As long as the battle between Darwinism and Lamarckism was raging, it was quite impossible to undertake an unbiased evaluation of Lamarck. For this we are now ready, after it has been demonstrated conclusively that the various causal explanations of evolution, usually designated as Lamarckism, are not valid. Not that it really needed this final proof, but the recognition that DNA does not directly participate in the making of the phenotype and that the phenotype, in turn, does not control the composition of the DNA, represents the ultimate invalidation of all theories involving the inheritance of acquired characters. This definitive refutation of Lamarck’s theory of evolutionary causation clears the air. We can now study him without bias and emotion and give him the attention which this major figure in the history of biology clearly deserves.

The past study of Lamarck (1744–1829) has tended to suffer from one-sided approaches. Sometimes he was discussed under the heading, “Lamarck and Darwin”: Did he anticipate Darwin? Did Darwin build on a foundation laid by Lamarck? Did Darwin fail to give him sufficient credit? It would be futile to try to reach a well-balanced evaluation of Lamarck through answering such one-sided questions. Other authors have limited their study to a comparison of Lamarck’s ideas with those of such eighteenth-century philosophers as had an interest in evolution, like Diderot, Maupertuis, or Robinet. This approach utterly fails to consider the contributions made by Lamarck’s professional interests. After all, he was not primarily a philosopher, but made his living as a naturalist who studied plants and animals for more than fifty years, from 1770 (when he was twenty-six) to the 1820’s (when he was in his eighties).

Some recent historians (Gillispie, 1956, 1959; Willkie, 1959; Simpson, 1961, 1964) have perhaps stressed too strongly the negative aspects of Lamarck’s work. They have stated, not with-
out justification, that his theory of evolution was neither new nor valid; that he did not propose a feasible mechanism of evolution; that, as an evolutionist, he was hardly ever mentioned by his contemporaries; that he seemed to have had singularly little influence on the subsequent development of evolutionary thinking; and that, when later in the nineteenth century his name was applied to evolutionary mechanisms, it was usually to ones not at all stressed by Lamarck himself.

All this is largely true, and yet it does not do justice to Lamarck as a figure in the history of biology. There are two excellent evaluations of Lamarck's work in French. That of Daudin (1926) is largely limited to Lamarck's taxonomy, a subject which I will not discuss here, since I plan to treat it elsewhere. That of Guyénot (1941:415–439) is a sympathetic and reliable introduction into Lamarck's thought (and its connections with his predecessors), but it does not pretend to be a full analysis. There is also Landrieu's (1909) extensive biography of Lamarck.

A truly penetrating study of Lamarck is still a desideratum. Eventually we will want to know far more about the growth of his thought, both before and after 1800. We will want to know to what extent his system of thought consisted of widely (at his time!) accepted "truths," such as the inheritance of acquired characters, and to what other part it was based on special philosophies and beliefs, such as deism, the concept of plenitude, and various aspects of the philosophies of Leibniz, Newton, or Descartes. This will require an extensive study of the thought of the eighteenth century.

Only one of Lamarck's biological publications, the Philosophie zoologique (1809), was ever translated into English, and even that one not until more than 100 years after its publication (Lamarck, 1914). For ease of reference I am basing my analysis almost entirely on the Philosophie zoologique, even though I fully realize that it is a confusing and repetitive work. One sometimes has the impression that Lamarck had merely gathered together his lecture notes over many years and combined them with portions of the Discours d'ouverture (Lamarck, 1907). How else can one explain that the identical topic is sometimes treated on six or ten different pages and his conclusions stated on these pages in virtually identical sentences? On the other hand, since no Lamarck "Notebooks" are in existence, this somewhat chaotic work may permit a better insight into the workings of Lamarck's mind than the more polished final revision that was published as the introduction to the Histoire naturelle des animaux sans vertèbres (1815).
The emphasis in my own treatment is on three aspects of Lamarck's work. It attempts (1) to bring out as clearly as possible what Lamarck actually thought and said; (2) to show where Lamarck got himself entangled in contradictions, in part because his findings as a zoologist were in conflict with his philosophical concepts; and (3) to point out problems that are in need of further research. In other words, this essay is a prolegomenon to the study of Lamarck rather than a comprehensive work on this great naturalist. My comments are primarily those of a biologist, not those of a historian. I have made no attempt to analyze the non-evolutionary writings of Lamarck, as for instance Parts II and III of the Philosophie zoologique. Greene (1959) has indicated the importance of this sector of Lamarck's work. Nor have I attempted to follow in detail the changes in Lamarck's thought throughout his long life.

One of my major objectives is to help English-speaking zoologists to become better acquainted with Lamarck's work. Extensive quotations from the Philosophie zoologique are provided under each subject heading, and I hope that they will show the reader not only how manfully (and often futilely) Lamarck struggled with facts and concepts, but also that Lamarck was a better observer and more perceptive thinker than he is usually given credit for.

**PSEUDO-LAMARCKISM**

Paradoxically, and as a consequence of a long tradition of historical interpretation, one must begin a discussion of Lamarck by emphasizing what the naturalist did not say. Two explanatory principles, in particular, are consistently but quite wrongly claimed to be the cornerstones of Lamarck's thinking: (1) direct effect of the environment, and (2) evolution through volition.

(1) Direct effect of the environment

When one checks the literature of Neo-Lamarckism to find out which concept is most consistently designated as "Lamarckian," one finds that it is the belief in a direct induction of hereditary changes in organisms by the environment. Curiously, as Simpson (1961) points out, Lamarck himself emphatically rejected the

1. Virtually all recent treatments of Lamarck merely provide an abstract of Lamarck's ideas. This is legitimate for most purposes. The particular flavor of Lamarck's reasoning, however, is lost by the mere summarizing of his ideas. I hope that the exact page references will help future students to find their way through the Philosophie zoologique, which is not an easy work to read. All page references (in parentheses) after quotations from the Philosophie zoologique refer to the Elliot translation.

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existence of such an evolutionary cause. However, since he speaks again and again of "the influence of the environment," he realizes the need for an explanation:

"I must now explain what I mean by this statement: The environment affects the shape and organization of animals, that is to say that when the environment becomes very different, it produces in the course of time corresponding modifications in the shape and organization of animals.

"It is true, if this statement were to be taken literally, I should be convicted of an error; for, whatever the environment may do, it does not work any direct modification whatever in the shape and organization of animals" (p. 107).

He then explains how he himself envisions the effect of the environment. Lamarck believed that "alterations in the environment of animals lead to great alterations in their needs, and these alterations in their needs necessarily lead to others in their activity" (p. 107). This interpretation is repeated many times throughout the Philosophie zoologique (pp. 40, 41, 43, 45, 58, and 114).

In spite of this emphatic rejection of direct induction for higher animals which display "activity," one finds that Lamarck speaks equally freely of a modifying influence of the environment on plants and lower (e.g., sessile) invertebrates. Would this not indicate that, at least in immobile organisms, he did have some belief in direct induction? And to what extent did Étienne Geoffroy St. Hilaire owe his belief in direct induction to Lamarck? These are still unanswered questions.

(2) The effect of volition

The other explanatory principle erroneously ascribed to Lamarck is the effectiveness of volition. The popular cartoon on Lamarckism depicts an animal, preferably a giraffe, wishing to reach an objective and through this volition growing (or acquiring) the needed structure (let us say, a longer neck). The attribution of this belief to Lamarck goes far back, for even Darwin speaks of "Lamarck nonsense of . . . adaptations from the slow willing of animals" (letter of January 11, 1844, to J. D. Hooker). Actually, as pointed out by Cannon (1957), Lamarck never said anything of the sort. The error presumably arose from a mistranslation of "besoin" (need). Lyell already scolded Darwin (in a letter of October 3, 1859) for ascribing to Lamarck a theory of volition. And yet Lyell himself may have inadvertently been one of the causes of Darwin's error. In Principles of Geology he consistently translates Lamarck's besoin as the "wants" [noun]
of animals. Huxley in his famous Times review of the Origin of Species (December 1859) says that according to Lamarck "the new needs will create new desires, and the attempt to gratify such desires will result in an appropriate modification." There is great danger that the hurried reader will only remember the word "desire."

**LAMARCK'S EVOLUTIONISM**

To a modern the word evolution has only a single meaning, the theory of common descent. In the eighteenth and early nineteenth centuries when essentialism was still the dominant philosophy, the word evolution, if used at all, was exclusively employed in the context of embryological phenomena, to denote the unfolding of immanent qualities. Ordinarily it would be applied to the embryogenesis of an individual, but increasingly often it was employed in a somewhat metaphorical manner, to the "evolution" of the type. For instance, when Louis Agassiz spoke of evolution (Mayr, 1959b), it was usually this kind of process he had in mind. It is difficult for the contemporary scientist to think in terms of eighteenth-century concepts, but we may try to describe eighteenth-century directionism as an endeavor to fuse the concept of a temporalized "Scala naturae" (Lovejoy, 1936) with that of the unfolding ("evolutio") of the immanent potentialities of an archetype. This postulates that only the appearance of the type would change, but not its underlying essence. It would be, so to speak, a static evolutionism.

