Louis Agassiz and the Species Question

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On the centenary of the *Origin of Species,* Ernst Mayr published a vigorous essay exploring the reasons for Louis Agassiz's opposition to Darwinism.[1] Mayr presented evidence to suggest that in his youth Agassiz was indoctrinated with "lofty fallacies of idealistic philosophy,"[2] which found expression in his famous claim that a species is a thought in the mind of God. This typological concept of species, a version of the Platonic *eidos,* is supposed to have made it impossible for Agassiz to accept evolution, and even, on occasion, to have warped his powers of observation. Mayr's analysis is widely recognized as having importance as an illustration of the phenomenon of scientific belief; it deserves scrutiny in the light of evidence appearing during the past twenty years.

In the years since 1959, evidence supporting a different interpretation has been accumulating. Edward Lurie has published a sensitive and scholarly biography, William Stanton has examined the American debate on the races of mankind in which Agassiz was embroiled, Elmer C. Herber has shown us the letters Agassiz exchanged with another museum-builder, and Edward O. Wiley has studied some of the fish first named by Agassiz. My own concern with the ideas behind the founding of the Museum of Comparative Zoology has led me to reread Agassiz's "Essay on Classification," and to conclude that his view of species was more interesting and complex than the label "typologist" suggests. Certainly, he tended to minimize facts that did not accord with his expectations, but Mayr's claim that preconceived ideas forced Agassiz into biological absurdities can be questioned. Agassiz did cherish a high standard of scientific reasoning and objectivity, which he felt, with some justification, that evolution did not meet, but the stubbornness with which he main-

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tained his opposition to Darwinism seems to me above all a reflection of his personality, not his philosophy.

A modified view of Agassiz is worth developing, it seems to me, not for the sake of his own reputation—surely the dead care nothing for our opinion of them—but because the history of a science always forms part of the self-image and justification of living scientists. Anyone who understands the modern biological species concept, in all its subtlety and power, can see the folly of Agassiz's claim that only individual organisms are real, with species having no more existence than the genera and orders by which they are classified. If Agassiz's blindness to the virtues of Darwinism, indeed to the relationship between fish collected from the same school, grew out of a set of ancient religious and philosophical beliefs, then we may congratulate ourselves that we share none of these dangerous prejudices. We may comfort ourselves that we will be unlikely to drift so far from the mainstream of scientific progress as he did. I think such self-assurance would be a delusion. Authoritarianism and the unwillingness to entertain alternative explanations, which were so characteristic of Agassiz, and which are never conducive to the pursuit of truth, are not the product of any particular set of ideas, but are human failings to which all of us are prone.

The Difficult Road of True Science

Louis Agassiz thought of himself as an exemplary modern scientist, sophisticated in his awareness of the demands of scientific method. Recalling his own development, Agassiz saw in his career a lesson on the proper role of fact-collecting and theorizing in science. "At first, when a mere boy . . . my highest ambition . . . was to be able to designate the plants and animals of my native country correctly by a Latin name . . . . I did not then know how much more important it is to the naturalist to understand the structure of a few animals."[3] During medical studies at Zurich and Heidelberg, biological subjects occupied his full attention, but at Munich he attended lectures of the *Naturphilosophen* Schelling and Oken, as well as continuing his medical studies.

> My experience in Munich [1827-30] was very varied. With the embryologist Döllinger I learned to value accuracy of observation . . . . Among the most fascinating of our professors was Oken . . . [who could construct] the universe out of his own brain, deducing from *a priori* conceptions . . . . The temptation to impose one's own ideas upon nature, to explain her mysteries by brilliant theories rather than by patient study of the facts as we find them, still leads us away. . . . He is the truest student of nature who . . . admits that the only

true scientific system must be one in which the thought, the intellectual structure, rises out of and is based upon facts .... He is lost, as an observer, who believes that he can, with impunity, affirm that for which he can adduce no evidence.[4]

Agassiz admitted that he had been entranced by Oken and Schelling, and the seeds of some of his later favorite ideas may undoubtedly be sought in their influence, but his own feeling was that he had soon grown beyond the fantasy of *Naturphilosophie,* while benefiting from the enlarged understanding that science is not the mere accumulation of information, but the search for solutions to great problems.

