FORERUNNERS OF DARWIN: 1745–1859

EDITED BY *BENTLEY GLASS*

OWSEI TEMKIN

WILLIAM L. STRAUS, JR.

under the auspices of
The Johns Hopkins History of Ideas Club

BALTIMORE: *The Johns Hopkins Press*

Distributed in Great Britain by Oxford University Press, London

Printed in the United States of America by J. H. Furst Co., Baltimore

This book has been brought to publication with the assistance of a grant from The Ford Foundation.

The Library of Congress has cataloged this book as follows:

Glass, Hiram Bentley, 1906– *ed.*

Forerunners of Darwin: 1745–1859. Edited by Bentley Glass, Owsei Temkin [and] William L. Straus, Jr., under the auspices of the Johns Hopkins History of Ideas Club. Baltimore, Johns Hopkins Press [1959]

471 pp. illus. 24 cm.

Includes bibliography.

1. Evolution–Hist. I. Title.

QH361.G55 575.016 59–9978 ‡

Library of Congress

FIVE

DIDEROT AND EIGHTEENTH CENTURY FRENCH TRANSFORMISM

LESTER G. CROCKER

Diderot was bound to come to the idea of evolution. It was not only that his searching mind drank in the newest scientific notions and imaginatively grasped their furthermost implications. More specifically, he needed such a theory in order to complete the materialistic interpretation he was building of man and the universe.

It frequently happens that a concept which to a later generation has become a commonplace—often accepted without sufficient critical questioning, like current coin whose face we no longer examine—simply did not exist in the minds of an earlier period, and was conceivable to those who gave it birth only by dint of extraordinary intellectual courage, imagination, and travail.

> Yet naught there is
> So easy that it standeth not at first
> More hard to credit than it after is;
> And naught soe'er that's great to such degree,
> Nor wonderful so far, but all mankind
> Little by little abandon their surprise.
>
> (Lucretius, Bk. II)

The concept of biological transformism, which was to revolutionize man's thinking in manifold ways, is surely an idea of this sort. There were many obstacles to hinder its coming into being. Not the least of these was a version of the world and of life which bridled men's thinking all the more effectively by combining with the strength of universal acceptance the power of sacredness and the might of institutions committed to it. Scientific evidence of an incontrovertible nature, that might embolden a few courageous thinkers to risk martyrdom, was, to put it at the best, scanty. A dawning notion of geological history, the elements of a science of comparative anatomy —and even these hotly challenged—here was insufficient basis for a scientist to venture very deep into the dangerous waters of unorthodox speculation. This was for the philosophers to do, especially for those with an unreined poetic imagination.

But even a philosopher could not step unimpeded into the brightly illumined truth of organic evolution. He was separated from it by intellectual barriers. Were not animate and inanimate beings so totally distinct from each other, that life could not be conceived of except as an act of divine creation? Were not matter and mind—*res extensa*, *res cogitans*—so completely incompatible, that the presence of the latter could never be accounted for by anything that might happen to the former? Did not all living organisms, and all their organs, present such clear evidence of design, that a prearranged plan could alone explain them? Outside of God, there was only nature. Nature was matter and its laws. Of matter, Wollaston expressed the common opinion when he wrote, "Matter is incapable of acting, passive only, and stupid."[1] As for its laws, they were, in the prevailing Newtonian view, the geometrical regulators of a stable, equilibrated machine. Everything was in its proper place in the great chain of being.

All of these obstacles were to be vanquished in Diderot's mind. We shall try to follow, in his writings, the birth and growth of his evolutionary thinking.

In the late 1740's, Diderot began to formulate his concept of nature. Whereas both to Christians, and to Newtonian deists (like Voltaire), nature was God's completed and immutable creation, Diderot began to think instead of dynamic forces which, self-existent and self-directing, have evolved the universe we know from a primeval chaos, to which it might again return in the course of its necessary unfolding. In 1746, in his first original work, the *Pensées philosophiques*, Diderot is still a deist, but is clearly tempted by atheism. Two factors retard his becoming an atheist: the ethical and the cosmic. Only the second of these need concern us here. If Diderot clings to his deism, it is partly because he has not yet reached this concept of nature as a self-sufficient All, containing

[1] *The Religion of Nature Delineated*, London, 1726, p. 74.

within itself the origin and the explanation of all its phenomena. His position may be termed anti-evolutionary. Spontaneous generation is rejected as the source of higher forms of life. Only an act of creation can explain the existence of the germ cells from which we come. The wing of a butterfly, the eye of a mite—these are sufficient to prove intelligent design. Yet, at the same time, Diderot is strongly drawn to the atheist's argument: if we concede matter to be eternal, and if we grant that movement is inherent in matter, an infinite number of "throws of the dice" was bound to bring about the combination which is our universe. It should be noted that there is nothing evolutionary in this thought; it is a quantitative mechanism that offers no perspective of qualitative change. The inclusion of motion as essential to matter is, however, a first step in that direction. It was an idea that Diderot had probably encountered in the "radical" irreligious manuscripts that were freely though illegally circulated; he conceivably could have met it in Toland's *Letters to Serena*; and he had undoubtedly read it in the *Metaphysics* of Aristotle.

In 1749, Diderot published his next important work, the *Lettre sur les aveugles.* We are immediately aware that there has been a significant revision in his thinking. In the three preceding years, he had been swept away by the strong current of interest that turned his contemporaries towards the startling discoveries in the biological sciences. He had read Nieuwentijdt, Nollet, William Derham; Bonnet's and Réaumur's works on insects. Needham's *Account of Some New Microscopical Discoveries* seemed to him a convincing demonstration of spontaneous generation. But it is unlikely that he as yet knew Buffon's theory of "organic molecules," for he seems to have become acquainted with the newly published *Histoire naturelle* during his imprisonment in the dungeon of Vincennes, which followed publication of the *Lettre sur les aveugles.* A particularly important influence was that of Trembley's memoir on fresh-water polyps (1744).[2] Trembley's discovery of the regenerative powers of the polyp threw the biological world of France and England into a ferment; his conclusions were taken up by Bonnet, Réaumur, and others. Maupertuis, as early as 1745, expressed his amazement and saw new perspectives opening up. The

[2] *Mémoires pour servir à l'histoire d'un genre de polypes d'eau douce,* Leiden (and Paris), 1744. For an important discussion of its influence, see Aram Vartanian: "Trembley's Polyp, La Mettrie, and eighteenth century French materialism," *J. Hist. Ideas,* 11:259-86 (1950).

philosophical repercussions were even more startling. The animal soul was clearly shown to be material. The heterogenetic origin of life seemed to be confirmed. Bonnet suggested that the polyp bridged the animal and vegetable kingdoms, nullifying their supposedly complete separation. Later he declared the polyp to be the key to the interpretation of nature.[3] The most radical conclusions were drawn by La Mettrie, in his notorious *L'Homme machine*, published towards the end of 1747. In this work, La Mettrie excludes any spiritual principle from the universe and rejects the biological finalism of Newton. Trembley's polyp, he states specifically, proves that nature (read: *matter*) contains within itself the power that produces its activity and—most important—its organization. (One might consider this a rebirth, on a new scientific basis, of the Aristotelian view that there is no matter without directing purpose or form.) The mechanical atoms-plus-chance materialism of Lucretius and Gassendi is declared to be insufficient, for nature involves design—design which springs from the dynamics of matter in action, free from the finalism of an extra-natural intelligence.[4] The vital point in this concept of nature, which makes it of particular concern here, is that a theory of transformism could scarcely have been conceived without the belief that matter, and living organisms in particular, possess a self-organizing power or impulse.

The importance of Leibniz in the formulation of this new outlook has, at least in recent years, been largely overlooked. The biological developments must be given their full due. They were crucial, in imparting reality and concrete importance to a concept which, however, already existed in a different frame of reference. Thus, in the *Monadology*, Leibniz writes "that the natural changes of the Monads come from an *internal principle*, since an external cause can have no influence upon their inner being." (Par. 11.) All simple substances "have a certain self-sufficiency which makes

[3] *Oeuvres*, Neufchâtel, 1779, IV, 340.

[4] "We do not know Nature at all; hidden, inner causes may have produced everything. Just look at Trembley's polyp! Doesn't it contain within itself the causes which give rise to its regeneration? What absurdity, then, would there be in thinking that there are physical causes for [by?] which all has been brought about, and to which the entire chain of this vast Universe is so necessarily tied and subjected, that nothing that happens in it could not have happened? . . . Thus, to destroy chance is not to prove the existence of a Supreme Being since there may be something else which would be neither chance, nor God, I mean Nature. . . ." (*L'Homme machine*, éd. Maurice Solovine, Paris, 1921, p. 108-9).

them the sources of their internal activities and, so to speak, incorporeal automata." (Par. 18). Matter, too, is undergoing constant modification, perpetual change, within the integrity of its substance (*Théodicée*, par. 396). Finally, "every present state of a simple substance is naturally a consequence of its preceding state, in such a way that its present is big with its future." (*Monadology*, par. 22). The biological discoveries, then, and the speculations they aroused in several thinkers (whom we know to have been familiar with Leibniz) added little new to a concept which already existed full-blown, though only in the abstract. It was the startling and unexpected confirmation of abstract speculation by empirical observation that brought the former to life, and into an actively operational status, in a direct application to the problems of biology. I suggest, then, that this decisive reorientation of eighteenth century thought came about through the fusion of an idea and a discovery, a fusion of the thought of Leibniz with the observations of Trembley. This fusion was made by the men we are now discussing.

(Leibniz's contribution to the rise of the new biological thinking has generally been limited to his reformulation of the idea of a "chain of beings," or "principle of plenitude." Certainly this was a notion that permeated the thought of the eighteenth century. It was of consequence for the development of transformism, inasmuch as it tended to create a continuous series of links between all species and "kingdoms." For this static concept to become evolutionary, however, it had, in the first place, to be transmuted into the concept of a process of dynamic change, occurring through a vast period of time—a transformation Arthur O. Lovejoy has studied in his *Great Chain of Being*. But even this would not have been enough to produce a biological theory of transformism. A still more significant change in thinking was required. Nature had to be conceived of as a self-creating, self-patterning force, as an experimenting —and a blindly experimenting—force. Furthermore, in the actual history of the idea, the second step really preceded the first. Consequently, the new concept of transformism, though it was aided and abetted by that of the chain of beings, was so distant from it, that it cannot be said to have derived directly or mainly from it. And, curiously, one concept of Leibniz may thus have had a share in the later transforming of another of his concepts.)

Although La Mettrie is often given credit for having been the first to set forth the new concept of nature, Maupertuis had, in fact, preceded him by two years. In his revolutionary work, the *Vénus physique* (1745), Maupertuis attributed to nature such a self-organizing and self-patterning power, based on motion and gravitational attraction (which, he emphasizes, is a non-mechanical principle). In other words, he made development inherent in matter. We shall not go into his theories at this point, since they are concerned essentially with the processes of reproduction and variation; but inasmuch as he does seek analogies in non-living matter, the principle is adumbrated in general form.[5] La Mettrie was almost certainly familiar with Maupertuis' work; but his thinking seems to have evolved independently. He was inspired by the polyp, and Maupertuis by his observations on genetic variation. Both reached the same conclusion.

In *L'Homme plante*, published in 1748, La Mettrie takes one more step in building the foundations of the eighteenth century theory of transformism. Like Bonnet, he emphasizes the "chain of beings" concept, and places the polyp in the key position of bridge between vegetable and animal. If nature is dynamic and self-determining; if nature consists of an unbroken gradation of beings from simplest to most complex, with the specific difference inhering in their material organization—if these two propositions be established, then the third and concluding step becomes inevitable.

With this background, it is now time to return to Diderot. Since we are interested in studying the genesis and development of his idea of evolution, as well as that idea itself, there is an essential point to note at this stage. It appears probable that Diderot did not know La Mettrie's work until after the publication of the *Lettre sur les aveugles*.[6] What we find in the *Lettre* must not be attributed, as is sometimes done, to the influence of La Mettrie.

At the base of the *Lettre sur les aveugles* lies a firm belief in the unity of nature, and in its dynamism. The psychological phase of Diderot's discussion rejects psycho-physical dualism in favor of a physical explanation of mental activity. Similarly, as he views the formation of the universe, he sees no final separation between the organic world and the inorganic. Such a view of the unity of nature is another essential preliminary to a concept of organic evolution. How far do these ideas carry Diderot in 1749? Has he yet reached such a concept?

[5] See notes 33, 34 *infra*, and *Vénus physique* (*Oeuvres*, Lyon, 1756), II, 85 ff.
[6] *Lettre sur les aveugles*, éd. Robert Niklaus, Genève, 1951, p. xxi.

Significantly, he speaks first of animals. Breaking loose from the teleology which, in the *Pensées philosophiques*, struck him as a necessary conclusion from the obvious adaptive design of all living organisms, he proclaims this design to be independent of a divine intelligence, plan, or guiding hand. As the blind Saunderson explains it to his would-be converter, the minister Holmes, the error—and Diderot is aware that it had been his, too—lies in the assumption that this order always existed as we now see it in successful forms of life. But if we postulate, instead of a single and final act of Creation, an original chaos from which nature gradually formed itself, under the impulsion of its intrinsic dynamism, we get a picture that is in much closer agreement with the known facts. The principal facts that Diderot has in mind are the complete failure of some natural productions to embody a successful design, and the imperfection of others. Saunderson's blindness is evidence of the latter, and the production of nonviable "monsters" proof of the former. These facts tend to exclude God from the natural processes, since he could create only fit beings; and they simultaneously point to a persistent creative process in the initial formation of the world, a self-determining but blind impulsion to trial and error.[7] Such a process is equally alien to the workings of a Perfect Being. Let us now read Diderot's own words:

> Imagine, then, if you will, that the order which strikes you has always subsisted; but allow me to believe that it is not at all so; and that, if we went back to the birth of time and of things, and if we perceived matter stirring and chaos disentangling itself, we should encounter a multitude of shapeless beings for a few well-organized. . . . I may ask you, for instance, who has told you, Leibniz, Clarke and Newton, that in the very beginning of animal formation, some were not without a head and others without feet? I can assure you that some had no stomach, and others no intestines . . . that all the monsters were successively annihilated; all the imperfect combinations of matter have disappeared; only those remain in whose mechanism there was no imperfect contradiction and which could exist by themselves and perpetuate themselves. On this supposition, if the first man had had his larynx blocked, lacked proper food or properly formed genera-

[7] Then Nature, delivered from every haughty lord,
And forthwith free, is seen to do all things
Herself and through herself of own accord,
Rid of all gods. (*De rerum natura*, Bk. II)

> tive organs . . . what would have become of the human species? It would have been enveloped in the general cleansing of the universe, and that proud being who calls himself man, dissolved and dispersed among the molecules of matter, would have perhaps forever remained in the number of possibles. . . . But order is not so perfect, that there do not still appear, from time to time, monstrous productions . . . I therefore conjecture that in the beginning, when matter in fermentation produced the universe, my fellow men were quite common.[8]

Diderot then extends his concepts of trial and error and fitness to embrace the physical evolution of the cosmos.

> But why should I not apply to worlds what I believe of animals? How many misshapen worlds have dissolved, are reformed and dissolved again, perhaps at this very moment, in the immensity of space, where I cannot touch, and you cannot see, but where movement continues and will continue to combine accumulations of matter, until they have found an arrangement in which they can persist? Oh philosophers! transport yourselves with me to the end of this universe, beyond the point where I can touch and where you see organized beings; walk over this new ocean, and seek through its irregular agitation for vestiges of that intelligent Being whose wisdom you admire here! . . . What is this world, Mr. Holmes? a composite, subject to revolutions that all indicate a continual tendency to destruction; a rapid succession of beings that follow each other, push each other and disappear; a passing symmetry, a momentary order.