Some of the more extreme critics of Lamarck have implied that Lamarck's ideas on evolution were of this eighteenth-century vintage and that he did not truly propose a genuine evolutionary change, or, as we would now say, a genetic transformation. Are these critics right? Did Lamarck think only in terms of an improvement in the appearance of a fixed type without a change?

2. Lamarck, so far as I know, never used the terms evolution, evolutionism, or transformationism later employed in the literature of English or French evolutionary biology. The term "evolutionary" is used in this essay in its modern connotation.

3. Essentialism designates the philosophies, all ultimately based on Plato's concept of the *eidos* and variously referred to also as realism (in the sense of the scholastics) or idealism, according to which the unlimited variety of natural objects corresponds to a limited number of underlying essences ("types"). Applied to morphology and taxonomy, it resulted in a search for the "ideal type," in the neglect of variability, and in an exaggerated emphasis on discontinuities (e.g., gaps between taxa). The opposite pole is population thinking, which stresses that classes of biological objects constitute populations consisting of uniquely differing individuals (see Mayr, 1959a).
in its essence, or did he indeed support the idea of a genuine evolutionary change? What do Lamarck's own words tell us about this assertion?

There are numerous passages in Lamarck's writings which one might want to quote, but none of them documents the genuineness of Lamarck's evolutionary thinking better than his discussion of aquatic animals in the *Philosophie zoologique*:

I do not doubt that . . . water is the true cradle of the entire animal kingdom.

We still see, in fact, that the least perfect animals, and they are the most numerous, live only in water . . . that it is exclusively in water or very moist places that nature achieved and still achieves in favorable conditions those direct or spontaneous generations which bring into existence the most simple organized animalcules, whence all other animals have sprung in turn (pp. 175-176).

. . . after a long succession of generations these individuals, originally belonging to one species, become at length transformed into a new species distinct from the first (pp. 38-39).

The principle of an evolutionary transformation through time could not be stated more clearly than that!

Historians concerned with the two hundred-year period prior to 1859 tend to go either to one or to another extreme. They either interpret any deviation from a strictly static description of the world as an anticipation of Darwin or else they regard it as a purely philosophical speculation that has nothing to do with true evolutionary thinking. The truth lies somewhere between these two extremes. As the exploration of the world accelerated in the seventeenth and eighteenth centuries and as, following Leeuwenhoek, the study of small aquatic organisms and micro-organisms became ever more popular, the Great Chain of Being (Lovejoy) acquired increasing substance. And with this came a belief in continuing change. After Leibniz (1693) had said that "even the species of animals have many times been transformed," it was stated more and more boldly by various eighteenth-century authors (as, for instance, by Maupertuis, Diderot, Robinet, and Bonnet) that the entire organic world is the product of evolution (see Lovejoy, 1936:256-286). Most of these authors were philosophers with only a limited knowledge and understanding of the world of organic beings, and their pronouncements were made rather casually and with little attempt at substantiation.

However, this cannot be said of Buffon, the foremost naturalist of his day. He might have based his entire *Histoire naturelle*
on a theory of descent if he had really believed in it, but this he
did not do. Even though Guyénot (1941:401) is convinced that
Buffon must be considered “not merely a forerunner, but, indeed,
a veritable founder of the theory of evolution,” Lovejoy (1959)
cites many good reasons why Buffon’s statements must be
treated with caution. They might just as well, or even more so,
reflect his philosophical ideas and, in particular, his adherence to
the principle of plenitude.

It seems to me that Lamarck has a much better claim to be
designated “the founder of the theory of evolution,” as indeed
he has been by several French historians (e.g., Landrieu, 1909).
All others before him had discussed evolution en passant and
incidentally to other subjects or else in poetical or metaphorical
terms. He was the first author to devote an entire book primarily
to the presentation of a theory of organic evolution. He was the
first to present the entire system of animals as a product of
evolution.

THE EVIDENCE FOR EVOLUTION

A specific set of observations gave rise to the evolutionary
thinking of each of the founders of evolutionism. In the case of
Lamarck the decisive observation, more than anything else, was
the perfect correlation between the structural adaptations of
organisms and their environment. This was not, of course, a new
observation since the very same evidence had induced the
natural theologians to extol the wisdom and foresight of
the Creator in creating only perfectly adapted beings. Natural
theology, however, was based on the belief in an essentially
static world. This dogma Lamarck was unable to accept, owing
to his far better understanding of the continuing geological and
climatic changes on the surface of the earth and of its great age.
To him, the geological, climatic, and geographic evidence indicated continuous, dynamic, and sometimes rather severe changes in the physical environment of the world. If there had been only
a single organic creation and yet all the mentioned subsequent
changes of the physical environment, then all organisms ought
to be by now very poorly adapted. However, since we find that
every organism is perfectly adapted to the particular environ-
ment in which it occurs, in its structural modifications as well
as in its habits, it is obvious that organisms, in order to survive,
must have the capacity for change. Anyone who wants to dis-
prove the validity of this argument, says Lamarck (p. 127),
must prove two points:

(1) “That no point on the surface of the earth ever undergoes
variation as to its nature, exposure, high or low situation, climate, etc., and

(2) "That no part of animals undergoes ... any modification due to a change of environment or to the necessity which forces them into a different kind of life and activity from what has been customary to them."

I believe that the cogency of this argument of Lamarck has not been adequately stressed in the past. Organisms, in order to remain perfectly adapted at all times, have to adjust to these changes; they have to evolve (p. 106). This leads Lamarck to "the conviction that according as changes occur in the environment, situation, climate, food, habits of life, etc., corresponding changes in the animals likewise occur in size, shape, proportions of the parts, color, consistency, swiftness and skill" (p. 109).

There is a great deal of vagueness in Lamarck's discussion of this problem, perhaps largely owing to his lack of interest in species. The changes in organisms, which he describes on p. 109, must affect representatives of various species. Is it possible that these modifications of individual species will be compounded in time until they affect the very organization of the classes to which they belong? (This, indeed, as we now know, is the case). If not, what are the "units" of the classes whose improvement leads in time to the origin of higher types of organization?

The need for having to remain adapted to the constantly changing environment is for Lamarck the most powerful causal factor for evolution. It would have seemed an easy matter for Lamarck to supplement this purely inferential deduction by citing chapter and verse for such effects of the environment. Geographic variation would have been the most obvious evidence in favor of the ability of organisms to adapt. Lamarck was fully aware of the adaptation of "races" to a particular locality owing to the influence of the environment:

Localities differ as to their character and quality, by reason of their position, construction and climate: as is readily perceived on passing through various localities distinguished by special qualities; this is one cause of variation for animals and plants living in these various places. But what is not known so well and indeed what is not generally believed, is that every locality itself changes in time as to exposure, climate, character and quality, although with such extreme slowness, according to our notions, that we ascribe to it complete stability (p. 111).
Lamarck Revisited

It would have seemed logical to extend this to geographically vicarious species, as Buffon had done in his comparison of certain elements of the European and North American faunas. Indeed, throughout Buffon’s writings there are scattered references to the effects of geography on organisms. They stress the effects of climate rather than those of isolation, but they do stress geography. Zimmermann’s volume on biogeography, Pallas’s frequent comments on the subject, and particularly those of Alexander von Humboldt, culminating in his famous essay on plant geography (1805), all document the increasing preoccupation of naturalists with problems of geography at this period and show how much by 1809 this subject was “in the air.” However, this aroused no response in Lamarck; perhaps the fact that he had traveled so little was responsible for his lack of interest. In this he differs strikingly from the Darwinian generation. Geography, particularly the distribution of closely related forms in space, played a decisive role in the evolutionary thinking of Darwin, Wallace, Asa Gray, Moritz Wagner, Gulick, Karl Jordan, and other leading evolutionists from 1850 on. This permitted the careful, scientific analysis of innumerable “experiments of nature” and helped, more than anything else, to remove the evolution theory from the realm of pure speculation. Lamarck’s lack of interest in concrete species deprived him of the opportunity to take full advantage of the already available geographical evidence.

SPECIES AND THEIR ORIGIN

The species was the key unit in Darwin’s theory of evolution. For Lamarck, whose primary emphasis was on levels of complexity in the organization of animals, the species played a subordinate role. His Philosophie zoologique was not an Origin of Species. While still a botanist, Lamarck—presumably under the influence of Linnaeus—still believed in the constancy of species, and he dealt with them as if they were well delimited. After he became an invertebrate taxonomist, he still treated them in a thoroughly conventional manner in his technical taxonomic treatises, but no longer in his more philosophical discussions. Here he stated that species are not constant; they “have really only a constancy relative to the duration of the conditions in which are placed the individuals composing it” (p. 36). He therefore finds no conflict between his concept of the impermanence of species and the fact that the mummified animals found by the French expeditions to Egypt were indistinguishable from the living ones, because “the position and climate of Egypt
are still very nearly what they were” three or four thousand years ago. Hence there was no cause for them to change (see below for time in Lamarck’s thought).