As Mayr and Lurie have pointed out,[5] the evolutionary ideas that Agassiz encountered in the 1830s—Oken's transcendental unification of all life, Lamarck's progressive chain of transmutation, and Geoffroy St.-Hilaire's morphological transformation of insect into vertebrate—were all so highly speculative that few experienced naturalists could take them seriously. Agassiz was in Paris in the early 1830s when Geoffroy St.-Hilaire's morphology was debated by Cuvier in the Académie des Sciences. Cuvier countered with no alternative theory, but with an insistence that any theory be checked against carefully determined facts. Agassiz was attracted to Oken and to comparative morphology, but he saw Cuvier's approach as more scientific and considered him henceforth his prototype.[6]

The next fifteen years, during which Agassiz traced the succession of fossil fishes and developed the theory of the Ice Age, did nothing to alter his rejection of evolution. Fossils did not, after all, fall into the smooth progression with transitional forms that a Lamarckian would expect. When the paleontologist Adam Sedgwick informed Agassiz, in 1845, that "The opinions of Geoffroy St. Hilaire and his dark school [a new book on evolution had just appeared, the anonymous *Vestiges*] seem to be gaining some ground in England," Agassiz shared Sedgwick's feelings of dismay. He felt alarm and dread, he wrote back, of "arid" *Naturphilosophie* in all its forms and also of "religious fanaticism" that would "prescribe to scientific men what they are allowed to see or to find in Nature. Between these two extremes it is difficult to follow a safe road. The reason is, perhaps, that the domain of facts has not yet received a sufficiently general recognition, while traditional beliefs still have too much influence upon the study of the sciences."[7]

Upon his arrival in America the next year, Agassiz met and came to admire[8] Samuel George Morton, whose painstaking accumulation of facts was leading him to ideas about the history of mankind that offended traditional religious beliefs. Morton's extensive evidence that human skulls showed constant differences according to race,[9] and that the same racial distinctions could be traced back thousands of years in skulls from Egypt and pre-Columbian America, flew in the face of the Christian belief that all men were descended from Adam and Eve. The bold assertion of Josiah C. Nott that the so-called races of man must be viewed scientifically as separate species, in spite of their ability to cross-breed and produce fertile offspring, stimulated Morton to reconsider the definition of species in biology. He learned that fertile hybrids between what unquestionably were good species do occur and concluded that interbreeding was no proof that the human races are not distinct species.

In Europe, Agassiz had been content to regard mankind as a single species, unique in its worldwide range, as in so many other ways. But as soon as he learned from Morton that racial characteristics had remained constant over thousands of years and over wide ranges of climate, Agassiz realized that to insist that mankind was nevertheless descended from one common ancestor would be to demonstrate evolution. Many genera of animals and plants include species that differ no more from one another than do the races of mankind. The scientist struggling to keep to the narrow road of fact-based inference, pulled aside neither by speculative philosophy nor religious dogma, was put in a peculiar position by the question of the unity of man, because, in this case, both the evolutionists and the fundamentalists were pulling in the same direction—for the unity of the human species. Unquestionably, his rethinking was also influenced, as Stanton and Lurie have pointed out, by his revulsion at the thought that the black people he saw in America could be kin to himself.[10] Agassiz was rather prone to the fallacy that because he was a scientist, his opinion on every issue was a scientific one. But Morton seemed to be the very pattern of the unbiased observer of facts, slow to theorize, attentive to detail. Agassiz's announcement in favor of the multiplicity of human species was made in the name of scientific objectivity.

Agassiz had evidently never before reflected upon the difficult business of defining species, treating them rather as primary facts of experience. The naturalist simply observes that certain forms remain constant, if he is careful to discount differences in character resulting from differences of age or sex. He criticized colleagues who would treat as one species fossils that could be sorted, according to perfectly constant if slight differences, into two or more species. Agassiz had no sympathy with the pious assumption that all plants and animals were descended from original pairs, and he declared it inconsistent with the facts of geographical distribution. Rejecting the ability to interbreed as a criterion for specific distinctness, Morton proposed his own definition of species:

"primordial organic form." "Bravo, my dear Sir!" wrote Agassiz to Morton, "you have at last furnished science with a true philosophical definition of species."[11] Agassiz liked Morton's definition because it contained no unprovable assumptions about creation or common descent. Pointing to the horse, ass, and zebra, or the black bear, polar bear, and grizzly bear, Agassiz declared: "The ground upon which these animals are considered as distinct species is simply the fact, that, since they have been known to man, they have always preserved the same characteristics."[12] We can recognize these species, and we observe that their characters remain constant generation after generation, Agassiz thought.

