probability to genetics over a century before Mendel; who undertook experiments in animal breeding to throw light on his theories; who formulated a theory of heredity that was particulate and involved the mutual attraction of analogous particles provided by each parent, and that implied segregation, dominance, and independent assortment; and finally, who formed a theory of organic evolution based upon mutation, natural selection, and geographic isolation. Surely he ranks above his contemporaries in biology. Instead, we must compare him with the mighty figures of a later time.

Thus, in the company of Lamarck, of Karl Ernst von Baer, who

⁷⁶ L. Eiseley, *Darwin's Century: Evolution and the Men Who Discovered It*. Doubleday and Co., Garden City, N. Y., 1958.

⁷⁷ Guyénot, *op. cit.*, p. 393.

⁷⁸ J. and M.-L. Dufrenoy, Un bicentenaire oublié: La *Vénus Physique*, 1746; ou Maupertuis, précurseur de la Pathologie comparée, *Rev. Pathol. comp.*, 48: 107-115, 1948.

eventually disposed of the preformation theory, of Blumenbach, the father of anthropology, and of Darwin and Wallace, Mendel and Hugo de Vries, Maupertuis at last takes his rightful place. A man too far before his time, he was the most many-sided genius of them all. Only now, when the separate strands of genetics, embryology, anthropology, and evolution are woven together, and the Principle of Least Action is seen to be basic to them all, are we in a position to recognize in Maupertuis one of the greatest luminaries of eighteenth century science.