His species definition is the logical consequence of these views: “It is useful to give the name of species to any collection of like individuals perpetuated by reproduction without change, so long as their environment does not alter enough to cause variation in their habits, character, and shape” (p. 44). The concept characterized by this definition does not entirely fit into any scheme. Clearly it is closest to the nominalistic concept in its emphasis on the existence only of individuals and in the incomplete, if not arbitrary, delimitation of species against each other. However, Lamarck does not have the concept of variable populations. All the individuals that are forced by their environment to adopt similar habits will be essentially identical. Even though he does not accept the existence of an underlying essence, his species concept becomes curiously similar to that of the essentialists when he accepts the uniformity of “classes of individuals.” This is particularly puzzling since, as a working taxonomist, he must have been aware of the phenomenon of individual variability. And this phenomenon was the keystone in Darwin’s evolution through natural selection. Selection, as we know from the researches of Zirkle (1941) and others, was by no means an unknown concept by 1800, but it did not fit at all into Lamarck’s thinking. Furthermore, since individuals will change their habits whenever their environment (their “circumstances”) changes, adaptation through change of habit achieved for Lamarck all that Darwin later ascribed to the effect of natural selection.

It is remarkable how little Lamarck says on the multiplication of species, considering how many years he had been working on groups of closely related species and their distribution. For him “development of new species” simply was phyletic evolution. Individuals exposed to a changed environment “after a long succession of generations . . . originally belonging to one species, become at length transformed into a new species distinct from the first” (p. 39). For the origin of new species Lamarck, therefore, does not require saltations, as does the essentialist, nor isolation combined with natural selection, as does the pop-

4. The term “origin of species” confounds two biologically distinct phenomena, the gradual transformation of a phyletic line into a different species and the splitting of a single species into several daughter species. It is the explanation of the latter process, also referred to as multiplication of species or speciation, which caused the early evolutionists the greatest trouble. Essentialists and population thinkers were forced to propose entirely different explanatory mechanisms (see Mayr, 1970).
ulation thinker. Simple adaptation does the job, as far as Lamarck is concerned. Any multiplication of species would have to be sympatric speciation\(^5\) by ecological specialization. He describes this process as follows (p. 39): A "plant that grows normally in a damp meadow" sends out colonists into dryer and dryer terrain until "it reaches little by little the dry and almost barren ground of a mountainside. If the plant succeeds in living there and perpetuating itself for a number of generations, it will have become so altered that botanists who come across it will erect it into a separate species. The same thing happens in the case of animals that are forced by circumstances to change their climate, habits, and manner of life."

Lamarck, in these discussions, concentrates exclusively on two aspects of the new species, their differences ("so altered") and their occupation of a new niche (changed "habits and manner of life"). He nowhere mentions the key aspect of the modern biological species concept, the formation of a new, reproductively isolated community. Naturalists did not become conscious of the importance of this aspect of the biological species until more than fifty years later.

As an alternate mechanism Lamarck suggests, following in the footsteps of Linnaeus, that new species might originate by hybridization. Such hybridization he says will "gradually create varieties, which then become races, and in course of time constitute what we call species." Lamarck uses similar arguments to explain the origin of breeds and domestic races. This discussion is particularly interesting because Darwin uses the very same evidence as one of his major arguments in favor of the importance of natural selection. Lamarck in his discussions (pp. 110–111) does not mention the breeders' selecting activities, but ascribes the origin of the differences to the environment.

Lamarck's view that the species is largely an arbitrary aggregate of individuals exposed to "the same circumstances" and not sharply separated from other species was presumably strongly influenced by his studies of molluscan variability. There is perhaps no other group of animals with so conspicuous a variability as the land and freshwater molluscs. Indeed, they often show three superimposed kinds of variability: (1) genetic polymorphism, as in the European banded snails (Cepaea), where many different color types occur in a single population, (2) nongenetic

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5. Sympatric speciation is defined by the evolutionist as the origin of isolating mechanisms within the dispersal area of the offspring of a single deme (= population). The counterpart is geographic speciation, the acquisition of isolating mechanisms by a population during a period of geographic isolation.
modifiability, as in freshwater mussels (*Anodonta*, etc.), in which the species responds at each locality to the constellation of chemical and physical water conditions by producing a different phenotype, without necessarily changing genetically, and (3) genetically founded geographic variation which occurs in extreme form in many land snails, particularly in the Mediterranean region and on archipelagos. Although modern studies have shown that this variability rarely affects the sharpness of the borders between species, this was not at all evident in Lamarck's day, particularly to an author with nominalist tendencies. This leads him to describe the variation as follows: "... some of these individuals have varied, and constitute races which shade gradually into some other neighboring species. Hence, naturalists come to arbitrary decisions about individuals observed in various countries and diverse conditions, sometimes calling them varieties and sometimes species" (p. 36). As the amount of material in our museums grows, "we see nearly all the gaps [between species] filled up and the lines of demarcation effaced. We find ourselves reduced to an arbitrary decision which sometimes leads us to take the smallest differences of varieties and erect them into what we call species, and sometimes leads us to describe as a variety of some species slightly different individuals which others regard as constituting a separate species" (p. 37). "These species merge more or less into one another so that there is no means of stating the small differences that distinguish them" (p. 37). On the next page he refers to some of the well-known large genera of insects and states, "these genera alone possess so many species which merge indefinably into one another" (p. 38).

In these discussions Lamarck makes no distinction between, on one hand, individual variation or the formation of local ecotypes (neither of which normally leads to speciation) and, on the other hand, geographic variation (which—combined with isolation—may lead to speciation). Lamarck was fully aware of geographic variation (see also above, p. 62). "When the observing naturalist travels over large portions of the earth's surface and sees conspicuous changes occurring in the environment, he invariably finds that the characters of species undergo a corresponding change" (p. 112). Such geographic variation is described in even more detail in his *Natural History of Invertebrates* (1815), but it is nowhere contrasted with individual variation. What is missing, in particular, is any reference to the effects of isolation. The closest Lamarck comes to this is in his description of the domestication of the dog:

> No doubt a single, original race, closely resembling the wolf,
Lamarck Revisited

if indeed it was not actually the wolf, was at some period reduced by man to domestication. That race, of which all the individuals were then alike, was gradually scattered with man into different countries and climates, and after they had been subjected for some time to the influences of their environment and of the various habits which had been forced upon them in each country, they underwent remarkable alterations and formed various special races (pp. 110–111).

And he continues that the various races of dogs which are now so extremely different were “formed in very distant countries.” There is an intimation of the role of isolation in various of these statements, but it is nowhere clearly identified as an important factor.

Evidently not realizing that species are reproductively isolated populations and believing that the characteristics of organisms are (indirectly) the result of the environment, Lamarck could not appreciate the importance of isolation for speciation. Nor would it be important according to his theory because when a race returned to the place from which it had originated, it would have to return to its original appearance, owing to its being again exposed to the ancestral environment. Since each species is the product of its environment and since all environments merge into each other, it is only natural that all species should integrade with each other (pp. 37, 112).

Much of what Lamarck says about intermediates between “species” is quite correct when we deal with allopatric⁶ populations. This is why the modern taxonomist so often combines groups of such allopatric “morphological species” into widespread polytypic⁷ species. What is amazing, however, is the fact that Lamarck was so totally blind to the drastic difference between the situation he described for geographically variable polytypic species and the sharp, bridgeless gaps of coexisting, sympatric species, such as the working naturalist encounters everywhere. These he never mentions nor does he anywhere refer to the isolating mechanisms that help to maintain these gaps. Since an explanation of the origin of isolating mechanisms is the very essence of an explanation of the origin of species, it is obvious how distant Lamarck was from the solution of the problem of speciation (see fn. 4 above). Indeed, his entire conceptual

⁶. Allopatric, when applied to populations or species, means that they replace each other geographically. They are “vicarious,” in that they do not coexist at the same locality.

⁷. A species taxon is polytypic when it consists of several geographic races or subspecies.
framework was ill-adapted to explain the occurrence of concrete units such as species and their origin. Though he speaks so much of “branches” among evolutionary lines, Lamarck failed to notice that evolutionary divergence, i.e. the origin of such branches, must originate at the species level. It is rather evident that he was simply not thinking in terms of species, and least of all of species as biological populations.

THE CAUSES OF EVOLUTIONARY CHANGE

The principal reason why Lamarck failed to make more of an impression on his contemporaries and successors was that his explanatory principles were not convincing. There were primarily two processes the occurrence of which Lamarck postulated in order to account for evolutionary changes, but he never supplied any proof for either:

(1) Evolution toward perfection

Lamarck took it completely for granted that all classes of animals form a unique and graduated series from the simplest to the most perfect. As Daudin points out quite correctly (1926, 2:111), this is “his central thesis, his master doctrine on which he insists in his lecture courses and books more than on any other.” According to Lamarck (p. 60), it is not difficult to place all major types of animals in a linear series based on their “affinities.” Furthermore, “if one of the extremities of this series is occupied by the most perfect of living bodies, having the most complex organization, the other extremity of the order must necessarily be occupied by the most imperfect of living bodies, namely those whose organization is the simplest.” Similar statements are found in the introduction (Discours Preliminaire) of his Flore françoise, 1778 (1779). Since the evolutionary change led from the simplest to the most complex, it is necessary in a classification to adopt the same sequence. Lamarck chides Aristotle for having chosen a descending classification: “This classification furnishes the earliest example of an arrangement, though in the opposite direction from the order of nature” (p. 62). However, he fails to notice that in Chapter V, 15, of the Historia animalium, when discussing the genesis of animals, Aristotle does indeed start with the simplest organisms and proceeds


9. For his second principle, branching evolution and adaptive radiation, see below.
methodically through the animal kingdom up to the live-bearing ones.