This approach to species, which was mere common sense to Agassiz, but seems to us riddled with circular reasoning, was exemplified in his 1850 descriptions of fishes he had collected in Lake Superior. There he followed standard taxonomic practice, giving thorough descriptions of each species that was new to science. He would give a scholarly discussion of what was already known of a particular kind of fish, and point out various ways in which the ones he found seemed to differ. He closely examined the teeth, the gill-arches, the scales, and the number of bony rays in the fins. All such description, however, was not meant to prove that the difference was great enough to justify giving a fish a new name, but rather to enable other ichthyologists to decide whether a specimen they might have before them was Agassiz's species or some other. No rule stated how much difference had to exist; the question was rather whether any differencs that did exist were found consistently. This could only be found out by experience.

In this study, Agassiz treated varieties as taxonomic errors to be corrected either by combining them into one species or discovering by closer study the constant character differences that reveal them to be distinct species.

> The species common to a fauna are subject to individual variations which run over the whole range of the species. ... In a series of more than forty individuals of the yellow perch of America, we can no longer trace the limits of separation between the *Perca granulata, serratogranulata, acuta* and *gracilis*, which all belong as mere varieties to the *P. flavescens* .... The species [of the minnow family] ... appear to be mere varieties. These difficulties occur also in all genera which have numerous species ... but, far from impressing naturalists merely with the monotony to be overcome, they should render them attentive to the most minute details which characterize, in a permanent manner, natural groups in the animal kingdom.[13]

But it would be wrong to imagine that Agassiz's "Fishes of Lake Superior" was merely a series of descriptions of new species. The accepted method was first to characterize the entire family and then the genus to which each species belonged, and Agassiz did this carefully and thoughtfully. He raised questions about the relative systematic position a group should occupy, its relationship to fossil groups, patterns of geographic distribution, and taxonomic inferences to be drawn from its embryology.

The Essay on Classification

With encouragement from friends and colleagues, Agassiz in the 1850s considered himself the leading zoologist in America. Asa Gray, James Dwight Dana, Spencer Fullerton Baird, and even the profound Jeffries Wyman had not the equal of Agassiz's professional European training. Agassiz knew how the great museums of Europe were organized, he was familiar with the latest improvements in microscopy, and he had learned from the teacher of Karl Ernst von Baer how to trace the development of germ layers in an embryo. He had experience supervising the work of illustrators and research assistants, orchestrating grand projects through publication. Never mind that his "scientific factory" in Switzerland had collapsed in debt, for his visits to local natural history societies in the New World assured him that this optimistic democracy would support an expensive work of science. In 1855, he called for subscribers to an illustrated series, *Contributions to the Natural History of the United States of America.*

The time was ripe, Agassiz felt, for a new level of synthesis in biological science. That laymen were confused about the principles of scientific proof was demonstrated to Agassiz by the popularity in America of the anonymous *Vestiges,* whose author believed that an electric battery could generate insects and a goose's egg hatch out a rat. American naturalists, though too aware of the facts to be impressed by the *Vestiges,* were also uncertain in areas where Agassiz's uncertainties had long ago been resolved. The discovery of cave-dwelling fish whose eyes were rudimentary they took as evidence that darkness had caused the eye to atrophy; they were unable to see the logical necessity of agreeing with Agassiz that the human races had had separate origins; when a former servant of his, Charles Girard, published a catalogue of snakes, the American naturalists did not share Agassiz's scorn. Lurie documents the growing atmosphere of expectation surrounding Agassiz in his first decade in America.

Between January 1854 and July 1856, Agassiz was composing an introductory essay for his *Contributions,* an essay that would enable the general public and his professional colleagues to share his own sense of certainty of the direction in which scientific knowledge was progressing. During this period, he reexamined all his earlier scattered thoughts on species and on classification. He was very pleased with his results and wrote to Baird at the Smithsonian:

I have made some investigations of great importance upon that eternal question of species .... I shall not wait till it is *published* to send you my Chapter on Classification. The results are so practical that even my students of one years standing with these rules are able to trace for themselves in lots of unlabelled specimens of any class I put in their hands, the natural limits of genera and families and they actually do it better than our old practiced Zoologists. So you see it will tell in the progress of science.[14]

Agassiz knew that great things were hoped for from him, and he was satisfied that he had arrived at some significant new insights. His "Essay on Classification," completed in August 1856, was published in the fall of 1857. However wrong we believe the "Essay" to be, we must admit, on comparison with his contemporaries and predecessors, that Agassiz had indeed developed an original and interesting viewpoint.