The influences that have shaped Diderot's thinking are obvious. The disentangling chaos and the importance of monsters hark back to Empedocles, Epicurus, and Lucretius, whose philosophy he knew well, and to a later echo in Shaftesbury's *The Moralists.* There are also evidences, in the *Lettre*, of the impact of Cartesian philosophy.[9]

[8] Diderot, op. cit. p. 42-3.

[9] It is not probable that Diderot knew of Hooke's speculations which, according to Louise D. Patterson, enlarged the Cartesian physics to include the organic world in a sort of evolutionary theory. See "Hooke's gravitation theory and its influence on Newton," *Isis*, 40: 327-41 (1949); 41: 32-45 (1950). While this statement is perhaps too sweeping, there are several points of interest in Hooke's *Micrographia* (London, 1665). He finds nothing to make him "positive" that animal and plant are "altogether *heterogeneous*, and of quite differing kinds of nature," some species being, on the contrary, transitional or undecided (p. 124). He sees no fixity in species. One kind of creature "may produce several kinds" (p. 193-4). A plant, though produced

Doubtless Descartes' concept of the physical universe as necessarily evolving under fixed law (in contrast to the static Newtonian universe) was a factor of some importance. If we add to these influences that of Trembley, we can understand how Diderot was led to express a view that links the organic and inorganic worlds in a process of creation, patterned according to necessary laws that impel matter to find temporary stability of physical organization and viability of organic form. The motion inherent in matter lies at the base; as Diderot later wrote, thinking of Leibniz, "In general there is no force whatever that is not a principle of change." Time and becoming, the continuity of process (once more we cannot help thinking of Aristotle), and the selection of the fit—all these have brought him to the threshold of a theory of organic evolution.

To the threshold—but not across it. Some critics have erroneously seen in Diderot's statements the first announcement of such a theory. Actually, his concept applies only to the fundamental dynamism of nature. But he has no notion, as yet, of *transformism*, that is, of a species having itself a history, of becoming what it is out of something else that it was. Matter spawns its productions as fully formed species, whose "fitness" or "monstrosity" consists essentially of internal viability. Thus men were produced, in the original disentangling process, along with all the rest, even as Lucretius describes it in his fifth book. The very process of the universe is that of creation, growth and destruction.

Geburt und Grab,
Ein ewiges Meer,
Ein wechselnd Weben,
Ein glühend Leben.
(*Faust*, Part I)

It must further be noted that chance persists (even as it does in modern biology) alongside inherent laws of viable structuring; and that there are only quantitative combinations, with no concept of qualitative change. Diderot has not yet escaped (as it is often

by spontaneous generation ("casual putrefactive production") may germinate and thus "propagate its own, that is, a new species" (p. 124). However, he sees new species produced by putrefaction as inevitably of "inferior" or degenerate rank (p. 122-3), reminding one somewhat of Buffon's later theories. Although Hooke's influence in France has not been studied, his description of salts taking on shapes resembling living things (p. 129-130) is too close to Maupertuis' description (*Système de la nature*, *Oeuvres*, and *Vénus physique*, I, 85-86) not to suspect a direct influence.

asserted) from mechanical materialism. The persistent, creative dynamism of his nature concept rests perhaps on a broader base than the Lucretian; but it still terminates in stability, which is dissolved in a cycle of formlessness and reformation. An evolutionary or a dialectical materialism, on the other hand, requires a dynamism that drives through stability, in a process of advancing *neo*-formation. In fact, there is not a single idea, in all we have quoted, that does not seem directly and immediately inspired by the second and fifth books of *De Rerum Natura*.[10] There is also no doubt that the notion of nature's self-creative dynamism was becoming widespread, and Diderot had assuredly read these lines in Pope's popular *Essay on Man:*

> See, thro this air, this ocean, and this earth,
> All matter quick, and bursting into birth.
> (I, 233-4)

The definite exposition of a theory of transformism comes at last in 1753, in the *Pensées sur l'interprétation de la nature*. Many influences, accumulated during the intervening five years, had been working on Diderot's mind.

Mention must first be made of Benoît de Maillet's *Telliamed* (which, despite its 1748 date, had no apparent influence on the *Lettre sur les aveugles*). Historians agree that this work was the first to contrive a genuine notion of transformism; but it is a very limited concept. *Telliamed*, a remarkable fantasy composed of a mélange of shrewd intuition and absurd credulity, reminds one of the imaginary voyages of the seventeenth century sceptic, Cyrano de Bergerac (to whom it is dedicated). De Maillet develops a theory that the seas once covered the earth, and are still receding. This accounts for the presence of what we now call fossils. In the last section of his book, he takes up the origin of animals and man. He mocks both spontaneous generation and the materialist hypothesis of atoms combining, comparing such theories to primitive myths of man formed from the earth. His own theory is that the universe is filled with seed ("semences") of all species, and that the sea acted as the female matrix which allowed their development. From the sea, species "transmigrated" to the land. Thus every species of land animal has its marine equivalent. Flying fish became birds.

[10] For a contrary view, see A. Vartanian: "From Deist to Atheist," in *Diderot Studies*, ed. Torrey and Fellows, Syracuse, 1949, p. 46-63.

There are "sea-dogs," "sea-monkeys," and of course, a "sea-man." He quotes many instances of "sea-men" having been observed, and assures us that if we do not come upon them more frequently, it is only because they dwell by preference near the poles. There is no notion of transformism in all this. What impressed others, however, was his idea that there is a limited adaptive change in the process of accommodation to the new milieu, which may in some few cases be abetted by the crossing of species. Thus one traveler had observed that a Hollander who, by a not unusual reverse process, had become a "sea-man," was covered by scales and had hands like fins.[11] De Maillet here foreshadows the theory of transmission of acquired characteristics.

A more important influence on Diderot was surely the great impact of La Mettrie's writings, as we have described them above, and as they were completed by the publication, in 1750, of the same writer's *Système d'Epicure.* It has in fact been claimed that La Mettrie was the first eighteenth century writer to suggest, in his *Système d'Epicure*, the fundamentals of transformism.[12] Actually, the most that can be said is that he skirts the edge of such a theory. He never reaches it. What he gives us, first of all is a variation of de Maillet's theory. The seeds of all the species are in the air. When the oceans receded, they left the "human egg" on the shore, "where it incubated in the sun's heat." Thus "man and all other animals left their shells, as certain ones still do in warm countries." [13] The hatched human nourished himself, helped by kindly animals. When La Mettrie says that men have not always "existed as they

[11] *Telliamed, ou Entretiens d'un philosophe indien avec un missionnaire français*, Basle, 1749. *Telliamed* went through four editions between 1748 and 1755. La Mettrie specifically refers to it in his *Système d'Epicure*, and Bonnet, in his use of terminology such as "lion-marin," "veau-marin," and in his insistence on the orang-outang as an "homme sauvage," also reveals de Maillet's influence. (See *Contemplation de la nature* (1764), *Oeuvres*, IV, 105, 116). The latter notion will again appear in Monboddo's theories. Even Buffon's "organic molecules" may owe something to him. It has also been said that de Maillet suggested the origination of men from mermaids or sirens; on the contrary, he rejects this as an illusion due to posture (p. 336-7). Among the fantastic incidents recounted by de Maillet is the capture of a "sea-girl" who felt inevitably drawn back by the sea; it is curious that this is precisely the case of the heroine of a recent Spanish play, Casona's *La sirena varada.*

[12] Cf. Raymond Boissier: *La Mettrie* (Paris, 1931, p. 45-64); A. Vartanian: "Trembley's Polyp," p. 273.

[13] *Oeuvres philosophiques*, Amsterdam, 1764, II, 141-2, 152-3. He also says the "seeds" develop now in the matrix of the spermatic vessels.

are," he means only that "the earth must have served as uterus to man, that she must have opened her bosom to human germs, already prepared." Beyond this, La Mettrie, who followed Diderot's writings closely, echoed the ideas expressed in the *Lettre sur les aveugles* about monsters and viability. "The first generations must have been very imperfect," some being without esophagus, generative organs, etc. Only the viable survived. Nature had to essay many combinations before coming up with a perfect animal. At this point La Mettrie expresses an idea which might be construed as containing a hint of transformism. Through how many more combinations of matter did animals pass, he exclaims, "before generations became as perfect as they are today!"[14] It is probable, however, that La Mettrie is here referring only to the elimination of "monsters" in reproduction, or "generation." The context of the passage and the surrounding ideas justify only this interpretation. Similarly, when he speaks of animals being produced before men, "because it requires more time to make a man" than an imperfect being, he is referring to his idea that nature reworked the same matter into various combinations.[15] The essential element of transformism, that present forms *depend* on earlier forms, is lacking in La Mettrie. The closest we come to it is in this reference to a hypothesis he does not firmly embrace: "The animals which hatched from an eternal germ, whatever it may have been, the first to come into the world, by mingling among each other have, according to some philosophers, produced this handsome monster called man; and the latter, in turn, by his mixture with animals, may have brought about the different peoples of the universe."[16]

An important role in the development of Diderot's thinking was undoubtedly played by the writings of Maupertuis, especially the *Système de la nature* (1751, 1754). Curiously, Diderot failed to see the tremendous significance of Maupertuis' greatest anticipation—his work on a genetic theory of heredity.[17] Maupertuis clearly per-

[14] Ibid., p. 144-6.

[15] Ibid., p. 153, 140. Cf. *L'Homme machine* (p. 100): "animals formed from the same matter which lacked only a degree of fermentation . . ."

[16] *Système d'Epicure*, p. 157.

[17] See Bentley Glass: "Maupertuis and the beginnings of genetics," *The Quarterly Review of Biology*, 22:196-210 (1947). The *Système de la nature* was first published in 1751 as the *Dissertatio inauguralis metaphysica*, and translated into French in 1754. Diderot had read it in the Latin. The essentials of the theory are already outlined in *Vénus physique* (1745), but there is no evidence to indicate that Diderot was familiar with that work.

ceived in genetic mutation and recombination the possibility of an explanation of biological variation, and in this respect he stands, a unique figure, enouncing a truth others of his time were unable fully to grasp. Diderot did not realize until much later how remarkably Maupertuis had accounted for the monsters which had struck him as evidences of nature's dynamic trial and error process.[18]

Why did Diderot, always so avid for new ideas, fail on this occasion? A good part of the explanation probably lies in the language used by Maupertuis, in the attribution to his genetic particles of a low form of intelligence, a property "akin to what in us we term desire, aversion, memory."[19] Diderot could not accept this panpsychism, even as he was not able definitely to accept the quality of Buffon's "organic molecules" which had been adopted by Maupertuis in his theory. Both concepts implied a hylozoic view of ultimate particles; and the "organic molecules" perhaps also involved a final separation between the inanimate and animate world. Furthermore, Maupertuis specifically denies the possibility that matter plus motion could, ultimately, as a result of organization, produce sensation and then intelligence, a belief which is at the heart of Diderot's materialist evolutionism.[20] Maupertuis avoids this obstacle by redefining matter to include "intelligence." Now this hypothesis is unacceptable to the materialist, even though it does lead Maupertuis to an important coincidence of thought with La Mettrie. Maupertuis, influenced, like Diderot, by *L'Homme machine*, is emboldened to develop the idea of nature he had sketched in *Vénus physique*. He declares that the old atoms-plus-chance materialism does not explain how matter combines into living forms possessing purposeful design. There had to be properties and laws of matter, and a selective power in the genetic particles that were actively self-regulating. Maupertuis believed his redefini-

[18] Ibid., p. 206. See Arthur O. Lovejoy: "Some eighteenth century evolutionists," *The Scientific Monthly*, Sept. 1950 (reprinted from *The Popular Science Monthly*, 1904), p. 167. For the "production of new species," and its relation to recombination of genetic materials by chance or by human design, and for an explanation of the disappearance and reappearance of variations, see *Vénus physique*, p. 108 ff., and 119 ff. In the *Système de la nature*, Maupertuis emphasizes his new concept of matter, and the possibility of "mutations"; however the latter is not conceived of as resulting from any change in the inner structure of genetic particles themselves, but only in their accidental or spontaneous displacement and recombinations.

[19] *Système de la nature*, II, 157-8; also p. 149 ff.

[20] Ibid., p. 139-41, 146-7, 153-6, 166-7.

tion of matter (to include "memory") solved the difficulty.[21] At the same time, he rejected atheism and led the ultimate explanation back to the Divine Intelligence, a view which could only grate upon Diderot's atheism.[22] Still a third reason for Diderot's failure to grasp the significance of Maupertuis' discovery was the influence exercised on his mind by the Leibnizian principle of plenitude. *Natura non facit saltus.* This may be said to have been a preconception that blocked his view.

If Maupertuis' brilliant apprehension of the principles and problems of heredity and genetic variation did not inspire Diderot, he did find another passage in the *Système de la nature* which he could enthusiastically embrace. We shall shortly see how it left its mark on him. Granting his theory of variation, continues Maupertuis,

> Couldn't we explain in this way how the multiplication of the most dissimilar species might have resulted from two single individuals? Their origin would be owing only to a few accidental productions in the embryo, in which the elementary particles would not have retained the arrangement which they had in the father and mother animals: each degree of error would have created a new species; and by dint of repeated divergences there would have come about the infinite diversity of species which we see today, which will perhaps increase with time, but to which the passing of the centuries perhaps brings only imperceptible additions.[23]

---

[21] Ibid., p. 146-7 (XIV), 183. See A. O. Lovejoy, loc. cit. Maupertuis also applies this theory to inanimate or inorganic matter (p. 150-5); for the earlier version, in the *Vénus physique*, see pp. 85 ff.

[22] Ibid., p. 156-8 (XXIX, XXXI). Of particular interest is Maupertuis' separation of the moral intellect and his attribution of it, along with our knowledge of God, to the distinctive human soul (p. 159-61, XVII).

[23] Ibid., p. 148-9 (XLV). Dr. Glass (op. cit., p. 206), correctly points out that Maupertuis largely limits variation to genetic recombination and mutation. In other passages of the *Vénus physique*, however (p. 121 ff.), and in the *Système* (p. 159), Maupertuis seems to accept the possibility of transmission of acquired characteristics, as by repeated mutilation.