Lamarck defends this linear sequence even though he is fully aware of Linnaeus' map-like, two-dimensional arrangement and, at least in the *Histoire naturelle* (1815–1822), of Cuvier's denial of any relationship whatsoever among the four major "embranchements" of the animal kingdom (Cuvier, 1812). He particularly rejects the suggestion that the relationships of families could be presented in the form of a network (p. 58).

"In each kingdom of living bodies the groups are arranged in a single graduated series, in conformity with the increasing complexity of organization and the affinities of the objects"¹⁰ (p. 59). Instead of "complexity" he calls his principal classifying criterion sometimes "ever greater perfection," but rarely specifies by what standards he determines "perfection." When he finally does so, he adopts the traditional criterion of the *scala naturae* (p. 71):

"Man . . . presents the type of the highest perfection that nature could attain to: Hence the more an animal organization approaches his, the more perfect it is." It is as simple as that!

The *scala naturae* is basically a static concept. When it is combined with the concept of evolutionism, it leads to conflicts and contradictions which Lamarck does not resolve—indeed, which he does not even seem to have been aware of. For instance, combining the image of a staircase and upward evolutionary movement leads almost by necessity to the simile of an "escalator," and this is how Gillispie¹¹ quite rightly characterizes Lamarck's *scala naturae*. Yet, how does such an escalator operate, when it involves only the "masses" (= major taxa), while the development of the species within each of these major taxa is regulated by "circumstances"? If one were to take the escalator simile seriously, one would have to conclude that every kind of organism moves upward to ever greater perfection. Since the supply of the simpler organisms is continuously depleted by this process (they move up the scale and become more complex), their number has to be replenished continuously by spontaneous generation. The simplest organisms thus are the ones most recently generated, and an arrangement of organisms based on their complexity will result in a classification that will "lead us to a knowledge of the order followed by nature in bringing the subdivisions of the animal kingdom into a graduated series."¹⁰

¹⁰ Notice that only the major types ("groups," classes) are arranged in such an ascending sequence, not individual species (see below).

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various species into existence" (p. 9). When classifying, naturalists “are obliged to follow the actual order observed by nature in giving birth to her productions” (p. 29). Indeed, this is the order which Lamarck adopted in Chapter VIII (pp. 128–169), entitled “of the natural order of animals, and the way in which their classification should be drawn up so as to be in conformity with the actual order of nature.”

The steady upward movement of the major animal groups (“masses”), if this is indeed what Lamarck postulates, creates a conflict with certain consequences of the principle of plenitude. Either all groups of organisms move upward at the same rate, or else some “masses” move faster than others and cause the production of gaps, the existence of which Lamarck denies steadfastly (pp. 23, 33, 37, 57, 66). Yet, when speaking of man’s continuing evolution, Lamarck says: “This predominant race, having acquired an absolute supremacy over all the rest, will ultimately establish a difference between itself and the most perfect animals, and, indeed, will leave them far behind” (p. 171) [Italics mine]. He does not attempt to reconcile such a gap with the principle of plenitude.

When trying to account for the causes responsible for the movement of the escalator, Lamarck abandons the firm ground of experience and becomes philosopher, speculating on forces, movements, and subtle fluids. The upward movement of the scale of complexities, he says on one occasion, is simply due to the “power [pouvoir] of life.” “That says no more than that the main movement is an inherent characteristic of life, which certainly explains nothing.” 12 Certainly not to a modern biologist. The analysis of Lamarck’s theories on life and vital processes is outside the scope of the present essay; it will be dealt with by R. W. Burkhardt in a forthcoming publication. 13

In this context one should also remember that Lamarck was a deist and that this colors some of his explanatory models. He evidently believed in a “Sublime Author” or “Supreme Being,” words he uses not infrequently and with apparent sincerity in the Philosophie zoologique. Lamarck believed in “creation” but not in a simplistic, once-and-for-all creation that would result in a static world. Ever since St. Augustine there had been two schools among the Christians with respect to creation. Lamarck evidently accepted the concept of continuing creation, later espoused by Darwin’s friend Asa Gray. Consequently, he con-

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cidered it rather absurd to think that the Sublime Author should have to look after each detail separately. "Could not his infinite power create an order of things which gave existence successively to all that we see as well as to all that exists but that we do not see?" "Shall I admire the greatness of the power of this first cause of everything any the less if it has pleased him that things should be so, then if his will by separate acts had occupied itself and still continued to occupy itself with the details of all the special creations, variations, developments, destructions and renewals, in short, with all the mutations which take place at large among existing things?" (p. 41). Nature can bring into existence an apparent order among organized beings "from powers conferred by the Supreme Author of all things" (p. 60; a similar statement is made on p. 130). When evolution is thus interpreted as continuing creation, it can be reconciled with the belief in a supreme being.

SPONTANEOUS GENERATION

One consequence of Lamarck's conception of evolution as the movement of organisms on an endless escalator is that the lower reaches of this escalator would be gradually vacated by this upward movement unless there is a steady replenishment at the lowest level. This, Lamarck says, indeed takes place through steady spontaneous generation, a phenomenon he considers so important that he devotes to it an entire chapter (Chapter VI of Part II). Spontaneous generation, according to Lamarck, does not have the power to produce higher organisms.

It is exclusively among the infusorians that nature appears to carry out direct or spontaneous generations, which are incessantly renewed whenever conditions are favorable; and we shall endeavor to show that it is through this means that she acquired power after an enormous lapse of time to produce indirectly all the other races of animals that we know.

"Justification for the belief that the infusorians or most of them owe their existence exclusively to spontaneous generation is found in the fact that all these fragile animals perish during the reduction of temperature in bad seasons" (p. 103). A similar statement is found on p. 40: "Nature began and still begins by fashioning the simplest of organized bodies, and that it is these alone which she fashions immediately, that is to say, only the rudiments of organization indicated in the term spontaneous generation" (see also p. 130).

According to these discussions there had to be a minimum of
two types of spontaneous generation, one which gives rise to infusorians and higher animals and another which originated the plant kingdom. In his famous diagram (p. 179) he admits, however, two roots even for the animal kingdom and says in the text, “in my opinion the animal scale begins by at least two separate branches . . . each of these branches derives existence only through direct or spontaneous generation” (p. 178). One of these starts with the infusorians, which in turn give rise to the polyps and these to the radiates. The other, actually more important, branch starts with “worms.” More detail about this is provided in the *Histoire naturelle* (1815, p. 455). Here Lamarck states firmly that this second line does not pass through an infusorian stage, but “with the help of particular matter (matériaux) found in the interior of already existing animals, she [nature] has given rise to spontaneous generations which are the source of the intestinal worms, among which perhaps certain ones, after having passed to the outside, have given rise to the free-living worms.” The belief in the spontaneous origin of intestinal worms was thoroughly destroyed within a few decades by the brilliant researches of v. Siebold, Küchenmeister, and others on the life cycles of cestodes and trematodes. The work of Pasteur and Robert Koch uprooted the last remnants of a belief in the possibility of spontaneous generation, already undermined by Redi and Spallanzani prior to Lamarck’s day.

### The Origin of Evolutionary Novelties

Lamarck characterizes each “stage of organization” in his series of ever greater perfection by a newly arisen structure or capacity through which it is distinguished from the next lower stage. For instance, he characterizes his Class VI (Arachnids) as having “stigmata and limited tracheae for respiration; a rudimentary circulation”; his Class VII (Crustaceans) as having “respiration by gills; a heart and vessels for circulation,” etc. But how do the more perfect organisms acquire these new structures? About this Lamarck is as explicit as his theory permits him: New environments create new needs; new needs require new efforts and habits; and these, in turn, lead to the production of new structures. By insisting on the primacy of behavior over structure, this would have been a remarkably modern explanation if Lamarck had not believed in the wrong mechanism. At the turn of the twentieth century the mutationists proclaimed the

14. For a historical treatment of the discovery of the reproduction of intestinal parasites, see Foster (1965).
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primacy of structure over behavior by asserting that mutations produce new structures and that thereby the use of these structures is predetermined. Some of Lamarck’s contemporaries seem to have had similar ideas, for he explains: “Naturalists have remarked that the structure of animals is always in perfect adaptation to their functions, and have inferred that the shape and condition of their parts have determined their use.15 Now this is a mistake: for it may be easily proved by observation that it is on the contrary the needs and uses of the parts which have caused the development of these same parts, which have even given birth to them when they did not exist, and which have consequently given rise to the condition that we find in each animal” (p. 113). Elsewhere he states the same principle in these words:

It is not the organs, that is to say, the nature and shape of the parts of an animal’s body, that have given rise to its special habits and faculties; but it is, on the contrary, its habits, mode of life and environment that have in course of time controlled the shape of its body, the number and state of its organs and, lastly, the faculties which it possesses (p. 114).

He repeats this statement, in slightly different words, once more on pp. 127 and 174.