Naturalists struggling with "that eternal question of species" had created a false problem, Agassiz decided, since in reality only individual organisms existed as physical objects of study. We should notice that he was using the word "species" in two different senses, as we still do, and it might be helpful to distinguish them. Most commonly we mean by "species" the kinds of living things we know from experience, like the horse, the gray squirrel, or the African violet. Of course, there are also kinds of nonliving things, like chairs or rocks, but biological species carry extra conviction, because members of a species have the marvelous trick of producing offspring like themselves. Another meaning of the word "species" arises from the practice of scientific classification. If we compare the hierarchical divisions of the living world—phylum (Agassiz's "great types or branches"), class, order, family, genus and species—to the military categories (corps, divisions, brigade, regiment, battalion, and company) then the species, like the company, is the final category.

The recognition and precise description of biological species had long been accepted as one of the important tasks of science. This in itself is by no means a simple problem, because specimens belonging in fact to the same species can differ remarkably from one another, while specimens belonging in fact to two biological species sometimes differ only slightly. But it is further necessary to gather species together into sets and subsets in order to talk rationally about them, because they number in the millions. How should they be classified? Any artificial arrangement, such as an alphabetical one, would help, but it has always been perceived that some groups of species are more natural than others; as Aristotle explained, birds are a natural group recognized by everyone, the bees, ants, and wasps form another natural group, though it has no common name, and the "two-legged animal" is an unnatural group, combining man with birds. The genius of Linnaeus was to outline a program for the gradual improvement of botanical classification. His arrangement made use of many unnatural groups, but his method encouraged the correction of his arrangement as biological knowledge increased. Cuvier's emphasis on internal anatomy provided a firm basis for the recognition of more and more natural groups in zoology.

One of Agassiz's favorite techniques for turning into scientists the young naturalists who came to him at Harvard was to give them one dead fish and instruct them to study it. When they produced after many hours or days a description that they thought covered every possible detail, such as would permit one species to be distinguished from a similar one, Agassiz would express dissatisfaction and send them back to stare at the fish for another week. What he wanted from them was insight into the general structure of their specimen, beginning with its bilateral symmetry and including all those obvious features, such as skeleton and scales, which made that object a fish. The specific characters were really the least important. The scientific naturalist, Agassiz always affirmed, must be as concerned to delimit the natural orders or families as he is to identify a new species.

As scientific research gives us progressively more natural arrangements of species, it should become ever more obvious, thought Agassiz, that biological classification is not at all like the gathering of companies into battalions, regiments, and divisions. Every naturalist knows of some natural family containing only very few species, while a seemingly endless number of new species are being added to another family, a family equally true to nature. If a country could muster only a hundred soldiers, it would be absurd to describe them by brigade, regiment, and battalion. But the arrangement of any good textbook of zoology or botany shows that in biology the idea is not absurd. If just one species, say the common lobster, were the only arthropod in existence, a scientific description of that animal still would involve, Agassiz claimed, all those elements that would be found in the orderly delimitation of its class, order, family, and genus.

By examining the groups generally acknowledged as being true to nature, Agassiz hoped he could identify what sort of characteristics were found to best delimit each category. The overall shape of the body, for example, obviously plays no part in deciding whether a given specimen belongs to the Class Pisces, for seahorses are fish while porpoises are not. Families, on the other hand, did seem to Agassiz to consist of species that have in common their overall shape. Following, so he thought, the inductive method of science, he reviewed the natural categories and arrived at the new analysis that would, he was sure, "tell in the progress of science."

The highest category presented no difficulty. Agassiz adopted the *embranchements* of Cuvier as his four "great types," the Vertebrata, Mollusca, Arthropoda, and Radiata. Although Cuvier himself thought of these four "plans" in terms of physiological interdependence of parts, morphologists like Richard Owen described them in terms of abstract archetypes. There was never any doubt in Agassiz's mind about the correctness of the concept that there are fundamentally different underlying plans of animal structure and that Cuvier had recognized them. A few years ago I described his defense of the Radiata, in spite of growing evidence of major differences between coelenterates and echinoderms;[15] he likewise insisted that one day the various protozoans and worms would be found properly to belong to one or another of Cuvier's four branches. If most of his fellow zoologists were ready to disagree with Agassiz's stubborn conviction that the number of great types was exactly four, at least they would all understand what concept he had in mind. That became less clear as he proceeded on to the other categories.