Note should be taken of a passage in an earlier work by Maupertuis, the *Essai de cosmologie* (Oeuvres, I, 11-12), in which he argues against the proof of God from biological design. "But could we not say that in the chance combination of Nature's productions, as only those could subsist which embodied relationships of fitness, it is not astonishing that this fitness is found in all species now existing?" Only a few animals, he continues, were so constructed by the workings of chance; "animals without a mouth could not live, others lacking generative organs could not perpetuate themselves: the only ones which have endured are those which possessed order and fitness; and those species, which we see today, are only the smallest part of what a blind

Buffon's influence is more uncertain. Diderot toyed with his theory of organic molecules, which possessed the merit of explaining development by the inherent power of an internal design. But Buffon, precisely because transformism stood in contradiction to this favorite theory of organic molecules as the direct source of all creatures, was opposed to the idea of evolution. In the fourth volume of the *Histoire naturelle* (1753—the year of Diderot's *Pensées*) he maintained that no new species have come into existence, despite infinite combinations of matter and of living things.[24] Buffon makes this denial despite the fact that he is impressed by anatomical similarities among animals. At the same time he denies categorically the possibility that some species may be degenerate forms of a prototype. Buffon includes in his speculation a curious passage. If it were true that a single species had been produced by degeneration (such as the ass from the horse), "there would no longer be any limits to Nature's power, and one would not be wrong in supposing that from a single being she has been able to draw, with the passage of time, all other organized beings. But no, it is certain, through Revelation, that all animals have participated equally in the grace of creation, that the first two of each and every species came fully formed from the Creator's hands."[25] Scholars have disagreed in reading this passage as a sincere or an ironical asseveration. Expression of heretical theories *via* ironical disclaimer were common at the time; and yet, Buffon provides no solid evidence elsewhere of his accepting a notion of transformism until much later.[26] In view of the fact that in this same passage he goes

fate had produced." Some have seen in this passage an early expression of such evolutionary processes as adaptation and survival of the fit (cf. Lovejoy: op. cit., p. 164-5). The date of this work (1750) is, however, significant. This passage is obviously an echo of Diderot's statement, which we have quoted, in the *Lettre sur les aveugles* (1749). Again, there is no relation to environment, or gradual selection, but only an immediate inherent viability dependent on chance. This Lucretian position, as we know, was soon to be surpassed by both men; although Maupertuis (and probably Diderot, too) kept a greater role for chance, in his theory of variation, than some scholars allow (cf. Vartanian, "Trembley's Polyp," p. 281).

[24] *Histoire naturelle*, Paris, 1753, IV, 182-3.

[25] Ibid.

[26] In a much later work (1766), he admitted the origination of certain new species by a process of "degeneration," but denied this was a general process. It was not until 1774 that he propounded his geological theory of "les époques de la terre." Buffon's greatest contribution was his insistence on homologies of structure in different species. For further discussion, see Buffon: *Oeuvres philosophiques*, éd. Jean Piveteau, Paris, 1954, p. XXXII-XXXV. The question,

on to affirm, in specific terms, that animals are not related to each other and do not have a common origin, and the fact that he insists on the fixity of species, it seems to me that Buffon is sincerely protesting against Linnaeus' classification and its consequences, and perhaps also against the passage we have previously quoted, on the same subject, from Maupertuis. On the other hand, we know from Diderot's own words that although he, too, accepted Buffon's sincerity, he preferred to read Buffon's lines in the way that suited *him*.[27] The reader may judge for himself the relation between Diderot's theory, to be quoted below, and the statements of Maupertuis and Buffon.

It is not possible to give an account of all of Diderot's readings during this period. There is ample evidence, in his *Pensées sur l'interprétation de la nature* and elsewhere, to show that he seriously followed the latest biological developments, including embryology, that he studied physiology and chemistry, and absorbed Daubenton's findings in comparative anatomy. He was also to make fuller use, here and in future writings, of Bonnet's development, in his *Traité d'insectologie* (1745) of the popular scale-of-beings concept, in which the polyp served as bridge between the plant and animal worlds.

Bringing to a focus all his studies, and his own earlier ideas on the inherent force in nature, on change, cycles, and viability, Diderot, in 1753, in the *Pensées sur l'interprétation de la nature*, reaches a concept of evolutionism which is the most complete and brilliant speculative exposition of that doctrine in his time. He refers to transformism three times in the course of this brief work.

There is a general statement, based partly on Leibniz' assertion that no two blades of grass or grains of sand can ever be identical:

> If beings change successively, passing through the most imperceptible nuances, time, which does not stop, must eventually put the greatest difference between forms that existed in ancient times, those which exist today and those that will exist in far-off centuries; and the *nil sub sole novum* is only a prejudice based on the weakness of our organs, the imperfection of our instruments and the shortness of our lives.[28]

---

however, is more complicated than Piveteau realizes, because of Buffon's extremely broad concept of species.

[27] *Oeuvres complètes*, éd. Assézat et Tourneux, Paris, 1875, II, 15nb. 2, 16.

[28] Ibid., p. 55.

There is a more specific declaration:

> Just as in the animal and vegetable kingdoms, an individual begins, so to speak, grows, exists, declines and dies, is it not the same with entire species? . . . Would not a philosopher without religious faith suspect that the necessary elements for animal life have existed from the beginning of eternity; that it chanced that these elements united, because such a thing was possible; that the embryo formed by these elements has passed through an infinity of forms and developments; that it had, successively, motion, sensation, ideas; . . . that millions of years passed between each one of these developments; that there are others yet to come, unknown to us; that there has been or will be a stationary period . . . that it [animal life] departs or will depart from this state by an eternal decay . . . ; that it will disappear forever from nature, or rather that it will continue to exist in it, but in a different form and with different properties than we see in it in this instant of its duration? Religion spares us many wanderings and much labor.[29]

Here, finally, is a still more detailed outline of Diderot's conjectures:

> It seems that Nature has taken pleasure in varying the same mechanism in an infinity of different ways. She abandons one kind of production only after having multiplied its individuals in every possible respect. When we consider the animal kingdom and perceive that among quadrupeds, there is not a single one whose functions and anatomy, especially internal, are not entirely like those of another quadruped, would we not naturally conclude that there has never really been but one first animal, prototype of all animals, some of whose organs nature has only lengthened, shortened, transformed, multiplied, obliterated? Imagine the fingers of the hand drawn together, and the material of the nails so abundant that, spreading and swelling it envelops and covers the whole; instead of a man's hand you will have the hoof of a horse. When we see the metamorphoses of the embryo bringing closer the different kingdoms by imperceptible degrees . . . who would not be impelled to believe that there was only one prototype of all beings? But, whether we accept this philosophical conjecture as true, as does Dr. Baumann [Maupertuis], or reject it as false, like M. de Buffon, it cannot be denied that we must entertain it as a hypothesis essential to the progress of experimental physics, to that of rational philosophy, to the dis-

[29] Ibid., p. 57-8.

covery and explanation of phenomena which depend on organization.[30]

The essential ideas presented by Diderot are these: (1) each species has had a history; (2) it has evolved over a long period of time; (3) new species appear through a process of variation, but maintain a relation to each other. Despite his regrettable failure to utilize Maupertuis' genetic findings, it is noteworthy that he does introduce, in addition to comparative anatomy, a reference to embryology, to the recapitulation theory. No one yet could call upon fossil evidence. But it is clear that Diderot, working on the most advanced findings available, has united them with his general philosophy of nature to produce this animated vision of biological history. Another important shortcoming in his theory is the absence of what Julian Huxley has termed the quintessence of Darwinism—the selective action of external conditions. The history of species is accounted for entirely on the grounds of internal dynamism and viability.

The concept of transformism takes its place, in Diderot's mind, in an expanding philosophy of materialism. Several points must be noted briefly, as strictly complementary to the theory itself. His materialistic monism seeks the fundamental unity of nature. All of nature's manifestations, he asserts, must be reducible to one basic law, and all phenomena must be interdependent. Nature "has perhaps produced only a single act." The absolute independence of any single phenomenon would disrupt the whole and vitiate nature's order. Eventually, he predicts, such phenomena as matter, weight, electricity, gravitation, and magnetism will be unified in a single law. Nature's dynamism, in its constant flux, is not submitted entirely to chance. "Chaos is an impossibility; for there is an order inherently consistent with the primary qualities of matter." Molecules, because of their shape and attraction, have definite interrelationships.

It would be similarly impossible to admit a definitive separation between inert and organic matter. On the one hand, Diderot is dubious about Buffon's "organic molecules." But he is undecided,

[30] Ibid., p. 15-16. For the comparison of the horse's hoof and a man's hand, Diderot refers in a note to Daubenton's description in Buffon. This description points out "a general, primitive pattern" underlying animal variations from fish to mammals, but attributes this to God's wishing "to use only one idea and vary it at the same time in as many ways as possible, so that man could admire equally the magnificence of the execution of the simplicity of the design." (Op. cit., IV, 379.)

speaks himself of "organic molecules," and even says, "it is evident that matter in general is divided into dead and living matter." Yet he immediately inquires, "How is it possible that matter is not one, either all inert or all living? Is inert matter really inert? Doesn't living matter die? Doesn't inert matter ever begin to live?" On the other hand, he cannot go all the way with Maupertuis' materialization of Leibniz' monad (or spiritualization of Epicurus' atom), although he is attracted by it. Maupertuis, he says, should have kept his system within proper limits. It is enough to include in the concept of matter, in addition to mass and movement, the notion of sensitivity—a dull, blunted sensitivity, much inferior to that of the lowest living things. However, Diderot does not as yet clearly extend the idea of sensitivity beyond "organic molecules," to "dead matter." As it will appear in his later writings, he is not certain whether sensitivity is an attribute of all matter, or whether it is an emergent from organization. He will alternate between these two positions. As a result of this sensitivity, there would be for any living molecule "only one situation more comfortable than others," which it would tend to assume through a kind of "automatic restlessness." [31]

Here, then, is a key to a question which, philosophically at least, is inseparable from that of organic evolution, that of the origin of life. Life is materialized, but matter is partially vitalized. "Is there any other difference," queries Diderot, "between dead matter and living matter, except organization, and real or apparent spontaneity of movement?" [32] This, of course, implies spontaneous generation; but we will be less shocked by it if we remember that this theory, in a more sophisticated form, is the accepted doctrine of modern biology.

Clearly, an important change in the thinking of Diderot, as well as of Maupertuis, had come about shortly after 1750. A glance back at the chronology will be fruitful. The two crucial events had been the work on the polyp and Maupertuis' discovery of genetic variation. In exposing the latter discovery, in the *Vénus physique*

[31] Ibid., p. 49. The idea of sensitivity appears in La Mettrie's *Traité de l'âme* (La Haye, 1745, p. 29-36), where he is equally hesitant about its inherence in matter as an actuality or a potentiality. It was also suggested to Diderot by the discovery of muscular irritability (contractility), first mentioned in La Mettrie's *L'Homme machine* (1747, p. 113 ff.), and then in Albrecht von Haller's *Elementa physiologiae* (1757). Haller may have derived the notion from the seventeenth century English doctor, Francis Glisson.

[32] Ibid., p. 58-9.

(1745), Maupertuis had simultaneously brought out the central idea of the new materialism: the self-patterning force of nature, containing in itself the laws of its organization and development. This view was to enable materialism to advance from the mechanical atoms-plus-chance concept, to that of the emergence of novelty from the increasingly complex organization imposed by natural process. At the time, Maupertuis based this force on an "attraction," or selective affinity, between chemical particles, essentially similar to the gravitational attraction between celestial bodies.[33] He also extends this principle to non-organic chemical substances.[34]

In 1747, La Mettrie had taken the next step of formulating this concept of nature in a more general and, simultaneously, a more precise fashion.[35] Diderot's *Lettre sur les aveugles* in 1749, and in 1750, Maupertuis' *Essai de cosmologie* both express a theory of universal change and cosmic evolution, of organic trial and error based on internal viability. Meanwhile, in 1749 Buffon had given out his important notion of organic molecules. Again in 1750 (*Système d'Epicure*) La Mettrie insists on nature's creative dynamism, and brings together de Maillet's *Telliamed* and Bonnet's "chain of being." In 1751, Maupertuis revises his notion of the self-organizing power of organic and inorganic matter, by the attribution of sensitivity and elementary intelligence and memory. At the same time, he hints at the possibility of evolution from a common ancestor. Buffon, in 1753, again expresses the latter idea, but apparently rejects it. Finally, towards the end of 1753, Diderot brings together all these ideas in a synthesis that is sharper, firmer, more cogently developed, more clearly evolutionary.[36]

[33] "Why, if this force exists in Nature, should it not act in the formation of animal bodies? Let there be in each of the seminal fluids particles intended to form the heart, head, entrails, arms, legs; and let each of these particles have a greater uniting ratio (relation) with that one which, in order to form the animal, has to be its neighbor, than with any other; the foetus will form itself: and were it a thousand times more complex than it is, it would form itself." (*Oeuvres*, II, 89.) After Maupertuis, La Mettrie also proposed to explain the formation of specialized organs by "necessary movements" of the foetal matter (*L'Homme machine* [1748], p. 110; *Système d'Epicure* [1750], p. 149-50). For Bonnet's interesting absorption of this idea into the preformation theory, see Glass: op. cit., p. 207-8.

[34] Ibid., p. 85-7.

[35] See Note 4, *supra*. "Granted the least principle of motion, animated bodies will have all they need to move, feel, think, feel remorse and behave, in a word, in the physical realm and in the moral realm which depends on it." (*L'Homme machine*, p. 113.)

[36] In passing, some note should be taken of Rousseau's awareness of the

After 1754, Diderot turned to other fields of activity. He was not again to take up scientific questions until the late 1760's. His later work, however, was to remain unpublished until well into the nineteenth century. Despite the lapse of fifteen years, his writings present evidence of continuous reading in the field, and greater maturation of thought. Aside from von Haller, whose *Elementa physiologiae* (1757-1766) he studied intensively, the principal new influences were those of Bordeu, Robinet, and Bonnet. Bonnet, in his *Contemplation de la nature* (1764), develops further the idea that all is linked in nature, there being, in consequence, no essential difference between animal and vegetable. He also expands his "scale of beings" hypothesis, which he bases on Leibniz; since there are no jumps in nature, there is a gradual gradation of beings. Nevertheless, he rejects the idea of organic evolution, and—a metaphysician at least as much as a naturalist—is concerned with proving universal harmony.[37]

Robinet, in *De la Nature* (1761), also developed the idea of nature having varied a single prototype, from stones to men, forming a natural gradation of beings. The polyp is the proof of this chain of beings. The "prototype" is "a germ which tends naturally to develop itself. . . . Its energy cannot be repressed. . . . The

notion of transformism. In the *Discours sur l'origine de l'inégalité* (1755), he comments very explicitly on the possibility that man has originated, by a process of change and adaptation, from more primitive, non-human forms. He dismisses the hypothesis, not out of hand, but as unprovable in the present state of biological knowledge, and as superfluous to his particular theme. The close friendship between Rousseau and Diderot at the time, and the acknowledged influence of the latter on the writing of the *Discours*, seem to account for Rousseau's entertaining of the hypothesis. His references to it, however, are a precious indication of the intellectual ferment. (See Vaughan: *Rousseau's Political Writings*, Cambridge, 1915, I, 142, p. 198, note C. In note j on p. 208, Rousseau does accept the transmission of acquired characteristics.)