Once it is admitted that habits “control the shape of the body,” it is only a small step to believe in the origin of entirely new structures, owing to entirely new habits: “I shall now prove that the constant use of any organ, accompanied by efforts to get the most out of it, strengthens and enlarges that organ, or creates new ones [italics mine] to carry on functions that have become necessary” (p. 119). This is the section of the Philosophie zoologique which leads to the famous example of the giraffe (p. 122) which acquired a lengthened neck because it had “to make constant efforts to reach” the leaves of trees. In the same way wading birds acquired long legs owing to their “efforts to stretch and lengthen” them (p. 119). As critics have pointed out for the last 150 years, virtually nothing is said, however, as to how these modifications of the phenotype are converted into heritability.

When describing the acquisition of entirely new organs or organ systems, Lamarck often employs a language that is not too different from that which the idealistic morphologists used for their archetypes (pp. 82–83): “Nature attained to the

15. Could he have referred to anyone but Cuvier?
creation of a special organ of digestion," or "she subsequently established a special organ for respiration," or "when afterwards she succeeded in producing the nervous system." From the context it is clear, however, that Lamarck had nothing in mind but the gradual, slow advance toward perfection.

His dogma that the "more perfect" animals are characterized by the acquisition of new faculties and the required executive structures, demands that the newest and lowest of all animals, the infusorians, are devoid of most of the properties of higher organisms. It would be ridiculous, he says, to assume that such imperfect organisms could have any of the higher properties: "If we were to imagine that such animals possess all the organs known in other animals, but that these organs are dissolved throughout their bodies, how absurd such a supposition would be!" (p. 103). One more instance in which Lmarck made the wrong guess!

ASCENDING SCALE AND DEGRADATION

Considering how emphatic Lamarck is about the correctness of the ascending scale, it comes rather as a surprise that in his major discussion of the classification of animals (pp. 61–105) he follows a descending sequence. He entitles his Chapter VI, "Degradation and simplification of organization from one extremity of the animal chain to the other, proceeding from the most complex to the simplest" (p. 68).

In his discussion Lamarck says: "There exists from one end to the other of this chain a striking degradation in the organization of the animals composing it . . . This examination . . . convinces us that all the special organs are progressively simplified from class to class, that they become altered, reduced and attenuated little by little . . . and that finally they are completely and definitely extinguished . . . the degradation . . . is real and progressive, wherever its effects can be seen" (p. 69).

One is tempted to explain this singular contradiction by assuming that Lamarck had changed his ideas in the midst of writing the Philosophie zoologique and that he had maintained the original descending arrangement (customary in contemporary classifications) in Chapter VI and had switched to the newer, ascending order in Chapter VIII. However, such a recent change of mind is contradicted by the fact that he had adopted an ascending series already in his Flore française (1778), which led him from the "least complete" to the "most perfect" plant.

Then why was Lamarck so inconsistent and, more importantly, why did he adopt the descending sequence in his Chapter VI,
which is devoted to an exposition of the types of organization among animals? He nowhere gives a clear answer to this. He implies, but nowhere says so directly, that he adopts the descending sequence for didactic reasons (see p. 1 of the Preface and p. 72). Could it be that it is easier to describe and justify the loss of structures than the acquisition of new structures? I have mentioned above the insufficiency of Lamarck's explanation for this evolutionary phenomenon. He sidestepped this difficulty, presumably unconsciously, by describing the differences in complexity of organization in terms of degradation.\textsuperscript{16}

(2) \textit{Branching evolution and adaptive radiation.}

Lamarck, the philosopher of nature, firmly believed in an ascending linear scale toward perfection. A study of systems of organization in less perfect and more perfect animals had convinced him that all the manifold organizations could be ranked as less perfect or more perfect, and could be arranged in a single series, strictly on the basis of their complexity and without commitment on their actual derivation. It is this "unique and simple series which we are forced to adopt in order to facilitate our zoological studies" (\textit{Histoire naturelle}, 1, p. 451). He asserts dogmatically in the \textit{Philosophie zoologique} that "in each kingdom of living bodies the groups are arranged in a single graduated series, in conformity with the increasing complexity of organization and the affinities of the object" (p. 59).

Alas, the finely graduated scale of perfection of the philosopher does not exist in reality. As early as 1800 Lamarck\textsuperscript{17} points out that he does not really "speak of the existence of a linear series, regular in the intervals between species and genera: such a series does not exist, rather I speak of an almost regularly graduated series of the principal groups ("masses"), such as the great families; a series which assuredly exists, among the animals as well as among the plants; but which, when the genera and particularly the species are considered, forms in many places lateral ramifications, the end points of which are truly isolated." The same idea is stated, in part with identical words, in the \textit{Philosophie zoologique} (pp. 57–59).

The enormous diversity of living beings thus has convinced Lamarck, the naturalist, that "the genuine order of nature, that is to say, that which nature would have carried out if accidental

\textsuperscript{16} The problem of the acquisition of new organs also played an important role in the attacks against Darwin, particularly by Mivart (see E. Mayr, "The origin of evolutionary novelties," in S. Tax, ed., \textit{The Evolution of Life} [1960], pp. 349–380).

\textsuperscript{17} \textit{Discours d'ouverture}, An VIII, p. 29 (Lamarck, "1907").
Ernst Mayr

does not exist in reality. In the Discours of 1800, when Lamarck had just abandoned the dogma of the fixity of species, he limits the lateral ramifications to species and genera, and the same emphasis still seems to dominate the early chapters of the Philosophie zoologique.

A distinct advance in Lamarck's thinking is reflected in the later chapters of the Philosophie zoologique, particularly in a discussion embodied in Additions to Chapters VII and VIII (pp. 173–179). All pretense that branching is limited to genera and species is now given up. Indeed, in his famous diagram (p. 179) he entirely abandons a linear classification. The Infusorians, Polyps, and Radiarians are grouped entirely separately from the lineage that arises from the worms. Again, this line from the worms divides into two major assemblages, one terminating in the insects, arachnids, and crustaceans, the other leading to the annelids, cirripedes, and molluscs. The reptiles again lead to two branches, one giving rise to the birds, the other to the mammals. This diagram is certainly much more easily reconciled with the theory of evolution through common descent than with the scala naturae.

It is not only in the diagram but also in the text that Lamarck speaks quite freely of branching among the higher categories. He says of the aquatic mammals that they "were divided into three branches by reason of the diversity arising in their habits in the course of time; one of these led to the cetaceans, another to the ungulate mammals, and a third to the various known ungulate mammals," and summarizes animal evolution as follows: "This series of animals begins with two branches where the most imperfect animals are found; the first animals therefore of each of these branches derive existence only through direct or spontaneous generation" (p. 178).

Even more branching points are admitted in the Histoire naturelle, particularly among the invertebrates (pp. 451–460). Here Lamarck rather frankly admits that there is no real connection between the molluscs and the fishes (although he places them adjacent to each other in his diagrams). He establishes a new group for the ascidians, which he places provisionally after the radiarians, although he confesses "that they cannot be considered their continuation nor as derived from them" (p. 451). He now admits that the "order" which nature has produced "is anything but simple; it is branched and seems to consist of several distinct series" (p. 452).

Accepting evolution thus forced Lamarck to abandon the
simple series of the *scala naturae*, except as a sequence convenient for teaching and textbook writing. The rapidly increasing knowledge of the comparative anatomy of the invertebrates had forced Cuvier simultaneously also to abandon the single series. Cuvier, however, replaced it by a purely creationist and static set of four "embranchements," while Lamarck's mature arrangements (particularly those of 1815) approach the later concept of the phylogentic tree to a remarkable degree.

From 1800 on Lamarck had recognized two evolutionary processes, "progress in complexity of organization" and "anomalies due to the influence of the environment and of acquired habits" (p. 70). The latter were clearly labeled as "disturbances" in his earlier writings, due to "accidental causes." It would require a far more detailed analysis than I can offer here, but it is my impression that by 1815 the relative importance of the two processes had become reversed in Lamarck's mind. The series of perfection is now reduced to a didactic devise, based on a rational principle; the branching tree, however, reflects what is actually found in nature: "We must thus work on the composition and perfecting of two different tabulations:

One of them represents the simple series which we must make use of in our publications and lecture courses in order to characterize, distinguish, and make known the observed animals. This series we shall base, in general, on the progression which takes place in the composition of animal organizations, considering each one in the ensemble of all of its parts and making use of the precepts which I have proposed.

The other one represents the several particular series, with their simple side branches, *which nature seems to have formed when producing the different animals which actually exist* (*Histoire naturelle*, 1, p. 461) [Italics mine].

The empirical naturalist had finally gotten the better of the philosopher of the scale of perfection. More importantly, the disturbances and accidental causes become a dominant factor in the causation of diversity. "The reason is that nature's work has often been modified, thwarted, and even reversed by the influence exercised by very different and even conflicting conditions of life upon animals exposed to them throughout a long succession of generations" (*Philosophic zoologique*, p. 81; see also p. 107).

The causal sequence in this branching evolution is perfectly clear. The first step is invariably the entering of a new environ-
ment by an organism or a change in the environment at the traditional location. In essentially the same words it is incessantly repeated in the *Philosophie zoologique* (pp. 40, 41, 43, 45, 58, and 114) that "alterations in the environment of animals lead to great alterations in their needs, and these alterations in their needs necessarily lead to others in their activity" (p. 107).