The classes, Agassiz had discovered, represented ways and means of carrying out the plan; for instance, the bird and the fish are two very different ways of being a vertebrate. Morphologists often spoke of modifications of the typical plan as they compared one class to another, but Agassiz objected to their choice of words. The plan itself was never modified, he said, just expressed in a different manner. Orders, he continued, will only be natural if they are based upon relative degrees of complication of structure. While the bra..ches and classes are simply different from one another, Agassiz thought he saw the orders within any class falling naturally into a series, according to their simplicity or degree of superiority. Families, as we have seen, express overall shape or form, but Agassiz admitted that this was terribly vague and attributed his difficulties to the fact that zoological classification was still a heterogeneous mixture of natural and unnatural groups. The genus was easy to characterize, said Agassiz: two species do not belong to the same genus if they exhibit any structural peculiarity; members of a genus must be alike in every ultimate detail of their structure.

Up to this point, Agassiz's analysis had been entirely concerned with morphological characters. When he reached the species category, however, there were no details of structure left. He mentioned the few remaining physical characters—size, proportion of parts, and ornamentation—but he did not try to magnify their importance. He was, after all, an experienced naturalist, not a philosopher, so he knew first hand that a purely morphological analysis was of limited usefulness below the genus level. Having already publicly rejected the criterion of interbreeding, during the debate on the unity of mankind, Agassiz had to ask himself what else besides morphological detail and sexual preference enables a biological species to be recognized. His answer was, its characteristic mode of reproduction and growth, its geographic distribution and fossil history, and the manifold relations that the individual organism bears to the world around it. These include its habitat, food, associations with its fellows, and relationships to other organisms, such as parasites.[16] Agassiz concluded:

> Species cannot always be identified at first sight, ... it may require a long time and patient investigations to ascertain their natural limits .... Well digested descriptions of species ought, therefore, to be comparative; they ought to assume the character of biographies and attempt to trace the origin and follow the development of a species during its whole existence .... Among some species variation of color is frequent, others never change, some change periodically, others accidentally .... All this should be ascertained for each, and no species can be considered as well defined and satisfactorily characterized the whole history of which is not completed to the extent alluded to above.[17]

We come at last to the individual organism, the dignity of which Agassiz acclaimed in ringing tones. His insistence on the physical reality of the individual was certainly not, in his mind, a denial of the reality of the species. He had no conception of physical genes or of gene pools, of course, so it might be argued that his biological species was not as physically real as our own, but he would have thought it as absurd as we would to say that species do not exist. His purpose was rather to affirm the reality of all those relationships of similarity that are expressed in a natural classification. "Species then exist in nature in the same manner as any other groups, they are quite as ideal in the mode of existence as genera, families, etc., or quite as real .... Now as truly as individuals, while they exist, represent their species for the time being and do not constitute them, so truly do these same individuals represent at the same time their genus, their family, their order, their class, and their type, the characters of which they bear as indelibly as those of the species."[18]

Even before the "Essay" was published, Agassiz himself could not avoid seeing some of its weaknesses. His work on American turtles, which with the "Essay" would form the magnificent first volume of his *Contributions to the Natural History of the United States of America*, exposed some if its inadequacies. He confessed to Baird:

> I must be the first to disregard the critic I have made in my first volume of the manner in which species and genera are generally described and I find that to do it as I think it ought to be done it takes more time than I had expected ....
>
> I must once more go to work with *Cistudo* [the box turtle] and try to make out whether we have only one or several species; I can distinguish four forms, but so can a shepherd distinguish every breed in his flock. Differences are not necessarily specific differences and the more I study Nat. Hist. the more I am struck with the looseness of the admitted specific characters. *Emys picta* [the painted turtle] has become for me a very troublesome species, since I have got it from every part of the country. As long as I knew only the New England form I found no difficulty. So is also *E. elegans* [the red-eared pondslider], and *E. concinna* [the river cooter].[19]

Baird had been lending Agassiz every turtle the Smithsonian received from government explorations, and Agassiz's own careful cultivation of amateur naturalists, who shipped him specimens from the Eastern states, the South, and the Midwest, was having its effects. No other group of animals could have more clearly confronted him with the existence in nature of what we call subspecies.