[37] *Contemplation de la nature, Oeuvres*, IV, 38-115. He declares species to be invariable. Some importance has been attached to Bonnet's insistence on a possible close relationship between man and higher apes. He states that the orang-outang is probably only a variety of our species, an "homme sauvage" (p. 115-6 n.). It would once again be a rash (and I believe, erroneous) judgment to conclude from this that Bonnet entertained a belief in transformism as the origin of species. Aside from his own contrary statements, we must remember that the orang-outang-man *rapprochement* had been made earlier by Rousseau—from whom it seems that Bonnet borrowed it (*Discours sur l'inégalité*, note j, p. 208-9); and that Rousseau accepts the "homme sauvage" as a fact that exists in his mind quite outside of the hypothesis of transformism (which he had excluded as unproven), and not necessarily related to it. These are connections that we now inevitably make, in our intellectual frame of reference; but in the eighteenth century, they were not at all obvious.

germ develops, then, and each degree of development gives a variation of the prototype, a new combination of the primitive universal plan." The character of the prototype remains in all beings, and the only difference between stone, plant, and animal is "the measure in which they participate in that essence." Nature is then dynamic in its original formation of species; but they are formed by a series of trials, out of the same unformed material, which contains the germs of all beings. In 1768, in his *Considérations philosophiques sur la gradation naturelle des formes de l'Etre, ou les Essais de la nature, qui apprend à former l'homme*, Robinet expressed his theory even more strongly. "A stone, an oak, a horse, a monkey, a man are graduated variations of the prototype which began to form itself (*se réaliser*) with the least possible number of elements. A stone, an oak, a horse are not men; but they can be regarded as more or less rough types in their relation to a single primitive design, and in that they are all the product of a single idea, more or less developed." We must consider the succession of individuals "as so many steps of being towards humanity." [38]

The significance of Robinet's hypothesis should not be underestimated. Buffon had previously expressed the idea of the "prototype" in the fourth volume of the *Histoire naturelle*, but only within a single species. In enlarging it to cover all species, Robinet is drawing closer to a concept of organic evolution. He envisions nature as dynamic and continuously experimenting, and all species as related. In Robinet, the static concept of the chain of beings has become dynamic. Yet it would be too much to say that he had any clear idea of transformism. All that he postulates is a series of trials ("*essais*") in an ascending scale of complexity. But each trial is, so to speak, an entirely fresh start from the relatively unorganized stage of the *original* prototype. Now this concept certainly goes beyond the earlier one of Diderot, in the *Lettre sur les aveugles*, in which all of nature's trials took place within a single period of original disentanglement. It is close to the theory of La Mettrie which we have examined. But species are not conceived of by Robinet as having themselves had a history, nor as derivative in a directly unfolding process. Consequently, we are not surprised to see Robinet affirming the absolute fixity of species.

[38] P. 7. This idea is related to Daubenton's work. We may perhaps see in it an anticipation of the "unity of plan" concept that later formed our evidence of evolution.

He considers anatomical similarities to be deceptive, and insists that each species has a specific organization; else they would be variable, "could change, mingle and disappear."[39]

What may have been Robinet's most significant contribution to Diderot's transformism was an offshoot of his metaphysical theory of evil. This was his picture of a struggle for existence, which he considered the necessary mechanism, established by God, for maintaining the equilibrium of the species. This process of mutual destruction involves the sacrifice of the individual, whose only function is reproduction; it provides a balance among living things which, if destroyed by the supremacy of any one species, would lead to its own extinction by hunger.[40] It is possible that these ideas had an important influence on Herder. In Robinet's mind, however, there is no relation whatsoever of this struggle to any concept of natural selection, variation of species, or transformism.

Théophile de Bordeu, finally, one of the brilliant physicians of the age, was a friend of Diderot's and a collaborator in his *Encyclopédie*. He was a member of the Montpellier school of vitalists, and carried forward the thinking of Stahl and Boerhaave. His influence is found in several details of the *Rêve de d'Alembert* (1769), the great dialogue in which Diderot developed the most complete system of materialism in the eighteenth century. Diderot was also impressed by some of his more general ideas. Bordeu conceived the organs of the body to have an independent sensitivity and life of their own. Like Haller, he held the "fibre" to be the basic element of all animal structure, and described its properties as irritability, sensitivity, and elasticity.[41]

[39] *De la nature*, Amsterdam, 1761, I, 70; IV, 1-28 (1767).

[40] *Ibid.*, Première Partie. In an article shortly to appear in the *Proceedings of the American Philosophical Society* (Dec. 1958), Prof. Gilbert Chinard has brought to light the little-known development of Robinet's theory by Rétif de la Bretonne, in his *Ecole des peres* (1776). Rétif also sees a struggle for existence limiting population, and preventing undue domination by any one species. The harmony of the animal system is thus maintained. War, luxury and disease produce the same effect among men. Rétif also claims that all terrestrial animals descend from marine amphibians. He emphasizes nature's creative force, resulting in constant variation and the appearance and disappearance of "races" and "species." Unfortunately, his concept of "species" is so vague, contradictory and ambiguous that we cannot be sure of his real meaning. Once again the concepts of struggle and of evolution are not related.

[41] For a thorough study of Bordeu and Diderot, see Herbert Dieckmann: "Théophile Bordeau und Diderots *Rêve de d'Alembert*," *Romanische Forschungen*, 52:55-122 (1938).

In the *Rêve de d'Alembert*, Diderot envisions the universe, life, and man, under the light of a radical materialism derived from Spinoza, Descartes, and the science of his time. We shall here pass over his theory of a living universe, self-sufficient, perpetually reorganizing and renewing itself, forming an immense, unitary Whole. Diderot, in this development, is inspired by the Stoics and by the eighteenth century misinterpretation of Spinoza. But he further applies the concept in its conventional "chain of beings" form, to biology. "All beings circulate in each other. All is in perpetual flux. Every animal is more or less man; every mineral is more or less plant; every plant is more or less animal." [42]

At repeated intervals in the dialogue, the problems of life are taken up, one by one. How did life come to be? All matter, Diderot is now prepared to assert, involves sensitivity. There is only one substance, diversely organized. Change in organization converts "inert sensitivity" into "living sensitivity." This phenomenon occurs in the mineral-plant-animal cycle of nature, in the process of growth and nourishment.[43] Further, the act of fertilization is a mechanical process, changing the non-living germ cells into life, under the stimulus of heat produced from motion, in an embryological process that Diderot describes in some detail. Within the inert germ itself is the latent force or element ready to impose its organization. "And he who would expound to the Academy the progress of the formation of a man or an animal, would use only material agents whose successive states would be an inert being, a feeling being, a thinking being, a being solving the problem of the precession of the equinoxes, . . . an aging being, decaying, dying, dissolved and returned to vegetative earth." [44] But where did the germ first come from? queries d'Alembert. Diderot's reply relates the problem of the origination of life to the theory of evolution. "If the question of the priority of the egg over the chicken or of the chicken over the egg embarrasses you, it is because you suppose that animals were at first what they are now. What madness! We no more know what they were than what they will become. The imperceptible earthworm that wriggles in the mud is

[42] The reader will recognize La Mettrie, Bonnet, and Robinet as the sources of this idea.

[43] This idea Diderot may well have taken from Toland. See L. G. Crocker: "John Toland et le matérialisme de Diderot," *Revue d'histoire littéraire*, 53: 289-95 (1953).

[44] *Rêve de d'Alembert*, éd. Vernière, Paris, 1951, p. 13-14.

perhaps on his way to becoming a large animal. . . ."[45] If the sun were to be extinguished, and then rekindled, life would eventually start up again, but the results would be quite different; all in nature is connected, and to suppose a new phenomenon is to create a new world.

In Diderot's materialistic explanation of life and its variations, there are, in the order in which he takes them up, five interrelated steps: universal sensitivity (at least in virtuality); its transformation in the life-cycle (epigenesis); transformism; fertilization; and a repeated adherence to the theory of spontaneous generation.

We must neglect Diderot's brilliant psycho-physical explanation of thought, memory, and the self, a discussion which includes dreams, obsessions, illusions, and amnesia. Again the source is in La Mettrie, but Diderot goes far beyond him. A theory of moral determinism follows. Returning then to questions of biology, he discusses the nature of individual organs and their submergence in the unity or whole of the living body, by their submission to a collective life and consciousness—an idea whose sources are in Bordeu, Maupertuis, and the second book of Lucretius. It is this phenomenon that is peculiar to life. Abiogenesis is firmly adhered to. Once more the discussion leads back to problems of evolution. What is the mechanism of change and variation? Unfortunately, Diderot had not been impressed by the genetic theories of Maupertuis. He now suggests the alternative hypothesis of the transmission of acquired characteristics. Rejecting, on the one hand, Christian finalism, and on the other, the Lucretian theory that organs are prior to any use made of them, he coins an oft-quoted phrase: "organs produce needs, and reciprocally, needs produce organs."[46] Bordeu, speaking in the dialogue, avers that he has seen two shoulder-blades lengthen into stumps of arms—a purposefully fantastic exaggeration of regeneration in crustaceans, which Réaumur had studied long before.

[45] Here we can see the great difference between Diderot's theory—a true transformism—and those of Bonnet and Robinet, whom Vernière mistakenly considers as true evolutionists (p. LI-LII). In the minds of Bonnet and Robinet, the different species are separate "trials" by Nature, as she devises ever higher combinations. The species themselves are invariable. When Bonnet speaks of "passage" from one species to another, it is always contiguity in the chain that he has in mind.

[46] Ibid., p. 67. In the later *Réfutation d'Helvétius*, Diderot was to put the proposition in a more acceptable form, stating that exercise strengthens organs, and disuse atrophies them. (*Oeuvres*, II, 410.)

> Suppose a long sequence of armless generations, suppose continuous efforts, and you will see the two sides of this pincers extend, extend more and more, cross behind the back, return forward, and perhaps form digits at their extremities, and refashion arms and hands. The original conformation is altered or perfected by necessity and habitual function. We walk so little, work so little and think so much, that I should not think it strange if man ended up by being only a head. (p. 69)

It is to be observed that the stimulus to adaptation is not a changing environment, but internal dynamism, or an internal teleology. There are really three distinct theories of which we have given an account in this study, and they should be carefully distinguished. Benoît de Maillet is the true predecessor of Lamarck, in his rather fantastic notion of acquisition of new characteristics in direct response to environmental change, and their transmission. Maupertuis explains variation, in an entirely opposite fashion, as the result of random genetic change. Diderot, on the other hand, is impressed by the dynamism of life, and by its purposeful response to the self-contained needs of the organism.

In a remarkable passage which follows, Diderot describes the differentiation of organs in the embryo, which he attributes to the action of certain "threads," each carrying its own design and finality. Extract from the foetus one of the "threads," the corresponding organs will never develop; mutilate it, and a monster will result (Diderot has finally explained his monsters!); double the thread, and two heads may result, or six fingers; change their position, and the lungs or heart will be reversed. By a mechanical process of extracting "threads," a genius could theoretically be converted into an unorganized mass of flesh; then, by their appropriate restoration, this mass returned to its proper state. At last Maupertuis' genetic theory seems to have entered the picture; but Diderot fails to apply it directly to evolution. He develops one aspect of it, but only to explain the defects of his "monsters." Commenting on their irregular reappearance in different generations, "Bordeu" says,

> It takes two to make a child, as you know. Perhaps one of the agents repairs the defects of the other, and the defective network is reborn only at a time when the descendant of the monstrous race predominates and determines the formation of the network. The bundle of threads constitutes the original and primary dif-

> ference between all animal species. The variations in the bundle of any one species produce all the monstrous varieties in that species. (p. 91)

It is curious that Maupertuis, in his notion of "particles," foreshadows the concept of genes, while Diderot, with his "threads," anticipates the discovery of chromosomes. In making this claim, however, we must not fail to include an important reservation. Diderot's notion of the "threads" is developed in a highly ambiguous fashion. His first description of them would indicate that they are not related to our idea of chromosomes, but are materials that are formed epigenetically, as a *result* of fertilization, in the embryo. He seems to be thinking of the "threads" he may have observed in a fertilized chicken's egg.[47] As the discussion proceeds, however, the concept seems to change, and as we have seen in the passage quoted, the "threads" become themselves the constituents of heredity and the genetic constitution of species. Furthermore, we may even (if we wish to be so bold) see in Diderot's words an intuition of the theory of recessive genes.

Much of the remaining part of the dialogue completes Diderot's theory of materialism by its extension to ethical questions. Virtue and vice have no reality, except as social impositions; all actions, even the so-called abnormal, if they produce pleasure without hurt, are equally natural, and morally indifferent. We are reminded that Diderot's beloved Horace had said something like this in his third satire, "Nec natura potest iusto secernere iniquum." Implicit in this discussion is a theory previously developed in the *Neveu de Rameau*, and closely tied to Diderot's view of nature and evolution: in the competition for survival, all that matters is success. "There is nothing solid but drinking, eating, living, loving and sleeping," says d'Alembert in his dream. Life, and persistence in being are the only realities nature knows.

There is one more work in which Diderot touched for a last time on the questions of life and evolution. His *Eléments de physiologie* (1768-1780) are a series of notes, often daring or fantastic, stemming from his prolonged study of Haller. Organs, he states again, are differentiated by an inherent patterning power within the germ cell ("molecule"). The undifferentiated "molecule"

[47] "You were, in the beginning, an imperceptible point, formed by smaller molecules, scattered in the blood and lymph of your father or your mother; this point became a long thread, then a bundle of threads." (*Oeuvres*, II, 144.)

produces an eye "by an inherent tendency (*une disposition première*) which can, with nutritive material, produce no other effect." [48] Diderot is now somewhat doubtful about life arising from a complex organization that changes inert into active sensitivity. Irritability and sensitivity are different from all other forces, are life, and they do not exist without life.[49] What else can account, he inquires, for the difference between the living man and the corpse? Is there not, in living bodies, "*un principe vital*," the extinction of which is death, the presence of which animates, creating the unity of the Whole, and the continuity of the life process? He foresees the modern view that all life is organized energy engaged in a struggle, destined to failure, against entropy. "What is an animal, a plant? A coordination of infinitely active molecules, a linkage of small, living forces, against which all things are working together to dissolve. Is it then astonishing that these beings end so soon?" [50]

Diderot's *principe vital* is very close to Bergson's *élan vital*. Were there any reason to believe that he knew the work of Caspar Wolff, we should think it a reminiscence of the latter's *vis essentialis*.

Of the phenomenon of organic evolution he now expresses his firm conviction. "We must not believe that [animals] have always been and will always remain such as we see them. . . . Why could not the long series of animals be varying developments of a single one? . . . One of these [absurd] suppositions is that there is on the surface of the earth a single being, an animal which has always been what it now is." [51] His remarks on the mechanism of evolution fall under two heads. He repeats his belief in the inheritance of acquired characteristics. "Organization determines functions and needs; and occasionally needs revert upon the organization, and this influence can go sometimes so far as to produce organs, always so far as to modify them. . . . I am not averse to believing that the prolonged eradication of an arm would bring about a one-armed race." [52] Of greater interest is a new viewpoint that appears for the first time. The significant shift is now made from inner viability to successful relationship with environment. He definitely glimpses, though the

[48] *Oeuvres*, IX, 411. As previously stated, the sources are in Maupertuis and La Mettrie.

[49] Ibid., p. 269, 274.

[50] Ibid., p. 255.

[51] Ibid., 264-5.

[52] Ibid., p. 336, 419.

thought is still vague, the essential elements that had been lacking in his theory of transformism—adaptation to environment, and selection by environment. There is no question, he writes, of a tendency towards perfection as life evolves (an idea he conceivably might have encountered in Leibniz);[53] there is only a purge of ill-adapted beings. "Why cannot man and all animals be considered species of monsters that are a little more enduring? . . . What is a monster? A being whose survival is incompatible with the existing order. But the general order is ceaselessly changing; in the midst of this mutability, how can the continuance of the species remain the same? . . . The vices and virtues of a preceding order have brought about the existing order, whose vices and virtues will bring about an order to come, without there being any question of the whole getting better or worse." Diderot clearly implies that if the environment suddenly changed, the most "perfect" and "beautiful" beings would become imperfect, and perish unless they were able to re-adapt themselves. In this context of existence, he concludes, spanning nature and ethics, "the world is the house of the strong."[54]

To attempt a summary of Diderot's "theory of transformism" would be futile, since his thought was itself a process of ideological transformation. But we may recall some basic assumptions. Diderot could not believe that matter had to be defined solely in terms of human sense impressions (extension, impenetrability, etc.), and that it could have no other mode of existence. It also seemed incredible that matter could have two distinct ontological states, inert and living. But whereas modern biology, analytic and quantified, tends to study life in terms of its elementary components, or the non-living, Diderot took the other approach. To explain life (being a philosopher he could not merely accept it), he postulated "sensitivity" (and motion) in matter. When he doubted sentience, he doubted, too, the possibility of a materialistic explanation. He also required a theory of organism. The organism "controls" the behavior of its parts, in view of a goal. For this reason life possesses behavior, and ultimately, consciousness, thought and will. They cannot be explained through the activity of the components, but only through the organization. What matters is the dynamism of life, imposing design and creating change, ever seeking stability, never resting in it, always in process, always becoming. All this is

[53] See A. O. Lovejoy: *The Great Chain of Being*, Cambridge, 1948, p. 256-7.
[54] *Oeuvres*, IX, p. 418-9, 428.

far from the Darwinian combination of chance variations of undirected particles and environmental selection (which Diderot glimpsed too late).