There are special physiological mechanisms which permit converting the new "activities," "efforts," or "habits," as they are variously called by Lamarck, into structural changes. This is explained in the Preface (p. 2) of the *Philosophie zoologique*. Changes of habits cause changes in the movements of the fluids in the soft parts of organisms, and this results in a modification of the cellular tissues. These, as we now know, totally unsupported speculations are explained further in Part II (Physiology) of the *Philosophie zoologique*. These processes merely lead to changes in what we would now call the phenotype and are of no particular interest to the evolutionist.

Like Darwin's theory of pangenes, Lamarck's physiological interpretations are evidently influenced by his belief in the effects of use and disuse. Such a belief goes all the way back to antiquity (Zirkle, 1946) and is still widespread in our folklore. We know what an important role use and disuse played in Darwin's thinking. As I pointed out in the preface to the facsimile edition of the first edition of the *Origin of Species* (p. xxvi), Darwin invoked use and disuse on no less than thirteen pages. Lamarck does so on pp. 2, 12, 105, 107, 108, 112, 113, 115, 116, 118, 119–126, and 170 of the *Philosophie zoologique*. Much of this is based on extremely astute observations by an excellent naturalist, and that Lamarck surely was. Indeed, many of his explanations are surprisingly similar to those of Darwin. By attributing the presence of rudimentary organs to disuse (p. 115), he explains quite rationally, although incorrectly, what was such an obstacle for the argument from design. All the modern biologist has to do is to adopt natural selection as the agent through which disuse is converted into structural reduction, and most of Lamarck's statements become quite reasonable.

There is little difference between Lamarck and the modern evolutionists in giving the environment an exceedingly high rating as the major causal factor in evolution, but there is a radical difference in the mechanisms by which the environment is effective. Lamarck's conceptualization provided him with no opportunity to utilize natural selection. In spite of his nominal-
istic emphasis on the existence only of individuals, not of species or genera, Lamarck unconsciously treated these individuals as identical, hence typologically, just as an essentialist would. All of his statements on the impact of the environment are phrased in typological language: "As changes occur in the environment . . . corresponding changes in the animals likewise occur" (p. 109).

If a given environment induces very specific needs, Lamarck postulates that different organisms entering this environment will respond with the same activities and efforts and thus acquire similar structures and adaptations. Here was an opportunity for Lamarck, the experienced zoologist, to test his theory. For instance, when he cites the sloth (Bradypus) as an animal which, owing to its arboreal locomotion, leaf-eating habits, and existence in the hot tropics, has acquired all sorts of adaptations, including extreme slowness of movement, he should have asked himself whether other equally tropical and arboreal mammals with similar food habits, such as the leaf-eating monkeys, had become sloth-like. He would have found out that they acquired entirely different adaptations and have remained quick and lively. Would he then still have maintained his conclusion that different organisms respond to the same environment in the same way?

INHERITANCE OF ACQUIRED CHARACTERS

It is not enough in evolution for an individual to acquire certain modifications, let us say, by the increased use of certain muscles. The crucial point is the transfer of his new acquisition to his offspring. This is the sine qua non of the evolutionary process, and it is precisely this problem which Lamarck sidestepped. Whenever (in the Philosophie zoologique) Lamarck invokes the principle of an inheritance of acquired characters, he remains strangely silent about the mechanism by which the transmittal takes place. The most explicit statement is found on p. 124, where he makes this claim:

"Now every change that is wrought in an organ through a habit of frequently using it, is subsequently preserved by reproduction, if it is common to the individuals who unite together in fertilization for the propagation of their species. Such a change is thus handed on to all succeeding individuals in the same environment, without their having to acquire it in the same way that it was actually created." References to the inheritance of acquired characters on pp. 6, 11, 108, 109, and 175 are even less revealing. The inheritance of acquired charac-
ters is simply stated as a universally accepted principle, without a word on the mechanism of this inheritance. Lamarck considers this principle of such importance that it is stated as his Second Law (p. 113):

“All the acquisitions or losses wrought by nature on individuals . . . are preserved by reproduction to the new individuals which arise, provided that the acquired modifications are common to both sexes, or at least to the individuals which produce the young.”

LAMARCK’S CONCEPTUAL FRAMEWORK

It has often been remarked how different Lamarck’s philosophy is from that of such contemporary essentialists as Linnaeus (+1778) and Cuvier or from the later population thinking of Darwin. Indeed, it largely belongs to a seventeenth-eighteenth century tradition which by now has been completely superseded. Many of its elements are lucidly described in Lovejoy’s *Great Chain of Being*. Leibniz surely had a considerable impact on the development of this kind of thinking, but it is rather more likely that Lamarck’s Leibnizism is second-hand. I wonder whether Lamarck ever read any of Leibniz’s work. It will require considerable further research to determine which eighteenth-century authors, in addition to Buffon, had the greatest influence on the development of Lamarck’s philosophy.

Its elements include the following:

*Evolutionism* (see fn. 2 above): Lamarck’s rejection of a static world has been discussed above (p. 6).

*Anti-essentialism*: In an age which—at least on the European continent—was dominated by essentialism (see fn. 3 above), Lamarck was an avowed anti-essentialist. He consistently emphasized all the things which the essentialists ignored, such as continuity, the absence of gaps, change (and slow, gradual change at that!), the role of the environment, the absence of archetypes, the composition of classes (individuals, not types), the steady movement of levels of organization, and related ideas.

*Uniformitarianism*: His anti-essentialism was, one might say, automatically responsible for his uniformitarian views in geology (Carozzi, 1964; Hooykaas, 1959). Lamarck’s thinking was strangely unaffected by the rising tide of catastrophism around him. This presumably had various reasons. One is his faith in the potency of general laws that are responsible for events taking place in an orderly fashion and not by cataclysms. The
other reason is that Lamarck, presumably following Buffon, had rejected the dogma of the recency of the earth (about 6,000 years, according to most earlier authors) and postulated an extremely high age (see below). This permitted an explanation of even the most conspicuous features of the landscape as the result of gradual and slow processes. It may well be that Lyell’s uniformitarianism was more influenced by that of Lamarck than he himself realized. If this were the case, Darwin would also have been affected (via Lyell).

GRADUALNESS, CONTINUITY, AND PLENITUDE

Like many eighteenth-century authors, particularly the followers of Leibniz, Lamarck believed in the principle of plenitude, according to which “the range of conceivable diversity of living things is exhaustively exemplified” (Lovejoy, 1936). Any type of organism that is conceivable must exist, and the diversity of types must form a complete continuum without borders or gaps. Lovejoy has shown convincingly how pervasive this concept was in the seventeenth and eighteenth centuries and what formidable difficulties it created for its adherents. After all, the world is full of evident gaps and discontinuities, which require to be reconciled with the principle of plenitude. This cannot help but lead to contradictions, of which Lamarck’s work provides numerous illustrations (particularly with respect to extinction, see below). On the positive side, the principle of plenitude is far more suitable as a basis for evolutionism than is essentialism, and it was clearly one of the inspirations for uniformitarianism, which through Lyell had such an impact on Darwin.

One of its important consequences is the belief that “Natura non facit saltus,” an insight which is responsible for Lamarck’s constant reiteration of the slowness and gradualness of evolution.

“With regard to living bodies, it is no longer possible to doubt that nature has done everything little by little and successively” (p. 11). Speaking of the originally aquatic animals, “nature led them little by little to the habit of living in the air, first by the waters edge, etc.” (p. 70).

A direct consequence of the imperceptibility of evolutionary change is that it must have been extremely slow. This, indeed, is emphasized by Lamarck again and again; for instance:

“These changes only take place with an extreme slowness, which makes them always imperceptible.” (p. 30); “the imperceptible changing of species” (p. 43); “it is difficult to deny that the shape or external characters of every living body what-
ever must vary imperceptibly, although that variation only becomes perceptible after a considerable time" (p. 45). With reference to the evolution of thinking in man: "Not only is this the greatest marvel that the power of nature has attained, but it is besides a proof of the lapse of a considerable time; since nature has done nothing but by slow degrees" (p. 50). "An enormous time and wide variation in successive conditions must doubtless have been required to enable nature to bring the organization of animals to that degree of complexity and development in which we see it at its perfection" (p. 50). For nature, "time has no limits and can be drawn upon to any extent" (p. 114).

Few other authors, if any, insisted with equal persistence on the enormous time available for evolutionary changes and indeed required by them. This is why Lamarck was not in the least fazed by the discovery that the mummified animals found in the Egyptian tombs had not visibly changed in some 4,000 years. Darwin, who likewise postulated an extremely high age of the living world, is strictly in the Lamarckian tradition, as compared to the catastrophists, who tended in their chronologies to stay far closer to a literal interpretation of Genesis.

EVOLUTIONARY CONTINUITY AND THE SHARP DELIMITATION OF TAXA

According to the principle of plenitude, as well as on the basis of evolutionism, there should be no sharp discontinuities in nature. Yet, every student of diversity, certainly from the seventeenth century on, observed that "bridgeless gaps" between species and higher taxa were universal. The essentialists—Linnaeus, for instance (Mayr, 1957), solved this problem by declaring all species as tied and static. The evolutionists were deeply troubled by it, and Darwin's ambivalent treatment of the species (Mayr, 1959c) can in part be explained by this dilemma.