Agassiz's earlier references to "varieties" seem to represent no particular distinction in his mind between individual differences and the overall differences that may be traced in the character of a species across its geographic range. But there is a profound distinction to be made in biology, as Mayr has often emphasized, between the variant individual and the variant population. The distinction may perhaps be compared to that between the random motion of a molecule of water on a calm, sunny day and the motion of all the molecules in a breaking wave. The first, having no particular relation to all its fellows, simply contributes to the warmth of the sea, while the second, which for any particular molecule may be no greater absolute motion, can in concert pound upon the shore with visible force. How many individual animals must differ from a previously known form and how much must they differ before they deserve to be recognized with a Latin proper name? This is rather like the question, what size must a ripple be before we call it a wave? There has always been, and still is, a great range of practice among taxonomists, who describe one another as "splitters" or "lumpers," according to whether they will name a rather modest ripple or tend to wait until they see breakers pounding on the beach.[20]

Agassiz's survey of turtle classification was intended to demonstrate the value of the definitions of order, family, and genus in his "Essay"; the number of species of American turtle was, he knew, small enough to be manageable. He knew that each individual specimen would have its peculiarities, and his resolute policy was to acquire a series of individuals of each species, not just a representative male, female, and juvenile. He knew that he would find variability, in addition to individual peculiarities, but I think he expected to find, as his collections grew, that most variability would resolve itself into differences associated with age and sex. It was also his policy to add to his collection specimens from many localities. If someone from Ohio asked him if he could use another box turtle, he would say yes, even if he had plenty from Pennsylvania, for he knew there might be more than one species of box turtle in the United States. His letters give no indication that he expected to find significant geographic variability within species. But as more and more specimens poured into Cambridge, Agassiz found himself in a number of cases unable to decide whether he had one species with three or four well-marked geographic forms, or three or four good species. In the spring of 1856, he wrote to Baird, "The most troublesome is still *Cistudo carolina* [the box turtle]. I have now examined hundreds and am as wise as when I began .... I trust within a few days I shall have mastered the difficulties of the genus. But who should have supposed that it required such extensive comparisons to determine a few species of turtles?[21] His hope was not realized, and he had to go to press still undecided about the box turtle. Naming and briefly describing his four forms, he admitted that he could not judge the value of the differences between them. "The differences noticed may indicate different species; but they may also mark only varieties. There is, however, a remarkable circumstance connected with the specimens that come under my observations: their variations are limited to particular regions of the country. A satisfactory investigation of this genus would therefore involve the whole question of local and climatic varieties."[22] It is hardly surprising, in light of his decision on the races of mankind, that he had decided that each of the other "troublesome species" needed to be broken up into a small number of distinct species, for he had learned that he could consistently tell them apart, and, indeed, his species descriptions are quite good characterizations of the subspecies recognized today.[23]

Although Agassiz had evidently not expected to find geographic varieties in nature, he felt no need to deny their existence. He was able to incorporate them into the framework of his "Essay" in a single sentence. He confessed that sometimes the principal categories do have natural subdivisions like subclasses, suborders, or subgenera. This provided the context for him to state: "The individuals of a species, occupying distinct fields of its natural geographical area, may differ somewhat from one another, and constitute varieties, etc."[24]

But if the existence of varieties of box turtle did not seem a serious challenge to his analysis, the character of these varieties certainly should have. Elements of structure were supposed to have all been dealt with at the level of class or order; members of the same genus were supposed to differ in no detail of structure. Most species of turtle did satisfy this criterion, being distinguished from others in their genus by size, coloration, and minor details of sculpture. The number of toes, however, was certainly a structural character to Agassiz, for a section of his "Essay" compared "the structure of animals widely scattered upon the surface of our globe" using the example of a series of lizard genera with different numbers of limbs and toes.[25]

Agassiz's collection confronted him with four-toed box turtles from New England, one four-toed specimen from Texas, a three-toed variety from the South, and "three-toed specimens from North Carolina, . . . which agreed in every other respect with those of New England."[26] Because the Southern ones were smaller and paler, Agassiz was ready to consider them a distinct species, until he found pale, three-toed ones of larger size from other areas. Dissection of the Southern box turtle revealed a rudimentary fourth toe, "faded away."[27] It must have been anomalies like this that prompted him to include in his "Essay" this peculiar footnote:

> It is almost superfluous for me to mention here that the terms plan, ways and means, or manner in which a plan is carried out, complication of structure, form, details of structure, ultimate structure, relations of individuals, frequently used in the following pages, are taken in a somewhat different sense from their usual meaning, as is always necessary when new views are introduced in a science, and the adoption of old expressions, in a somewhat modified sense, is found preferable to framing new ones. I trust the value of the following discussion will be appreciated by its intrinsic merit, tested with a willingness to understand what has been my aim, and not altogether by the relative degree of

precision and clearness with which I may have expressed myself, as it is almost impossible, in a first attempt of this kind, to seize at once upon the form best adapted to carry conviction.[28]

Agassiz was pushing himself to meet his publication deadline, unpacking still more boxes of turtle specimens, and hoping his colleagues and his public would appreciate the value of his "Essay on Classification," when, to his great exasperation, the theory of evolution once again received publicity. At least the author of the *Vestiges* had been blatantly unworthy of scientific notice, but the Reverend Baden Powell was a professor of geometry at Oxford and a Fellow of the Royal Society. His 1855 *Essays on the Spirit of the Inductive Philosophy* was obviously a book the English-speaking scientific community would be taking seriously. Without offering any new evidence that species are mutable, Powell scolded the scientists who opposed evolution.

I wish to take a perfectly unbiassed and dispassionate view of the real tenour of the evidence; and more especially to analyse certain arguments often brought forward ... which ... appear to me involved in considerable doubt and fallacy. And though, in some instances, they boast the sanction of names eminent in physiology and geology, yet the question is rather one of general principles of reasoning, than of precise scientific details; and thus, without pretending to impugn their *science*, I venture to call in question their *logic*.[29]

He directed only a few of his remarks explicitly at Agassiz, but all of Powell's argument touched Agassiz's ideas. Powell claimed that Cuvier had only taken the immutability of species as an hypothesis, but that his followers were taking it as a law of nature, thus assuming what was to be proven. He recalled Cuvier's debate with Geoffroy St.-Hilaire, reviewed the speculations of Oken, and declared that embryology was uncovering connections between Cuvier's four plans of structure. The purpose of Powell's book was not to advocate evolution, however, but to explicate the proper relations between evidence and induction in true science. The implication was that by opposing evolution Agassiz was displaying a lack of understanding of scientific method. Yet the relation between fact and theory was one thing Agassiz was sure he understood.

Agassiz replied to Powell in a series of footnotes to his "Essay". "It is almost incredible how loosely some people will argue ... ," he said, "from a want of knowledge of the facts, even though they seem to reason logically."[30] The rapidly growing store of paleontological facts, Agassiz knew, contained no evidence whatsoever of one species being gradually transformed into another. Their beginnings seemed as abrupt as their end. Of course, there may be a similar species in an earlier geological period, but if we may infer that the later one is genetically descended from the earlier, then, Agassiz argued, we could as well infer that if two paintings in a museum resemble one another, the one had changed into the other. Unquestionably, Agassiz's knowledge of the facts of contemporary geology and zoology was much superior to Powell's, but his severe limitation of inference must have sounded like special pleading.

Whether it was because he took Powell's criticism to heart, I do not know, but Agassiz was very careful in the "Essay on Classification" not to include constancy in his definition of species. In a chapter on the "permanency of specific peculiarities in all organized beings," he dealt with the sorts of evidence that demonstrated the fixity of species through vast periods of time. A few years before, when he had been won over to Morton's view that the races of man were constant far back into history, he had left himself open to the charge of arguing in a circle. But there is no such circularity in his treatment of species in the "Essay." His statement of their constancy appears as a conclusion from observation, not an assumption.

I have purposely left aside until now all mention of Agassiz's statements about God. Because our standards of scientific writing demand the careful exclusion of religion, Agassiz's frequent reference to the One God, the Divine Intellect, and the plan of the Creator make it hard for us to read his "Essay" as part of the history of science. In fact, the standards of Agassiz's own day allowed only brief references to the Creator at the beginning or end of a proper contribution to science. Natural theology was regarded as a separate discipline, and Agassiz was conscious that his treatment would seem improper to many of his peers. But he was clear in his own mind and consistent in what he was doing. He was following to its logical conclusion the search for cause, carefully and precisely inferring cause from effect, he thought.