Diderot's theories of transformism, of which only the earlier group was known to his contemporaries, had little direct influence on the growth of that hypothesis. The notion itself, however, was disseminated among the encyclopedists, and eventually scientists in France, Germany, and England became absorbed in its development. It should be recalled that Lamarck was a student of Buffon's and a contributor to the later *Encyclopédie méthodique.*

Throughout the course of his writings, Diderot's theorizing reveals two principal characteristics. One is his absorption of all available suggestions put out by contemporary investigation and speculation. The other is the power of animation and synthesis which enables him to complete the idea, to vivify it, and—most distinctively of all—to perceive its connection with related problems. In Diderot's mind, the hypothesis of transformism is a vital link in a coherent philosophy of materialism that extends from inanimate matter to the decisions and ethical judgments of the being who embodies matter's most complex organization. In a real sense, the theory sprang from a materialistic view of nature, and in turn, it became an important contribution to that view, making possible its completion in a universal form.

Furthermore, the development of a theory of transformism is intimately related to the entrance of historicism into the European intellectual outlook. The rise of relativism in ethics and social thought, as evidenced in the writings of Montesquieu, Diderot, and others, is a complementary part of a general evolutionist view of the universe, which embraces the cosmos, life, and societies. The new historicism will counter the Greek and Christian vision of a universe stabilized by eternal laws. From it will grow some of the deepest conflicts of the contemporary world, as the evolutionist philosophy leads both to the relativism of social Darwinism (or to that of Existentialism), and to the absolutism of Hegel and Marx.

Finally, to anyone interested in the history of ideas, who cares to see how a vital concept germinates, comes to life, and grows, summoned forth by the discoveries and nourished by the speculative necessities of an age, the history of Diderot's theory of transformism and its relations with the thought of his time offers a revealing, unforgettable page from man's intellectual history.

since he saw clearly the imperfections of those of Tournefort and Ray. Through a treatise of Vaillant, *De sexu plantarum* (1717), Linnaeus became aware of Camerarius' discovery in 1694 of the male and female organs of flowers and the nature of fertilization by pollination. He may already, and quite independently, have reached the same conclusion regarding the significance of the stamens and pistils. At all events, he soon convinced himself that a workable classification could be based upon the differences and resemblances in these organs from group to group. The classification was extended to the animal and mineral kingdoms in the *Systema Naturae*.

Probably at this time Linnaeus, in the great pressure of his creative activity, had little time to think about the problem of variation. He was working out the details of his great scheme, and in four years published no fewer than eight significant books. He would be tempted to set aside vexatious complications, in the knowledge that he could return to them later. At least, it is clear that at this time he fully accepted the fixity of species. The *Fundamenta botanica* No. 157 (1736) contains already the famous dictum: *Species tot sunt diversae quot diversas formas ab initio creavit infinitum Ens*; and over and over through the works of these early years, up to 1751, there recurs the expression *nullae species novae*. This belief on the part of Linnaeus may have sprung partly, as Perrier has suggested, from his devotion to the idea of Leibniz that Nature has no gaps.[1] Every species must then be strictly intermediate between two other species, or the plenum would not exist. The belief perhaps sprang also from Linnaeus' rejection of spontaneous generation and his alliance with the ovists. In any case, it led him to make a great reduction in the number of species (7,300) he would admit as true, the remainder of Ray's 18,000 entries being reduced to the rank of varieties.[2] One must then ask what in Linnaeus' mind these varieties were. The answer is clear. In the *Philosophia botanica* (1751), the definition of "varieties" immediately follows the statement quoted above that "there are as many species as the Creator produced diverse forms in the beginning," and further that "these forms multiply and produce, according to

[1] E. Perrier, *La philosophie zoologique avant Darwin*, F. Alcan, Libr. Germer Baillère & Cie., Paris, 1884, p. 34.

[2] Ray himself did not regard them all as certainly deserving the denomination of species.

the laws of generation, forms always like themselves. This is why there are just so many species as there exist today diverse forms or structures." Linnaeus therefore yielded no consideration to hereditary variants. Varieties were simply "plants of the same species modified by whatsoever occasional cause . . ." such as "the climate, sun, warmth, the winds, etc." They relate only to "stature, color, taste, odor." Furthermore, upon the return of the plant to its former environment it reverts, so he thought, to its original type. Botanists need take no account of such slight and evanescent variations.

This was Linnaeus' original view. Yet even while he was still reiterating words in this tenor, his mind was troubled and undergoing a change. It seems to have begun in 1742, when a student named Zioberg brought him, from an island near Uppsala, a collection of plants of the common toadflax, or butter-and-eggs, *Linaria vulgaris*, among which were specimens of a quite unknown plant. This new form, in all respects like the common *Linaria* except in its flowers, instead of the expected snapdragon-like blooms had tubular flowers expanding into five uniform petals at the mouth, and having five spurs at the base instead of a single one. Linnaeus called it *Peloria*, and in the *Amoenitates academicae* of 1749 (through a dissertation by his student D. Rudberg) he speaks of it with admiration and excitement. The ancients, he said, imagined that rye could become transformed (*transmutari*) into barley, barley into oats, and oats into tares. The mutation of *Linaria* into *Peloria* is a metamorphosis even greater than such transformations ("*mutationibus illis multo adhuc majorem esse metamorphosin quam mutata in Peloriam Linaria subierit*"). Yet *Peloria* must be considered, he thought, a species, albeit a new one, since it formed perfect seeds and bred true to type. It thus becomes clear that this hereditary variation was to Linnaeus no mere variety unworthy of a name, but in fact a new species. To distinguish the difference he even uses the word *mutation* rather than *variety*.

Now such a phenomenon was not unheard of. According to Guyénot,[3] an apothecary of Heidelberg named Sprenger had in 1590 discovered in his garden, where he grew medicinal herbs, and among them celandine (*Chelidonium majus*), a new form of the latter with very greatly divided leaves. He named it *Chelidonia major foliis*

[3] E. Guyénot, *Les sciences de la vie aux XVII^e et XVIII^e siécles: l'idée d'évolution*, Albin Michel, Paris, 1941, p. 374.

et floribus incisis, and sent it to Bauhin and other botanists of the time, all of whom recognized it as a new and previously unknown species. It is still cultivated and is known as *Chelidonia laciniatum*. A more famous and fully documented case was the discovery in 1715 by J. Marchant of two new species of *Mercurialis* growing in his garden; one of them he named *Mercurialis foliis capillaceis*, and the other *Mercurialis foliis in varias et inaequales lacinias quasi dilaceratis*. Both were cultivated until 1719, when Marchant communicated his discovery to the Académie des Sciences.[4] "There would be reason to suppose," wrote Marchant, "that the Omnipotent, having once for all created individual plants, as models for each genus . . . these models, in perpetuating themselves, would finally have produced varieties, among which those that remained constant and permanent have constituted species, which, through the succession of time, and in the same manner, have made other different products." It seems that in the mind of the discoverer, and likewise of the Historian of the Académie, who commented upon the communication, there was no question: these transmutations constituted new species.

Linnaeus, faced with his *Peloria*, recognized that it could obviously not be one of those temporary varieties produced by the action of the environment. Not only did it breed true, but it had occurred in nature more than once. Gmelin in 1749 reported that a *Peloria* had been found in another species of *Linaria* near Nuremberg; Linnaeus mentioned several places in Sweden; and a M. Ludolfe, a locality near Berlin. Gmelin had moreover transplanted the only two Siberian species of *Delphinium* to his garden in St. Petersburg and thereafter found five or six new fertile forms. He concluded that besides the species originally created, the number had since the beginning "doubled, tripled, or multiplied to infinity." This speculation pleased Linnaeus. It permitted one to adhere to the principle of the immutability of original species and at the same time admit new species produced through hybridization. He set his students to work upon the problem of looking for hybrids between well-known species and even hybridizing species to originate new ones.

It may be pointed out that the theory was certainly extreme. Neither *Linaria* nor *Antirrhinum*, the snapdragon, nor other plants

[4] J. Marchant, Observations sur la nature des plantes, *Mém. Acad. Roy. Sci.*, 1719, pp. 59-66.

of the Scrophulariaceae normally have peloric flowers. Either one must assume that a hybrid between two similar forms could bring forth something completely new; or else the hybridization must have been between a *Linaria* and a plant completely outside its family. Yet *Peloria* was in all respects, except for its flower structure (and fruit), a typical *Linaria*. Why did no other characters of the presumed widely different parent show up? Today, since the peloric mutation has recurred many times in these species, we know that it may be produced by a single gene alteration, and that it breeds true upon self-fertilization because it is a recessive type and consequently homozygous. What a pity that Linnaeus did not undertake to hybridize the *Peloria* with the common *Linaria*. He might in that case have anticipated Mendelism! Instead, he and his students Dahlberg, Gråberg, and Haartman began looking for new species that might have arisen by hybridization whenever parent species from distant realms had been brought together in a garden.

A large number of genuine and purported hybrids were discovered in the ten or fifteen years following the first finding of the *Peloria*.[5] Only a few of them can be mentioned, to serve as examples. One was a hybrid thistle (*Carduus*), its putative parents the common hairy thistle and the thistle of the Pyrenees. Several were *Verbena* hybrids, one being presumably from a cross between *V. americana* and *V. humilior*. *Pimpinella agrimonoides* was regarded as a hybrid between the common pimpernel (*P. sanguisorba minor laevis*) and agrimony (*Agrimonia officinarum*), a truly startling combination of a member of the rose family with one of the primrose family, had it been authentic. Another, somewhat less dubious, was found in the Uppsala garden in 1750, and described in fullest detail by Haartman. It was named *Veronica spuria* by Linnaeus, and was held to have come from a cross of *Veronica maritima* female and *Verbena officinalis* male. This hybrid represents a cross between species of different families belonging to two distinct subgroups of the Tubiflorae. It was a perennial, multiplying only from the roots, since it was quite sterile. Like the other reported hybrids, its flower structure most resembled the female parent, but the stem and leaves were very like those of a *Verbena*. It seems that Linnaeus, faithful to an old idea of Cesalpino, con-

[5] A quite detailed account, including bibliography, is given in H. F. Roberts, *Plant Hybridization before Mendel*, Princeton University Press, Princeton, 1929, pp. 15-33; cf. Guyénot, op. cit., pp. 368-374.

sidered the stamens of a flower to correspond to the wood and the pistil to the pith. "It is impossible to doubt," Linnaeus wrote, "that there are new species produced by hybrid generation. From all these things, we learn that the hybrid is brought forth, as to the medullary substance or the internal plant or fructification as the exact image of the mother, but as to its leaves and other external parts it is as that of the father. These considerations, therefore, lay down a new foundation for the students of nature, to which many things contribute. For thence it appears to follow, that the many species of plants in the same genus in the beginning could not have been otherwise than one plant, and have arisen from this hybrid generation."[6] Where the pollen parent was unknown, as in the case of many of these purported hybrids, Linnaeus believed that he could deduce it from the nature of the leaves and stem of the hybrid, and the general availability of possible pollen-providers. The description therefore signifies only that the purported hybrid had vegetative features somewhat resembling those of a *Verbena*. No one appears to have repeated this cross, or even to have regarded it as worth the attempt. Did Linnaeus deceive himself?

There was, notwithstanding, one hybrid which Linnaeus himself produced in his garden in 1757 through an artificial cross of *Tragopogon pratense* female by *T. porrifolius* male. It was reported in the *Disquisitio de Sexu Plantarum* (1760), which was submitted to the Imperial Academy of Sciences in St. Petersburg along with some of the seed of the *Tragopogon* hybrid. It thus chanced that Koelreuter had an opportunity to grow the hybrid and examine it when it bloomed in the spring of 1761. His comment that it was a mere "half-hybrid" was based on an erroneous theory of his own, and there seems no particular reason to doubt the authenticity of this first artificial interspecific plant hybrid.

If any further evidence were needed to demonstrate how far Linnaeus had shifted from his early view of the fixity of species than the clear statement just quoted a paragraph above, it is to be found in his numerous references in the *Species plantarum* (edition of 1764) which express a conjecture that some particular species in question has been derived from some other. Green has compiled many of these:

---

[6] C. Linnaeus, *Disquisitio de sexu plantarum*, 1760, p. 127-128; the translation is that of Roberts, op. cit.

Thalictrum lucidum . . . The plant is possibly not so very distinct from *T. flavum.* It seems to me to be the product of its environment.

Clematis maritima . . . I should rather think it is derived from *C. recta* under altered conditions.

Achillea alpina . . . May not the Siberian mountain soil and climate have moulded this out of *A. ptarmica*? [7]

There are numerous others, all of which imply that Linnaeus not only had accepted the origin of new species through hybridization, but was wondering about the origin of good species—no mere temporary varieties—through the action of the environment over long periods of time. The *Metamorphosis plantarum* of 1755 deals not only with fixed species but also with monstrosities and varieties. If, as Linnaeus had heard, Réaumur had produced a hybrid between a rabbit and a hen, was it not more likely that hybrids within the order of anthropoids, which Linnaeus had proposed as a fancy, might indeed have occurred? And was man by any significant character not of the order of anthropoids?

In 1762, Linnaeus conjectures that the work of God in the Creation stopped at providing the common source of each genus, or maybe only of each order, and that diversification within the limits of these original groups has made the species. In 1766, he omits from the final edition of the *Systema Naturae* his famous dictum that there are no new species. Finally, in 1779, he expresses the view that "species are the work of time," and that one of the great scientific enterprises of the future will consist in demonstrating this truth.[8]

Was Linnaeus, the master proponent of the fixity of species, then transformed by the hard pressure of facts into an evolutionist in his later years? That would be saying too much, perhaps; for the old man hardly thought his way clearly through his puzzlement. How

[7] E. L. Greene, *Carolus Linnaeus*, Christopher Sower Co., Philadelphia, 1912, pp. 79, 81, 82.

[8] Quoted by J. Rostand, *L'évolution des espèces*, Libr. Hachette, Paris, 1932, p. 24, from *Amoenitates Academicae*, 1762; and again J. Rostand, *Esquisse d'une histoire de la biologie*, 12th edition, Gallimard, Paris, 1945, from *Amoenitates Academicae*, 1779. [I have not been able to consult the original.] Cf. also K. Hagberg, *Carl Linnaeus*, E. P. Dutton and Co., New York, 1953, chap. XII, "The Origin of the Species," for interesting sidelights in spite of a sketchy treatment of the subject.

clear and sharp scientific distinctions had been in his youth! How turbid the waters he now beheld! Nevertheless, the view here set forth is agreed to be correct by every modern student of Linnaeus' work and thought.[9] One can put it this way. In the end he believed in the evolution of the smaller systematic categories, of the species as he knew species, and maybe of the genera. But the original Creation was still that of a multitude of forms, distinct then and forever. In holding to this conviction his Lutheran conscience was salved.