The difficulty, however, is not limited to the species level. Another set of problems arises at the level of the higher taxa. Lamarck tries to ignore these difficulties as much as possible. He describes classes, orders, families, and genera as "artificial


19. This is no longer a problem for the modern evolutionist. Theories of geographic speciation and speciation by polyploidy have demonstrated that there is no contradiction. A discontinuity between populations and incipient species can be established without an interruption of the continuity of the lines to which they belong (Mayr, 1970).
devices in natural science" (p. 20). "Nature has not really formed" such higher taxa, "but only individuals" (p. 21). Taxonomists have struggled with such conflicts for another 150 years, and it is only within the last decade or two that the true source of the trouble has been clearly recognized (Mayr, 1969).

When a terminological distinction is made between taxa (zoological groups, like birds, bats, or beetles) and categories (the rank of the groups, e.g., family, order, class), it becomes clear that taxa are often well-defined and sharply delimited, while ranking in the taxonomic hierarchy is nearly always somewhat subjective, which makes the categories "artificial devices," as Lamarck had rightly said.

Even Lamarck was unable to conceal the fact that there are major gaps in nature:

It may be said that an immense hiatus exists between crude matter and living bodies, and that this hiatus does not permit of a linear arrangement of these two kinds of bodies, nor of any attempt to unite them by link, as has been vainly attempted.

All known living bodies are sharply divided into two special kingdoms, based on the essential differences which distinguish animals from plants, and in spite of what has been said I am convinced that these two kingdoms do not really merge into one another at any point, and consequently that there are no animal-plants, as implied by the word zoophyte... nor plant animals (p. 51).

However, he claimed, when it comes to the animal kingdom as such, there are no natural gaps, no genuine lines of demarcation. All lines of demarcation "except those... resulting from gaps to be filled... always will be arbitrary and therefore changeable" (p. 57). By adopting certain principles, "it is possible to draw boundaries between each system, in such a way that there is only a small number of animals near the boundaries," even though "nature does not pass abruptly from one system of organization to another."

When discussing the ten classes of invertebrates recognized by him (p. 66), he insists dogmatically that "races may, nay must, exist near the boundaries, halfway between two classes."

He has to make either of two possible assumptions to explain the absence of these postulated intermediates. One is that they will still be discovered in some remote part of the world (see below); the other that they are represented in the fossil state:

It is true, especially in the animal kingdom, that several of
[its sub-] divisions appear to be really marked out by nature herself; and it is certainly difficult to believe that mammals, birds, etc., are not sharply isolated classes formed by nature. This is none the less a pure illusion, and a consequence of the limitation of our knowledge of existing or past animals. The further we extend our observations the more proofs do we acquire that the boundaries even of the apparently most isolated classes, are not unlikely to be effaced by our new discoveries. Already the *Ornithorhynchus* and the *Echidna* seem to indicate the existence of animals intermediate between birds and mammals" (p. 23).

As a consequence, all borders which we establish between higher taxa are entirely artificial. "... the complete series of beings making up a kingdom represent, the actual order of nature ... the different kinds of divisions which have to be set up in that series to help us distinguish objects with greater ease do not belong to nature at all. They are truly artificial" (p. 33). "... existing animals ... form a branching series, irregularly graded and free from discontinuity, or at least once free from it. For it is alleged that there is now occasional discontinuity, owing to some species having been lost" (p. 37).

It is worth noting that all these confident statements on actual or suspected continuity between higher taxa are in the first 67 pages of the *Philosophie zoologique*. One has the impression that Lamarck is less sure of this gapless continuity in the later chapters and conspicuously less so in the *Histoire naturelle* (1815). As Carozzi20 has remarked for the *Hydrogéologie*, Lamarck often seems to have changed his ideas while writing a book, without ever going back over the earlier chapters. There certainly are ample indications that he changed his ideas concerning the continuity of the animal series in the decade and a half after the publication of the first Discours d'Ouverture (1800).21

**EXTINCTION**

Extinction was a real problem for many of the natural


21. Cuvier was in rapid ascendancy in the period from 1800 to 1815, and he and his followers presumably criticized Lamarck with an increasing feeling of superiority. It would be interesting to make a careful comparison of the *Histoire naturelle animaux sans vertèbres* of 1815 with the earlier chapters of the *Philosophie zoologique* of 1809 to see how many of his earlier ideas Lamarck had dropped in the meantime.
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philosophers of the eighteenth and early nineteenth centuries. We still lack a comprehensive treatment of the conflicting currents of thought dealing with this problem. If one believes in plenitude and in a marvelous capacity of nature for adaptation, as did Lamarck, one cannot really allow for extinction. Hence he insisted: "I am still doubtful whether the means adopted by nature to ensure the preservation of species or races have been so inadequate that entire races are now extinct or lost" (p. 44).

There are four explanations, none of them allowing for "natural extinction," that were advanced by various naturalists during this period.

(1) Extinct animals are those that were killed by the flood or some other great catastrophe. The most awkward aspect of this explanation was that so many of the extinct fossil species were aquatic. Lamarck, very decidedly, and for a number of reasons, rejects this explanation (p. 46). Instead, he advances several others.

(2) The supposedly extinct species might well be surviving in as yet unexplored portions of the globe.

Lamarck expressed this as follows: "There are many parts of the earth's surface to which we have never penetrated, many others that men capable of observing have merely passed through, and many others again, like the various parts of the sea-bottom, in which we have few means of discovering the animals living there. The species that we do not know might well remain hidden in these various places" (p. 44).

(3) The same species, the remains of which we find as fossils, still exists, but their outward appearance has changed so drastically that we no longer recognize them as the same.

"May it not be possible . . . that the fossils in question belonged to species still existing, but which have changed since that time and become converted into the similar species that we now actually find" (p. 45).

Louis Agassiz in his writing was a vigorous proponent of this idea. The problem requires far more research, but it seems that there may have been quite a fundamental difference between Lamarck's and Agassiz's interpretations. Agassiz was an essentialist and it gave him no trouble to conceive of a drastic alteration of the outward appearance without any change of the underlying essence. It is very obvious that Lamarck, who was not an essentialist, had a genuine evolutionary change in mind. However, since his evolution was largely a matter of the con-
tinuation of the various phyletic lines, "extinction" simply meant the preservation in fossilized condition of earlier ancestral states of still existing lines.

(4) Extinction is the work of man.

Finally, extinction might be due to man. "If there really are lost species, it can doubtless only be among the large animals which live on the dry parts of the earth; where man exercises absolute sway, and has compassed the destruction of all the individuals of some species which he has not wished to preserve or domesticate" (p. 44).

These are prophetic words! Even though man has nothing to do with extinction prior to the Pleistocene, it has become increasingly apparent during the past twenty years that the extinction of so many species of large mammals and flightless birds in the late Pleistocene and post-Pleistocene periods might well have been man's work (Martin et al., 1967). Man clearly was and still is an important agent of extinction. Lamarck was perhaps the first author to appreciate this possibility to its fullest extent.

LAMARCK'S MINOR CONTRIBUTIONS

There is perhaps no better way to prove that Lamarck was not merely an out-of-the-world philosopher but also an observant naturalist than to call attention to some overlooked contributions of his which indicate that he was often well ahead of his time.22 The history of none of these subjects has been written, and it is impossible to say whether Lamarck was the first ever to pronounce certain principles, or—as is more likely—only an early adherent. It is not my intention to hunt for priorities, but it adds to our appreciation of Lamarck to know how many perceptive observations he had made. Otherwise they might well remain unnoticed by the non-zoologist.

(1) Adaptation and the Role of the Environment

No writer prior to Lamarck appreciated as clearly the adaptive nature of much of the structure of animals, particularly the characteristics of families and classes. Even though he reiterated forever his statements on "growing perfection" and "increasing complexity," he nevertheless fully realized that the nature of evolution was dual and that an irregular phenomenon of ad hoc adaptation was often superimposed on the linear trend of increased perfection.

22. See Carozzi (1964) for Lamarck's pioneering contributions to geology.
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Lamarck's detailed presentation of his views on adaptation given on p. 58 of Philosophie zoologique were already cited above (under branching evolution), but he repeats these assertions in Chapter VI (p. 69), where he emphasizes once more that those differences between animals that are not a result of the linear scale of perfection are due to the influence of the different environments in which organisms live. “The environment everywhere produces variations in them. This is the special factor which occasionally produces in the course of the degradation...the often curious deviations that may be observed in the progression.

“It is obvious that, if nature had given existence to none but aquatic animals and if all these animals had always lived in the same climate, the same kind of water, the same depths, etc., etc., we should then no doubt have found a regular and even continuous gradation in the organization of these animals.” And then he observes that there are all kinds of water in all kinds of climates and “these provide as many special conditions which each act differently on the animals living in them. Now the races of animals exposed to any of these conditions have undergone special influences from them and have been varied by them all the while that their complexity of organization has been advancing” (p. 69).

Lamarck's critics have tended to stress the invalidity of his explanatory mechanisms while ignoring his observations on adaptation. By doing so, they have failed to notice that Lamarck was far ahead of the contemporary essentialist morphologists in recognizing that the particular conformation of the morphology of a kind of animals was neither an accident of nature (“lusus naturae”) nor the result of the inscrutable design of the creator, but the product of an analyzable interaction between structure and environment. In that sense Lamarck quite clearly was a forerunner of Darwin, who based much of his argument on that same relationship between structure and [in his case the selective factors of] the environment.

(2) Mosaic evolution

If the essentialist morphologist admits any “evolution” whatsoever, he can visualize it only as an unfolding (evolutio sensu stricto) of preexisting potentialities. A type evolving in this sense must evolve “harmoniously.” All parts, claims the essentialist, tend to retain the same position in relation to each other and change at the same rate. In reality this is not at all the way in which an evolutionary line evolves. Certain key structures are invariably the first to respond to new selection pressures while
others may lag way behind. Paleontologists, from Dollo on (Gould, 1970), have known this, although the term “mosaic evolution” for this irregular evolutionary advance (DeBeer, 1954) is quite recent. It comes as somewhat of a surprise to find that Lamarck was fully aware of this principle: “The organs that have little importance or are not essential to life are not always at the same stage of perfection or degradation; so that if we follow all the species of a class we shall see that some one organ of any species reaches its highest degree of perfection, while some other organ, which in that same species is quite under-developed or imperfect, reaches in some other species a high state of perfection” (p. 58). Not being an essentialist, Lamarck had much less trouble in perceiving the truth than most morphologists of the ensuing 100 years. An outstanding human anatomist told me only a few decades ago that Australopithecus could not possibly be ancestral to Man because it was a “disharmonious type,” some structures “already” being almost as in man, while others were “still” essentially those of an ape! Since Lamarck did not postulate the existence of ideal types, he did not need to insist on the “harmonious” development of the type.23

(3) Competitive exclusion

One of the most frequently discussed principles of modern evolutionary ecology is that of “competitive exclusion.” According to this principle, no two species can coexist in the same area for any length of time if both compete for exactly the same resources of the environment. It is still being argued whether or not exceptions to this principle occur (Mayr, 1970). This much is certain: the principle has considerable heuristic value and has led to many valuable investigations.

It is evident that Lamarck was not unaware of competitive exclusion. In his description of human evolution, for instance, he writes, “We can easily conceive:

1. That this race having obtained the mastery over others through the higher perfection of its faculties will take possession of all parts of the earth’s surface, that are suitable to it;

2. That it will drive out the other higher races, which might dispute with it the fruits of the earth, and that it would compel them to take refuge in localities which it does not occupy itself” (p. 170).

23. One more point where Lamarck’s ideas were almost diametrically opposed to those of Cuvier, who stressed co-adaptation to an extreme extent. Cuvier would have found it very difficult to accept a drastically different rate of evolution for different structures of the same organisms.
A competing species, according to Lamarck, thus is a powerful factor in evolution and can influence the evolution of any other species that might be in competition with it. Although he was seemingly aware of the principle, Lamarck apparently did not apply it to evolutionary change in any animal species.

(4) **Darwin's principle**.

Good taxonomists have long been aware that not all characters are of the same value as clues for relationship. Indeed, there are now a number of empirical rules available (Mayr, 1969, pp. 220-226) which help the taxonomist in weighting taxonomic characters. One principle which Darwin (1859, p. 414) particularly stressed is that characters of an animal taxon acquired as a result of specialized habits are less suitable to indicate broad relationships than characters that are not ad hoc specializations for highly specific conditions of the external environment. Lamarck, apparently, was aware of this relationship. When speaking of deviations from the scale of perfection, he said: “These irregularities in the perfection and degradation of inessential organs are found in those organs which are the most exposed to the influence of the environment; this influence involves similar irregularities in the shape and condition of external parts” (p. 59). However, such “irregularities in . . . the inessential organs” do not affect the basic organization of organisms, and their classification into higher taxa can and must therefore be based on the essential organs. In other words, adaptive specializations vary greatly from species to species (or genus to genus), while the important internal organs, such as heart, lungs, kidneys, or nervous system remain largely the same within a major higher taxon.

(5) **Man and his evolution**

Man is included by Lamarck in the evolutionary series without hesitation and without reservations. Man “assuredly presents the type of the highest perfection that nature could attain to: hence the more an animal organization approaches that of man the more perfect it is” (p. 71). Since evolution is a continuing process, man will continue to evolve. “This predominant race, having acquired an absolute supremacy over all the rest, will ultimately establish a difference between itself and the most perfect animals, and indeed will leave them far behind” (p. 171). It is this thought, expanded and elaborated, which is a dominant theme in Teilhard de Chardin’s thinking.

24. Similar thoughts were expressed by Buffon and can perhaps be traced back to antiquity.
ERNST MAYR

Even though man has now acquired certain characteristics not found in any animal or at least not to a similar degree of perfection, nevertheless man shares most of his physiological characteristics with the animals and these, very often, are more easily studied among animals than in man. In order to achieve a full understanding of man, it is therefore "necessary to try to acquire knowledge of the organization of the other animals" (p. 11). Aristotle had recommended the same strategy.

THE VERDICT ON LAMARCK

At the height of the fight between Neo-Darwinism and Neo-Lamarckism, everybody was a partisan, he was either for or against Lamarck. This fight is now a matter of history since the Darwinian interpretation of the causal explanation of evolution has gained a total victory; it is now accepted by every well-informed biologist. But does this relegate Lamarck to a negligible role in the history of biology? Far from it! His contributions to the classification of the invertebrates alone secure him an honored name for all time. But merely to give him credit for his achievements as a competent descriptive zoologist and to consider him a failure as a generalizer does not do him justice at all, for a number of reasons.

First and foremost, because it was Lamarck who in defiance of the Zeitgeist preserved and propagated a set of ideas unpopular among creationists, catastrophists, and essentialists. Curiously, Lamarck was often most right where he most differed from prevailing ideas, such as in his support of evolutionism and uniformitarianism, while the errors he is best remembered for, like use and disuse, the inheritance of acquired characters, and much of his physiology, were not at all original with him but represent widely held ideas merely adopted by Lamarck.

Darwin always stressed how little he owed to Lamarck (Rousseau, 1969). In a letter to C. Lyell (October 11, 1859) he said of Lamarck's work, "I got not a fact or idea from it." This may well be true, as far as the causal explanation of evolution is concerned, as well as for providing evolutionary facts which Darwin might have quoted. Lamarck's approach was Cartesian (deductive), and he virtually never supplied detailed factual evidence in support of his sweeping generalizations. But I suspect that Darwin vastly underestimated the role which Lamarck had played in preparing the intellectual climate for the subsequent Darwinian advances.

In an age still largely dominated by a belief in literal creation—a concept not at all unpalatable to most essentialists—La-
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Lamarck's daring and iconoclastic speculations could not help having considerable impact. Lyell's preoccupation with Lamarck is telling evidence for this. And a good case can be made for the thesis that Lyell's uniformitarianism owed much to Lamarck (see above; also Gillispie, 1959:266). I have pointed out above how important Lamarck's championship was also of such ideas as adaptation, the role of the environment, the length of time available for evolution, and, most of all, his consistent evolutionism.

Lamarck's evolutionism had numerous serious deficiencies, as pointed out by his critics then and now. Nevertheless, it is conceivable that, if Lamarck had had the personality to found a school, his theories might have become the starting point of an improved evolutionary interpretation. What was most needed was the proposal of a feasible mechanism (or system of mechanism). However, Lamarck had no disciples to rebuild the foundation that he had laid. It was also his misfortune to have to live in the shadow of such a giant as Cuvier (twenty-five years his junior!). There was no common meeting ground between the evolutionist-uniformitarian-nominalist ideas of Lamarck and the essentialist philosophy which dominated Cuvier's thinking on all subjects (catastrophism, embranchements, etc.). A head-on collision between the representatives of these two so utterly different philosophical systems was inevitable, and it was this rather than any zoological disagreements that was responsible for Cuvier's hostility toward Lamarck.

Lamarck supported rather uncritically a number of ideas that go far back in human history. These include a belief in the inheritance of acquired characters, the importance of the use or disuse of structures, and the existence in the organic world of a built-in tendency toward ever greater perfection. By his championship of such "folklore" ideas Lamarck had an unexpectedly large influence, particularly outside of science. Some aspects of Lysenkoism in Russia as well as the books of Teilhard de Chardin can be traced back to Lamarckian ideas. How direct this influence was and how important Lamarck's support was for the respectability of these ideas are questions that are still unanswered.

I enumerated above some of Lamarck's zoological generalizations, which document what an astute and original observer he was. Originality is less evident in his philosophical ideas. It will require a thorough comparative study of the writings of the philosophers and naturalists of the seventeenth and eighteenth centuries to determine to whom Lamarck owes a particular debt.
for such concepts as scale of perfection (directionism), plenitude, role of the environment, movement of fluids, competition, organization, and other concepts and principles that were integral components of his system. Like all major figures in the history of ideas, Lamarck was both the endpoint of a long antecedent history as well as the starting point of new developments.

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