II

Were further evidence necessary of Linnaeus' ultimate conversion to belief in the origin of new species, it would be sufficient to cite a contribution to the *Histoire de l'Académie des Sciences* made by Adanson in 1772. Entitled "Examen de la question, si les espèces changent parmi les plantes; Nouvelles Expériences tentées à ce sujet,"[10] this remarkable paper is concerned wholly with the refutation of Linnaeus' views. Quoting Marchant's opinion about the significance of his mutant *Mercurialis*, Adanson says: "This opinion remained forgotten until the year 1744, when M. Linnaeus after having regarded species as constant in 1740, commenced to doubt it, and even to believe in the production of new species when speaking of the plant he called *Peloria*; and after having cited the two examples of M. Marchant, he enumerated six others upon which we will report." Adanson thereupon proceeds to describe his own experimental tests of these reputed new species, and to demolish their claims to such status. Before considering this highly significant, though almost unknown, piece of eighteenth century evolutionary controversy, a sketch of the earlier career of Michel Adanson, the botanist involved, will be relevant.

Adanson is a figure of disputed stature in the history of science. To Julius Sachs, whose *History of Botany* (1875) has become a classic, it seemed clear that the "first great advance in the natural system" was due to Antoine Laurent de Jussieu (1748-1836), prin-

[9] Including Loren Eiseley, in his recent book, *Darwin's Century*, Doubleday & Co., Garden City, 1958, pp. 16-26.

[10] *Histoire de l'Académie Royale des Sciences*, 1769 (publ. 1772), pp. 71-77 (commentary of the Historian of the Académie) and *Mémoires*, pp. 31-48.

cipally by providing the families of plants with distinctive characters.[11] The work of the uncle, Bernard de Jussieu, marked little advance over the effort of Linnaeus, who, in his *Classes plantarum*, had formulated the basis of a natural classification of plants that would take account of all characters and show true affinities, instead of being admittedly arbitrary and artificial like his empirical reliance on the sex organs of the flowers in the *Species plantarum*. Sachs remarks:

> Adanson's claims of priority over Bernard de Jussieu may be passed over as unimportant. The natural system was not advanced by Adanson to any noticeable extent; how little he saw into its real nature and into the true method of research in this department of botany is sufficiently shown by the fact, that he framed no less than sixty-five different artificial systems founded on single marks, supposing that natural affinities would come out of themselves as an ultimate product,—an effort all the more superfluous, because a consideration of the systems proposed since Cesalpino's time would have been enough to show the uselessness of such a proceeding.[12]

On the contrary, a more modern historian of science, Émile Guyénot, hails Adanson as the true founder of the natural method of classification and the greatest botanist France ever produced—a man at least the equal of Linnaeus in genius.[13] The reasons for Adanson's eclipse and the neglect of his work appear to lie, like those relating to Maupertuis, in the machinations of an evil genius, in this instance his rival Antoine Laurent de Jussieu, who through nepotism succeeded his uncle as director of the Jardin des Plantes and successfully devoted himself throughout his life to the derogation of Adanson and the enhancement of the reputation of his uncle. The facts seem to be as follows.

A precocius youth with a passion for the natural sciences, Adanson at 21 lacked the financial resources and influence needful to obtain a post in the limited scientific world of the time; and in 1748 he went as a business agent to Senegal, where he spent four years and a half. Two years later he wrote to his onetime teacher, the elder

[11] J. von Sachs, *History of Botany (1530-1860)*, trans. by H. E. F. Garnsey, rev. by I. B. Balfour, Oxford, at the Clarendon Press, 1890, p. 116. Original German edition, 1875.

[12] Ibid.

[13] Guyénot, op. cit., pp. 29-38; 366-367; 377-379.

de Jussieu, of the inadequacies he had found in the systems of Tournefort and Linnaeus in classifying tropical plants, and of his conviction that such systems were faulty because they selected a single part of the plant as a basis for classification. One must compare all parts minutely, he thought, and thus there will arise the character of the whole organism which can lead to a natural classification. On this basis, he at once met with a startling success, by divining the status of the great tropical baobab tree as a member of the mallow family, the Malvaceae. After returning to France, he published in 1757 his mémoire on the baobab, and immediately set to work on the plan of the great *Familles de plantes*, the outline of which he read to the Académie in 1759, while the entire work was completed in 1763. It was based on his natural method, which, he declared, is one wherein the classes contain "no plants which do not agree together" in the *ensemble* of their characters. Reliance upon this method was necessary, in Adanson's mind, because of his complete and implicit belief in the Great Chain of Being and the Principle of Continuity. From a belief that nature makes no leaps, that there are no real voids between organic forms, he, like Buffon in the beginning, held that in nature there are really only individuals, and neither genera, nor classes, nor species. The latter, he thought, are conveniences of the classifier's mind. The reality was the individual and the variability of those individuals. Nevertheless, upon close examination one can discern fissures in the apparent continuity, "lines of separation." These may be the result of our ignorance of intermediate forms, or of their disappearance, the latter being especially evident from "the bones of monstrous quadrupeds, the skeletons and impressions of fishes and of plants, and a prodigious number of shells, so different from those which live today in the seas." [Adanson, while in Senegal, had made huge collections of plants and animals, especially mollusks, and was the first to recognize, in a monograph of 1752, that the shipworm *Teredo* is a mollusk. One must not judge by the shell, but by the nature of the animal itself, he emphasized.][14]

A corollary of Adanson's view of variability was that it is very difficult to determine what is a variety and what is a species, Hence he deplored Linnaeus' exclusion from his system of all varieties and

[14] M. Adanson, *Histoire naturelle de Sénégal: Coquillages*, Paris, 1752. Cf. Guyénot, op. cit., p. 84.

his great reduction in the number of admitted species. "Seeds," said Adanson, "are the source of a prodigious number of varieties, often so changed that they could pass for new species, especially when they reproduce [again] by means of seeds. . . ." He did not think that these supposed new species—and he mentions specifically as examples the two mercurialis of Marchant, Linnaeus' *Peloria*, and Gmelin's delphinium—came from hybridization between species, as Linnaeus proposed. Among seedplants similar changes may be procured "either by the reciprocal fecundation of two individuals differing in some character, although of the same species, or by culture, soil, climate, drought, humidity, shadow, sunlight, etc. . . . These changes are more or less prompt, more or less enduring, disappear after one generation or perpetuate themselves for several generations, according to the number, the force, the duration of the forces which unite to form them." [15]

That was in 1763. Three years later a remarkable new strawberry was discovered by the Duchesnes, father and son, horticulturists of Versailles. It had a simple, entire leaf instead of the three distinct leaflets characteristic of the ordinary strawberry. The younger Duchesne concluded it to be a new species, and proceeded to a hypothesis that all existing kinds of strawberries had probably been derived by variation from one original type, by the influence of climate or unknown causes.[16]

At the Jardin des Plantes Adanson proceeded to investigate very thoroughly and scientifically the nature of this monophyllous strawberry, together with Linnaeus' *Peloria* species, the *Mercurialis* species of Marchant, Vaillant's Miracle, or Smyrna, wheat, and a variety of barley Adanson had bred himself, with 4-ranked instead of 2-ranked ears but otherwise possessing the characteristics of the 2-ranked sugar-barley (*orge sucrion*). Stating that to start with he had himself been inclined to agree with the suppositions of Linnaeus regarding new species, Adanson was convinced to the contrary only by repeated and painstaking experiments, continued over the space of seven years.

The *Mercurialis* of Marchant which Adanson had at his disposal had lower leaves like those of the common mignonette (*Reseda*). Hence Adanson not only crossed the *Mercurialis*, which was a male

[15] Adanson, *Familles des plantes*, Paris, 1763. Cf. Guyénot, op. cit., p. 377.
[16] Duchesne fils, *Histoire naturelle des Fraisiers*, Paris, 1766. Cf. Guyénot, op. cit., pp. 375-377.

plant, with two ordinary female *Mercurialis* plants, but also attempted to pollinate ordinary *Mercurialis* by mignonette and flax plants, respectively, since according to Linnaeus' conjectures the new species might have arisen as a hybrid between *Mercurialis* and one of the two latter species. The seeds of the cross of the abnormal *Mercurialis* by the normal *Mercurialis* germinated poorly (hardly 10 per cent). All of the plants which grew from these seeds or from a second, third, fourth, or fifth generation were ordinary *Mercurialis*. The attempted crosses with the mignonette and flax plants were wholly sterile, except for a few ordinary *Mercurialis* progeny that were produced—Adanson concluded—by contamination with pollen from neighboring gardens in spite of all his care, or perhaps by the presence of some male flowers on the female *Mercurialis* plant, a phenomenon Bernard de Jussieu had reported as occurring. Adanson concluded from these experiments that the *Mercurialis* with dissected leaves was no new species, but a monstrosity—as we would say today, a mutant—and this seemed to be confirmed by its numerous defective features not only of leaves but of vessels, veins, and stamens. Today we know that Adanson was unquestionably correct. The laciniated *Mercurialis* is a simple mutant variety.

Adanson's next experiments were done with *Peloria*. Contrary to Linnaeus' report, this form failed to breed true, either in the original variety which Linnaeus had sent to the Jardin des Plantes, or in a new peloric type which had arisen there in a Spanish species of *Linaria*. In both, reported Adanson, peloric flowers and typical flowers were borne on the same stalk, or plants might have only typical irregular flowers, or only peloric flowers; but in every case the peloric blooms were sterile. The only seeds came from the ordinary flowers, and these seeds yielded now ordinary *Linaria*, now *Peloria*. Once again Adanson was forced to conclude that the supposed new species was a monstrosity, with certain organs developed to excess (*monstre par excès*) and others developed weakly or not at all (*monstre par défaut*).

As for the strawberry with simple leaves, Adanson bred this too, and found that the leaves were in actuality quite variable in the basic defect of the veins of the leaves, so that it was apparent that the single-lobed leaf was an imperfect fusion of the three lobes of an ordinary leaf. The flowers, too, had more petals and sepals than usual, while the number of stamens was reduced; and both stamens and fruit were malformed. Here, then, was another example of a mutant, "monstre par excès dans le calice et la corolle; monstre par défaut dans les feuilles, les étamines, et la fruit." Every botanist was familiar with monstrosities: "one knows sufficiently what a difference there is between a species and a monstrosity; a species is comparable to a new species, but a monster can be compared only to an individual of the species from which it originates."

The barley studied by Adanson had a 2-ranked ear, but he noticed a slight tendency in some plants for the ear to become quadrate. Through selection continued over five or six years (10-12 generations), he raised the frequency of 4-ranked ears until all were of that sort, although within the ears there was still variability and a tendency to revert to a 2-ranked type. As for the famous Miracle wheat, which Linnaeus for some reason had ignored in the *Species plantarum*, this too proved to be a "monstre par excès." Among its branched heads, when carefully examined, there proved to be two to four per cent of simple heads; and by sowing the wheat too late or in spring, or in an earth too poor or too dry, virtually all branching of the heads would disappear. [Premonition of Lysenko!]

From these repeated results on every variety of supposed new species he could obtain, Adanson came to the conclusion that Linnaeus was quite wrong. ". . . The transmutation of species has not taken place among the plants, no more than in animals. . . ." Finally, a most pregnant conclusion: "To see the harmony which reigns in all parts of the Universe, every reasonable philosopher is at first moved to believe that these deviations also have their laws and their limits: in fact, the more one observes, the more one convinces himself that these monstrosities and variations have a certain latitude, necessary without doubt for the equilibrium of things, after which they return into the harmonious order preestablished by the wisdom of the Creator."

It is surprising that the erudite author of *Les sciences de la vie aux XVII^e^ et XVIII^e^ siècles* failed to discover this final mémoire of Adanson's career, for it has been referred to by Rostand[17] and others. Guyénot consequently arrived at a rather dubious conclusion, in holding that Adanson had not conceived clearly the idea of evolution. On the contrary, he furnished crucial experimental evidence to destroy the principal form in which it existed in his

[17] Rostand, *L'évolution des espèces*, p. 25.

time. Nevertheless, we are scarcely in error if we grant that his achievement of a truly natural classification based on real affinities, his emphasis on the variability of species and the analysis of mutant forms, his suggestion of the causes of hereditary variation, and his emphasis on fossils as indicating the demise of species which once filled the plenum of Nature, were all more in the true direction of the ultimate evolutionary theory than Linnaeus' theory of the origin of new species by hybridization. What irony in the fact that the tested "new species" of Linnaeus were all demonstrably mere mutants, although in principle he was right, since new species of plants can and do arise by hybridization upon occasion! The fate of Linnaeus' theory of the origin of new species within the bounds of the originally created forms, call them what you will, reminds us forcibly of the similar fate of Hugo de Vries' mutation theory, which was likewise wrong in the particular instances on which it was based, yet right in principle.

The last years of Adanson were lamentable. Even Lamarck may be considered to have been blest in comparison. Thirty-seven years were to pass after the publication of Adanson's last great mémoire before he died—years during which he was not only excluded from every official post and opportunity, but was first vilified and then forgotten. When still only 62 years of age, at the outbreak of the Revolution, he was deprived even of his two pensions, the one royal, the other from the Académie. During ten years of penury he lived on the sugar and coffee provided by a loyal servant, a peasant woman who worked at night, unknown to him, to make the extra pittance necessary for that poor fare. Crippled with rheumatism, without light and without fire, he tasted the final despair of inability to continue his work. Only in 1799, when his pension from the Académie was restored, was there a measure of relief; but it came much too late to revive his efforts. He died in 1806, when Lamarck was in the ascendant—Lamarck who wrote the article on "Famille" in the *Encyclopédie methodique* without so much as mentioning Adanson's name, even when describing the plants brought by Adanson from Senegal.[18]

[18] Guyénot, op. cit. I have relied almost exclusively upon this work in the present treatment of Adanson, except for a careful study of the Mémoire of 1769. The facts of Adanson's life are recounted in A. Chevalier, *Michel Adanson*, Larose, Paris, 1934.

III

One further crushing blow was dealt Linnaeus' theory of the origin of new species by hybridization. This was through the analysis of numerous interspecific hybridizations performed by the first great plant hybridizer, Joseph Gottlieb Koelreuter, who reported them in detail in a "Preliminary Report" (1761) and three "Continuations" (1763; 1764; 1765).[19] Koelreuter's experiments were models until the time of Mendel. Applying the discovery made by Camerarius of the sexual organs of flowers, and relying on their exclusive pollination by insects which might be readily excluded from access to the flowers, he performed numerous artificial pollinations with success. In 1761 he obtained the first well-authenticated interspecific plant hybrid, from a pollination of *Nicotiana rustica* by *N. paniculata.* Perfect seeds were obtained, they germinated well, and the young hybrid plants, extremely vigorous and fast-growing, were intermediate in type between the parent species. However, when they came into bloom, the anthers of the hybrid's flowers were not filled with pollen, and the pollen grains present appeared under the microscope to be shrivelled and empty. The hybrid, in fact, proved to be completely self-sterile, and Koelreuter therefore called it a "mule-plant." However, when the hybrid was pollinated with pollen from either of the parent species, it set some fertile seed. In these back-crosses Koelreuter observed that the progeny tended most to resemble the maternal parent; but in successive crosses gradually to go back to the type of original species used in the backcross. Thus, according to his findings, Linnaeus' new species could not be true-breeding hybrids, as Linnaeus thought, for hybrids are sterile except in backcrosses, and then they tend to return to the original forms.

As to Linnaeus' one artificial hybrid, the *Tragopogon*, Koelreuter was dubious of that too, although for the wrong reason.

> For the hybrid goat's-beard, which the celebrated Linnaeus considers in his new prize essay, is not a hybrid plant in the real sense, but at most only a half hybrid, and indeed in different degrees,

[19] J. G. Koelreuter, *Vorläufige Nachricht von einigen das Geschlecht der Pflanzen betreffenden Versuchen und Beobachtungen, nebst Fortsetzungen 1, 2, und 3*, Leipzig, 1761-1766. Reprinted in *Ostwald's Klassiker der exakten Wissenschaften*, No. 41, Engelmann, 1893. Cf. Roberts, op. cit., chap. II, for a relatively extended analysis.

as I will clearly and plainly demonstrate at another opportunity, with many reasons which appear in part from the nature and peculiarity of the composite flowers, and from certain experiments instituted upon the time of fertilization of the same; in part from the structure of the above-mentioned presumed hybrid itself, which had been raised by me from seeds which Linnaeus had sent, together with his prize essay, to the Honorable Russian Imperial Academy of Sciences, and which have bloomed the past spring in the Academy's garden at St. Petersburg.[20]

What Koelreuter meant by a half hybrid is apparent from the context. He assumed that always in hybridizations there would be a "tincture" of self-fertilization, in proportion to the amount of pollen from the anthers of the maternal parent to the amount of foreign pollen placed upon the stigma. [This was before the time when it became common practice in cross-pollination to remove the anthers of the flower selected as the female parent before their dehiscence.] Kolreuter thought, in other words, that a given plant of the progeny could share inheritance from two male parents, in proportion to the relative amounts of pollen contributed by them. This belief was grounded in his observation that it required 50 to 60 pollen grains to fertilize all 30 ovules in an ovary of *Ketmia* or *Hibiscus*. The actual nature of the fertilization process was not to be discovered until a century later; but Koelreuter himself soon showed that when the stigmas of a flower are pollinated by their own pollen and foreign pollen at the same time, fertilization is through the former. His theory of half hybrids was thus unfounded, and the objection to the validity of Linnaeus' hybrid *Tragopogon* may be rejected.

A more serious objection to Linnaeus' theory of the formation of new species by hybridization was, however, raised in this same communication (Erste Fortsetzung). Koelreuter showed that in his numerous crosses involving species of *Nicotiana* (tobacco), *Dianthus* (pink), *Ketmia* (a composite), *Leucojum*, *Hyoscyamus* (dogbane), *Verbascum* (mullein), and *Matthiola* (stock), in general only closely related species may be crossed at all, and not always even these. The wide hybridizations conjectured by Linnaeus on the basis of the supposed combination of maternal and paternal characteristics in the "new species" thus fell, and along with them were discredited

[20] Koelreuter, op. cit. Roberts' translation, p. 43.

his more reliable instances of species hybrids, among them, for example, the alsike clover and the artificially produced *Tragopogon*. In fact, it became common practice to say that Linnaeus had made no effort at all to test his theory experimentally (Duchesne, 1766; Sachs, 1875; Guyénot, 1941).[21]

The most significant bearing of Koelreuter's hybridizations upon the evolutionary theory lay in the results of the self-fertilizations of the hybrids and crosses of them to the original parent species. Many of these were performed, of which the *Dianthus* crosses may serve as example. There were 7 of these reported in the Erste Fortsetzung, 8 in the Zweite Fortsetzung, and no less than 29 in the Dritte Fortsetzung. Among salient observations were the following: (1) the F_1 hybrid was always very uniform in type but the progeny of selfings of hybrids and of backcrosses showed considerable variation; (2) at least three selfings were fertile; and (3) in a cross of *D. chinensis* by *D. hortensis* in which the latter had double flowers, all the progeny had double flowers.

One may emphasize first of all the great tendency to variation when the hybrids were bred. This observation was totally destructive of Linnaeus' theory of the formation of true-breeding new species from hybrids.

Of at least equal interest, however, were the self-fertile hybrids, even though the backcrosses had already demonstrated that many hybrids are not totally sterile, at least on the female side. This discovery of fertile hybrids between species rendered utterly untenable the sole criterion of species which Buffon, and after him Kant, were utilizing to maintain their views of the constancy of species.[22] Of course, it might be said that the test proved the parent types to be no true species, but mere varieties. Yet they had been well recognized by all systematic criteria as distinct species. The logical conclusion had either to be that the forms were not true species, or else that true species are able in some instances to cross and yield fertile hybrids. To accept the former view would lead to the expansion of the species until it engulfed the genus or even the entire family, and to admit that within its thus enlarged limits variation, hereditary or acquired, would have full scope. To accept

[21] Duchesne, op. cit., cited from Guyénot, op. cit., p. 373. Sachs, op. cit., p. 89; 400. Guyénot, op. cit., p. 373: "Il est à peine besoin de dire que les interprétations de Linné ne reposait sur aucune détermination expérimentale."

[22] See Professor Lovejoy's chapters on Buffon and Kant in this volume.

the latter view was more frankly to admit the probability that species may become altered by intermingling with other species. But then what keeps the species in nature breeding true to type?

Buffon chose the first way out of the dilemma: reduce the number of true species to a minimum—all quadrupeds to 38 species, for instance—and the criterion of hybrid sterility holds fast. But within each such " species " enormous modifications can take place. Linnaeus, so late in life, could not forsake his well-ordered system of species. He therefore abandoned the idea of the constancy of species, and resorted to the constancy of originally created " stocks " from which groups of related species have been derived. In reality, the difference between this conception and Buffon's is purely semantic. Koelreuter—and this is most curious—seems to have evaded altogether the issue of the nature of species and the light thrown upon it by his own experiments. It seemed enough that he had demolished Linnaeus' theory of new species through hybridization. He had saved the dogma of the constancy of species from the hands of its faithless creator. He did not see that in doing so he had in truth opened Pandora's box, since henceforth no one would ever be able to distinguish species from races and varieties by any simple criterion. Why did some, but only some, of Koelreuter's species hybrids manifest complete sterility, as among the mulleins (*Verbascum*) he intercrossed? Koelreuter remarks on the singular absence of such hybrids in nature, although some of the species involved in the crosses had lived in proximity for thousands of years. Was it not, he thought, teleologically, because of their very sterility? But in that case, why were the more fertile interspecific hybrids not formed either? The question indeed might lead one by minute gradations back to mere racial and varietal distinctions. Koelreuter failed to pursue it beyond the demonstrably greater potency for fertilization of a flower's own pollen than of foreign pollen.

The dominance of double flowers in the *Dianthus* cross might have provided a clue to the particulate nature of heredity; but these hybrids do not appear to have been backcrossed on the recessive parent. Koelreuter was not looking for purity of genetic character, since he had made many other crosses in which, even for simple traits, the hybrid had been intermediate in type. He had, for example, crossed *Mirabilis jalapa* red-flowered by yellow-flowered in reciprocal directions, and had done the same for *Leucojum* red-flowered by white-flowered, *Datura stramonium* white-flowered by

D. tatula violet-flowered, and the like. In each of these cases the flower color of the hybrid was intermediate, or at least not strictly like either parent. The *Mirabilis jalapa* hybrid had mixed red and yellow, or orange-yellow flowers; the *Leucojum* hybrid had whitish-violet blooms; the *Datura* flowers showed "a whitish color playing a little into the violet; the flower-tubes marked with five violet stripes, and the others [?] sky-blue." Undoubtedly results such as these and many others of like nature found in the succeeding century blinded Nägeli to the general significance of Mendel's discovery.

Finally, it should be apparent that Koelreuter's experimental findings, properly understood, constituted a body-blow to the doctrine of preformation in the form of emboîtement. Sachs has compared his influence in this respect with that of Caspar Friedrich Wolff.

> . . . Wolff is usually said to be the writer who refuted the theory of evolution [as Bonnet called his doctrine of preformation]. It is certainly true that in his dissertation for his doctor's degree in 1759, the well-known 'Theoria generationis,' he appeared as the decided opponent of evolution; but the weight of his arguments was not great, and the hybridization in plants which was discovered at the same time by Koelreuter supplied much more convincing proof against every form of evolution. Wolff conceived of the act of fertilization as simply another form of nutrition. Relying on the observation, which is only partly true, that starved plants are the first to bloom, he regarded the formation of flowers generally as the expression of feeble nutrition (vegetatio languescens). On the other hand the formation of fruit in the flower was due to the fact, that the pistil found more perfect nourishment in the pollen. In this Wolff was going back to an idea which had received some support from Aristotle, and is the most barren that can be imagined, for it appears to be utterly incapable of giving any explanation of the phenomena connected with sexuality, and especially of accounting for the results of hybridisation. Wolff may have rejected the theory of evolution on such grounds as these, but he failed to perceive what it is that is essential and peculiar in the sexual act.[23]

While this may be less than fair to Wolff, it certainly places the general significance of the studies of hybridization made by Koelreuter in a proper light. As Sachs well says: "It is impossible to rate too highly the general speculative value of Koelreuter's artificial

[23] Sachs, op. cit., p. 405.

hybridisation. The mingling of the characters of the two parents was the best refutation of the theory of evolution [read *preformation*], and supplied at the same time profound views of the true nature of the sexual union." [24] It is only fair, however, to point out also that Maupertuis' study of polydactyly and his views of the formation of the foetus had done the same, ten years earlier, and that Maupertuis' speculative extension of his views into the realm of evolution far exceeded Koelreuter's reluctance to grapple with the problem of species.

At all events, Koelreuter's experiments, though largely neglected in his own lifetime by the Linnaean school and most other systematists, bore fruit especially in the work of Konrad Sprengel, who took up Koelreuter's observations of insect pollination, demontrated the function of nectaries in flowers, and revealed the ingenious devices whereby, in dioecious plants, the fertilization of a flower by its own pollen is commonly prevented. In the next century the hybridizers Knight, Herbert, and Gärtner continued the analysis of species crosses; but—in Sachs' words again—"it was reserved for Darwin's wonderful talent for combination to sum up the product of the investigations of a hundred years, and to blend Koelreuter's, Knight's, Herbert's, and Gärtner's results with Sprengel's theory of flowers into a living whole. . . ." [25]

Lacking in the picture, of course, is Mendel, for Sachs wrote in ignorance of the revolutionary experiments with peas in the little monastery garden in Brünn. Yet Mendel, too, owed his inspiration to Koelreuter, whose work he knew so well. And if Nägeli and the other plant hybridizers of the time were so preoccupied with species hybrids and the seeming insolubility of the problem of species in relation to hereditary variation that they failed to understand Mendel, that preoccupation too stemmed from Koelreuter. How could one suppose that the study of simple variations of hereditary nature would one day throw more light on the nature of the origin of species than all the ten thousand crosses and three hundred and fifty different hybrids Gärtner had produced and described so painstakingly? Only Darwin might have understood, and fate kept Darwin and Mendel apart.

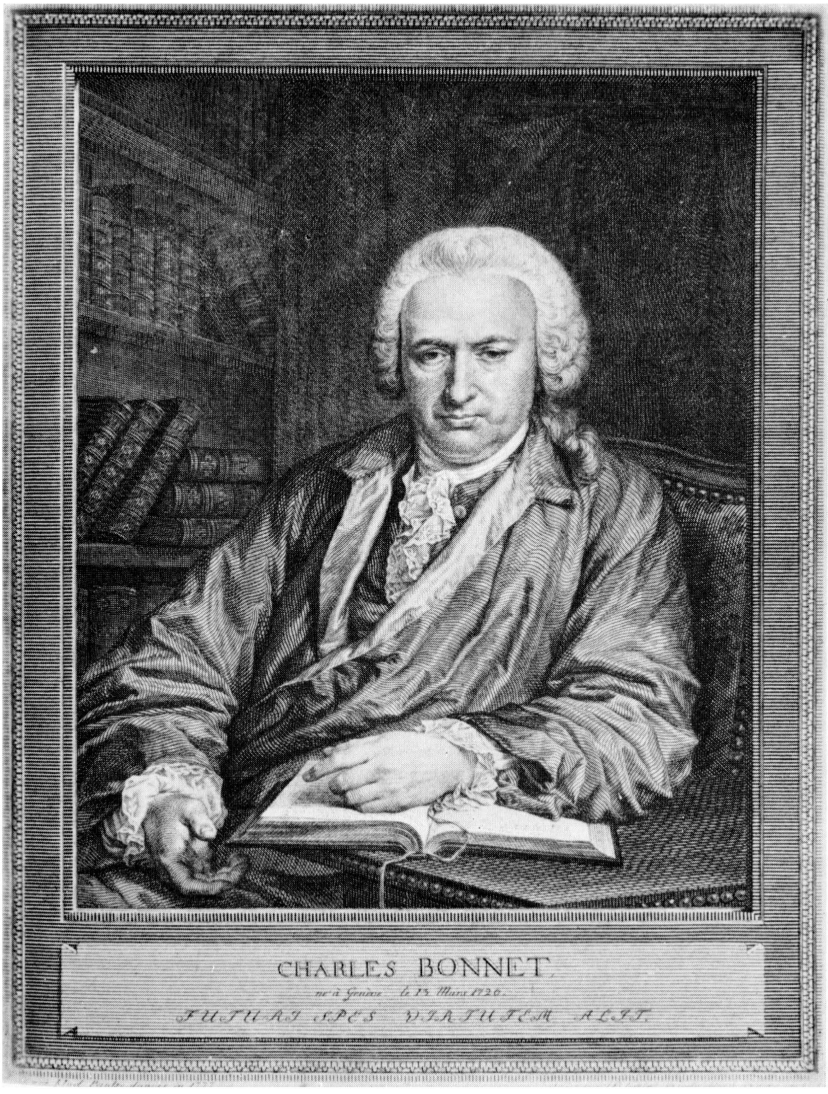
[24] Ibid., p. 413.
[25] Ibid., p. 431.

IV

In the eighteenth century, the theory of "evolution" was the theory of Charles Bonnet, and it had a far different sense than the theory of evolution of the nineteenth century. The older theory had reference to the evolution of the individual from the germ, which Bonnet supposed must always exist prior to fecundation, else there would be no heredity; and this led inevitably to emboîtement. The new evolution is the evolution of the species, presupposing hereditary change and variation, whereas the old evolution theory presupposed an unchanging species, based on the eternal conservation of its hereditary nature. In the new evolution, as we now see it and as Maupertuis saw it in the mid-eighteenth century, the ultimate event is abrupt change, mutation; as Bonnet saw it in his evolutionary scheme, the ultimate event was original creation. In the one conception, hereditary variation is ever new; in the other, it has been present from the beginning, requiring only the right conditions for its release and expansion. "Nature is assuredly admirable in the conservation of individuals;" said Bonnet, "but she is especially so in the conservation of species. . . . No changes, no alteration, perfect identity. Species maintain themselves victoriously over the elements, over time, over death, and the term of their duration is unknown." [26] From this position, as C. O. Whitman has ably set forth, Bonnet never wavered.

After wrestling with all the perplexing questions presented in Hydra; after accounting for sex as a means of diversifying the unity of the *beau physique*, and sexual reproduction as a device for expanding the germ and preserving regularity of specific form; after reconciling the existence of varieties with the permanence of species; after contending that a mule is a disguised horse and a hinny a disguised ass, and that the sterility of hybrids is to be regarded as fertility kept dormant by lack of adequate means to unfold; after reducing all heredity to likeness of original, contemporaneous, and independent creations, unfolding under similar conditions; after elaborating a scheme of "natural evolution" broad enough to take in any number of cosmic revolutions, and

[26] C. Bonnet, *Considérations sur les corps organisés* (1762), in *Oeuvres d'histoire naturelle et de philosophie*, Neuchatel, 1779, T. III, chap. VIII, sect. CXL, p. 90. Translation by C. O. Whitman, "Bonnet's Theory of Evolution—a System of Negation," in *Biological Lectures, Woods Holl*, 1894, p. 237.


CHARLES BONNET,
né à Genève le 13 Mars 1720.
FUTURI SPES VIRTUTEM ALIT.

> provide for the ultimate perfection of every organism as an immortal being;—in a word, after setting "Ferien" to all creative activity, Bonnet resolutely undertook to devise a scheme that would keep the holiday repose forever inviolable. With a zeal never daunted, and an ingenuity seldom baffled, never defeated, he piled mountain upon mountain of negation, rolling Ossa on Olympus and Pelion upon Ossa, until the whole organic world seemed to be completely buried under a stupendous mass of negations, blending in one infinite negation—No CHANGE.[27]

It is then truly of interest to see how Bonnet treated the problem of variation in relation to species.

Whitman points out that the passage immediately preceding (sect. CXXXIX) the words of Bonnet quoted above, is commonly taken to indicate that Bonnet had an evolutionary trend to his thought. The passage is as follows:

> One cannot doubt that the species which existed at the commencement of the world were no less numerous than those which exist today. The diversity and the multitude of combinations (*conjonctions*); perhaps also even the diversity of climates and nourishments have given rise to new species or to intermediate individuals. These individuals having mated in their turn the intergrades (*nuances*) have become multiplied, and in multiplying have become less detectable (*sensibles*). The *pear-tree* among *plants*, the *chicken* among *birds*, the *dog* among *quadrupeds* furnish us with striking examples of this truth. And in this respect we would not at all have to speak of the varieties which are to be observed among men derived originally from two individuals!

One is not surprised that Guyénot (op. cit., pp. 384-385) sees in this an expression of the multiplication of species through the action of the environment. But, as Whitman says, such passages must be read in context. Bonnet frequently indulges in seeming contradictions that, properly understood in his frame of thought, are no contradiction at all. Says Whitman: ". . . there is not the least inconsistency in it. Bonnet describes *appearances*, and he expects the reader to remember, what he has so often repeated, that appearances are deceptive. In many instances he uses the language of modern evolutionary doctrines without having any conception of them, and carrying always ideas that contradict them."

[27] Whitman, op. cit., pp. 239-240.

Nevertheless, so flat a contradiction as these two sections pose is very disconcerting. From the examples cited by Bonnet, it seems probable that he has here used the term "espèces" not in the Linnaean sense, but as signifying simply sorts or varieties. If so, he intended to say in sect. CXXXIX that various breeds and races, or "espèces," can be produced by the action of different conditions on the germ; and thereafter in section CXL to insist that the germ itself is unchanged, the real species unaltered. The germ of the barnyard chicken is the same as that of the wildfowl, the germ of the dog no different from that of the wolf, and all the races of mankind are brothers of the same species regardless of their environmentally induced distinctions.

Three aspects of the thought of Bonnet must be carefully distinguished. The over-riding conception is that of preformation. To this idea the theory of emboîtement was secondary, and indeed, as Bonnet found difficulties in applying it in every instance, it could conveniently be surrendered when necessary. What was essential to the major idea was not a practically infinite series of models of the adult each successively enclosed in turn within the preceding generation, but simply the existence of some organic preformation by means of which development could proceed under control. It was in particular the consideration of the formation of buds by the *Hydra*, the little "polype à bras" made so famous by his cousin Abraham Trembley, that forced Bonnet to these conclusions. The bud clearly can form anywhere on the body of the parent *Hydra* and does not contain parts within it, like the bud of a plant, all ready to expand and unfold. It is a mere bump, an excrescence on the parent's body. Yet, as it grows in size, it puts forth tentacles, develops a mouth in their center, becomes a fully formed *Hydra*. There must then be something, reasoned Bonnet, to make this happen, something present from the beginning—"certain particles which have been preorganized in such a way that a little polyp results from their development."[28] Since, too, the polyp can regenerate from any portion of its body when this is cut into small pieces, the particles must exist in every part of the whole. This consideration led Bonnet to the third concept of his theory, the concept of the germ.

[28] Bonnet, "Tableau des considérations," Art. XV, p. 68, *La Palingénésie philosophique*, 1769, in *Oeuvres*, T. VII.

"The germ need not be an actual miniature of the organism, but . . . merely an 'original preformation' capable of producing the latter," was Thomas Henry Huxley's rendering of Bonnet's thought.[29] The actual statement reads:

> I add here that I understand in general by the word germ every preordination, every preformation of parts capable by itself of determining the existence of a Plant or of an Animal.[30]

These words, written first in the *Contemplation de la Nature* in 1764 and repeated without change in the *Palingénésie* (1769; 1783), stand as the ultimate, mature reflection of Bonnet's natural philosophy. Bonnet's maturing concept of the germ is recapitulated as follows in the later work:

> *I at first assumed, as a fundamental principle, that nothing was generated*; that everything was originally preformed. . . .
>
> I postulated that all organized bodies derived their origin from a germ which contained *très en petit* the elements of all the organic parts.
>
> I conceived the elements of the germ as the *primordial foundation*, on which the nutritive molecules went to work to increase in every direction the dimensions of the parts.
>
> I pictured the germ as a network, the elements of which formed the meshes. The nutritive molecules, incorporating themselves into these meshes, tended to enlarge them. . . .
>
> Strictly speaking, I said (Art. 83, pp. 47, 48), the elements [inorganic] do not form organic bodies; they only develop them, and this is accomplished by nutrition. The primitive organization of the germs determines the arrangement which the nourishing atoms must take in order to become parts of the organic whole.[31]

Thus conceived, Bonnet's ingenious scheme is far different than the ludicrous view commonly attributed to him. The essence of the difference between his *germ* and the reproductive particles postulated by Maupertuis lies simply in the distinction that in Bonnet's thinking they could not, as Maupertuis supposed, be disorganized and dependent upon forces of mysterious nature, con-

[29] See Whitman, "The Palingenesia and the Germ Doctrine," in *Biological Lectures, Woods Holl*, 1894, p. 260.

[30] Bonnet, ibid.

[31] Bonnet, *Palingénésie*, Part VII, chap. IV, p. 205. Translation of C. O. Whitman, ibid., p. 246.

jectured chemical affinities resembling " what in us we term desire, aversion, memory," to bring each to its proper place in the body. The wholeness of the organism was something too intrinsic to be built up of inorganic matter. The organic fabric must exist, thought Bonnet, from the beginning. Hence preformation.

Hereditary differences–variations–thus existed for Bonnet as for other observers of Nature, but they were the consequence of the differences between germs, primordial, created once for all in the beginning, destined successively to enlarge and transform through varieties of nutritive condition, capable of metamorphosis to seemingly totally new forms under altered conditions, but in death reduced again to the undying germ. Even progress was envisaged.

> Perhaps there will be a continued progress, more or less slow, of all species towards a higher perfection, such that all degrees of the scale will be continually changing in a constant and determined order: I mean the mutability of each degree will always have its reason in the degree that shall have immediately preceded it.[32]

Now this passage has been taken by some writers to indicate that Bonnet too had conceived of evolution in the form of a transformation of species. But the entire context of his work shows this to be untrue. The germs, he believed, existed from the beginning of Creation. If there was progress, it took place *within* each species because the Creator had made the germs of each succeeding generation superior to those of the generation before. Plants might rise to the state of animals, oysters and polyps to that of birds and quadrupeds, monkeys to that of men, and men to that of angels; but for each it would be a metamorphosis, not a transmutation of species. Each germ had already within it, from the beginning, its potentiality to become something different, to take on a higher form, like the " evolution " of the butterfly from egg into caterpillar, caterpillar into chrysalis, and chrysalis into winged beauty.

Bonnet, of course, was profoundly right in seeing that there must be some organic entity persistent throughout all growth and change of form, some specific pattern or primordial foundation existing not alone at the origination of the individual but descending through the filiated generations. Today we call it the genotype. But he was just as profoundly in error in supposing that the genotype must

[32] Bonnet, *Palingénésie*, Pt. III, chap. III, p. 149-150. Cf. Whitman, ibid., pp. 255-257.

be static, or that it could not be generated in each new individual through the contributions of both parents. Having as a young man become famous for his discovery of parthenogenesis in plant-lice, he might be excused for naturally holding to the doctrine of ovism; but how could he blind himself to the clear implications of the biparental transmission of polydactyly in human families, or the presence in species hybrids of the features of both parent species?

In the *Considérations sur les corps organisés* (Part II, Chap. VIII, sect. CCCLV) Bonnet undertakes to consider the inheritance of ' sex-digitisme " in the famous Kelleia family, and in the final revision of this work (1779) he appended a note regarding Maupertuis' study of the Ruhe family of Berlin, of which he had been ignorant when the work was first written (1762). He adds comments regarding another report of inherited polydactyly in the *Journal de Physique*, November 1774, and concludes: "It seems, then, that one must recognize that polydactyly is transmitted or appears to be transmitted by the one and the other sex." [33] But does this conclusion force Bonnet to admit biparental heredity or even the possible inheritance of a monstrous germ? Not in the least. Just as earlier he had supposed that in the cross between a mare and a jackass the seminal liquor of the latter modifies the growth of the germ (which remains that of a true horse) so that the ears become longer, the natural fertility is impaired, and the modified larynx gives forth a bray, so now he suggests that the seminal fluid of a six-fingered male modifies the growth of the germ derived from a normal five-fingered female, but in no way changes the germ itself. As for the transmission through the mother, if abnormal conditions introduced by the semen of the male can modify the growth of the germ, why could not abnormal conditions in the intra-uterine development of the foetus convert a normal germ into a polydactylous one? Monsters are the accidents of nature. They arise through interference with the normal " evolution " of the germ.

No new generation! How apparent the link here between the faith in preformation and the rejection of spontaneous generation! For it was new generation of every sort, the origin of any living organism from separate organic particles rather than from a prior germ containing the essence of the whole, that was repugnant. The

[33] Bonnet, *Considérations sur les corps organisés*, Pt. II, chap. VIII, sect. CCCLV, p. 534 fn.

spontaneous generation of bacteria claimed by John Turberville Needham, the organic particles of Buffon, and the hereditary particles of Maupertuis were just as odious as the epigenesis of Caspar Friedrich Wolff. These views Bonnet shared with his friend and mutual admirer, the Abbé Spallanzani.

Lazaro Spallanzani was probably the greatest and most versatile biological experimentalist of the eighteenth century. His earliest studies, conducted at Modena, made him quickly famous. Needham, who had published a series of experimental studies on bacteria, was a close friend of Buffon, and an ardent believer in the reality of spontaneous generation, a view demanded by Buffon's theory of organic particles supposed to be disseminated throughout nature and to constitute a source of living organisms. In these experiments of 1745-50, Needham had placed meat broth in vessels corked and then sealed with mastic, after which he had set them by the fire and heated them to a temperature he supposed sufficient to kill all life in the flasks. After setting them aside for a few days, he invariably found the broth swarming with bacteria. Spallanzani (1765-76) repeated the experiments, but with greater care to assume perfect sealing. He used glass flasks with slender necks which could be fused in a flame, and thus sealed hermetically after the nutrient broth had been introduced. Thereafter the flasks were immersed in boiling water for three-quarters of an hour. (Needham had failed to record either the durations or the temperatures of the heat treatments he applied.) Spallanzani's flasks of broth remained clear and free of bacteria. When Needham objected that such severe heating had destroyed the capacity of the infusions to support life, Spallanzani triumphantly showed that when air was readmitted to the sealed vessels they were soon teeming with microbes. Just a century after the work of his compatriot Redi, Spallanzani had, at least temporarily, banished spontaneous generation from biology.

Spallanzani's conviction in the correctness of the preformation theory grew steadily during the succeeding years of experiment and communication with Bonnet. He turned to studies of the regenerative powers and reproduction of vertebrates, especially frogs and salamanders. Undismayed by the failure of so eminent an investigator as Réaumur, he succeeded in determining that the male frog emits seminal fluid at the very time when the female with which he is coupled lays her eggs. This he did by making for the male frogs little pantalettes of waxed taffeta, with suspenders to go over the shoulders. The pantalettes in no way interfered with the clasping of the female by the male, and when she laid her eggs Spallanzani was able to collect a glistening drop or two of the semen in the recesses of the garments. Not only did he then show that such eggs uniformly failed to develop, unlike those laid by females mated normally, but he also demonstrated that when the batch of eggs was divided and the diluted semen was added to one batch and not to the other, the eggs of the inseminated batch would develop normally into tadpoles, while the others failed to develop at all.

Notwithstanding this first successful artificial fertilization of animal eggs, Spallanzani failed to draw the correct conclusions. He had already determined, he thought, the existence of the germ in the frog's egg; and he held, in agreement with the views of Haller and Vallisneri, that the semen enters the egg by tiny pores and gently stimulates the heart of the foetus and sets it to beating. He tried many artificial agents–acids, poisons, blood, urine–nothing could replace the semen in this mysterious power. He heated the semen and found that it lost its fertilizing power after 2 minutes at 35°. He filtered it through fine cloth or blotting-paper. The power to fertilize was lacking in the filtrate; but pure water in which the filter was rinsed acquired the power to fertilize the eggs. Thus Spallanzani did every imaginable experiment needed to show that the spermatozoa were the active, fertilizing agent of the semen and that the fluid portion itself was impotent. Yet he failed to draw any such conclusion. No generation! The germ must be in the egg. The little animalcules of the semen, he knew them well; but they were neither the mediate nor immediate authors of generation. "Those of the man are not little men, those of the horse are not little colts." [34]

He tried one more experiment. Let a drop of semen evaporate, and watch it through the microscope as the spermatozoa recede from the edge of the drop and congregate in the center. Now immerse a needle in the edge of the drop and withdraw a droplet seemingly devoid of spermatozoa and apply it to an unfertilized egg. Success! it develops–the animalcules are after all not the source of the fertilizing power of the semen. Thus he performed what

[34] Quoted by J. Rostand, *La formation de l'être*, Libr. Hachette, Paris, 1930, chap. XII, p. 148. A valuable and graphic account of Spallanzani's work on fertilization. See also Rostand, *Esquisse d'une histoire de la biologie*, chap. VII; and Guyénot, op. cit., pp. 283-286.

seemed to be the crucial experiment, and thus he who had scorned Needham's subterfuges trapped himself in the delusion fostered by his own preconceptions.

For the time, preformation seemed firmly and permanently established. Wolff had been set down by the magisterial von Haller, who brushed away the young man's observations as those of a novice. Bonnet had met every argument of the epigenesists with subtle, untestable reasoning; and Maupertuis was dead. Spallanzani had overthrown the claims of Needham and Buffon regarding the spontaneous generation of bacteria and infusoria. The doctrine of the primordial, preorganized germs, created in the beginning, enduring unchanged until the end, reigned supreme. Perhaps in far-off Uppsala the old man whose brilliant youthful achievement had created a new biology pondered with failing mind the denial of his transformist views through the experiments of Adanson and Koelreuter, and thought: *nullae species novae.* Perhaps it was so after all. It would take a new generation to find out.

It would indeed take a new generation, the generation of Lamarck, and after that yet another, the generation of von Baer, before the transformation of species could be seriously reconsidered. And still beyond that time, another century would lapse ere the germ of truth embodied alike in the preformation theory and the epigenetic view of development would become reconciled in a higher synthesis, the genetic theory of development. And it would take that long, too, for the genetic analysis of variation to make clear the problem of hybrid sterility, to establish genetic mutation as the source of hereditary variation, and fully to characterize the species in dynamic, evolutionary terms.