Baden Powell criticized the reasoning of much current natural theology, but he regarded the cells of the honeybee as clear proof of a superintending Mind, not because of their adaptation to the needs of the bee, but because of their geometry. " . . . The proof of *mind* is independent of the consideration of a useful *end answered*: it depends on the conception and solution of what is to our intellects an abstract mathematical problem, by no means of an elementary or evident nature; and which is equally remarkable whether any *purpose* were *fulfilled* by its applications, or not."[31]

Agassiz's argument was similar. "No thoughtful naturalist," Agassiz believed, "can silence the suggestions, continually arising in the course of his investigations, respecting the origin and deeper connection of all living beings."[32] There had been no reason to expect that a hierarchical classification could satisfactorily contain the wonderful diversity of nature; the progress of knowledge had, after all, disappointed the earlier attempt to arrange nature into a progressive scale or great chain of being. There had been no reason to expect that the abstract analyses of comparative morphology could be carried very far, but morphologists were continually rewarded by the discovery of precise, extraordinary homologies. Since many structures seemed not at all the most effective means to an end, indeed, some were useless rudiments, and since it was by no means a trivial problem for our intellects to search out hidden homologies, the indication of the operation of intellect in nature seemed manifest to Agassiz. If we do not find Powell's reasoning compelling, neither will we Agassiz's:

"As long as it cannot be shown that matter or physical forces do actually reason, I shall consider any manifestation of thought as evidence of the existence of a thinking being as the author of such thought, and shall look upon an intelligent and intelligible connection between the facts of nature as direct proof of the existence of a thinking God, as certainly as man exhibits the power of thinking when he recognizes their natural relations."[33]

It certainly seems likely that Agassiz's belief in an intelligent God, one not above intervening in the world long after its initial creation, conditioned his search for natural order. However, part of Agassiz's image of himself as a scientist demanded that he should not derive his perceptions of the world from religious presuppositions, but only infer the action of Divine Intelligence from the fact that the organic world displays patterns of relationships, including those expressed in classification. He did assert that the species, like all the other taxonomic categories, was a thought in the mind of God, but he believed that he had discovered this, not assumed it.

Agassiz's Misnamed Fishes

The entire tone of the "Essay" is dogmatic. Unlike Darwin, Agassiz never mentioned the possibility that he might be wrong, only that he might be misunderstood. Any facts inconsistent with his system, like the three-toed box turtles, he ignored in the "Essay" (though he did not suppress them from the technical portion of the *Contributions*). Likewise, when the *Origin* was published, Agassiz often publicly denied that species could vary as Darwin's theory required, even though he knew how difficult it was to draw a line between species and geographic races, and even though he warned his students that some species displayed a wide range of differences among individuals.[34] But Mayr gave us evidence seeming to show that besides being so doctrinaire in his opposition to evolution that he would minimize or ignore facts, Agassiz actually was crippled in his powers of observation. "In his survey of the fishes of the Tennessee River," Mayr reported, "Agassiz encountered a number of species with high individual variability. His disbelief in the existence of 'varieties' forced him to describe several 'species' from schools of single species: *Lepomis megalotis* (*'sanguinolentus'*, *'inscriptus'*, *'bombifrons'*), *Aplodinotus grunniens* (*'concinnus'*, *'lineatus'*), *Fundulus notti* (*'guttatus'*, *'hieroglyphicus'*), and *Ictiobus bubalus* (*'urus'*, *'taurus'*).[35] Many readers of Mayr's influential paper have been struck with the vivid image of a man so influenced by a preconceived philosophy that he was no longer able to make reasonable judgments as a naturalist. Looking more closely into the case of these four kinds of fishes dispels that image, and reveals instead the complexity of the task that taxonomists still face.

A great many of Agassiz's new names for what he thought were species are now considered synonyms for names he knew about; he is regarded today as an extreme "splitter." How he compares with his own contemporaries I do not know,[36] but the practice of giving local varieties a specific name was very common in Agassiz's day; Hooker despaired over the state of botanical nomenclature because of it.[37] Agassiz's belief that the slightest difference could indicate a distinct species, if it occurred constantly and was not produced by climate, diet, or other environmental factors, would lead him to call a new form a species much more readily that we would. Certainly Agassiz shared with his contemporaries the conviction that differences due to age, sex, or individual peculiarity should not be recognized with a scientific name.

Of Mayr's four cases, two do not involve specimens from the same collection, or even the same locality. One species of buffalofish had already been described from the Ohio River (and another from Lake Pontchartrain, Louisiana), but Agassiz collected his "*taurus*"[38] in Mobile, Alabama, and the fish he named "*urus*" was sent to him from Huntsville, on the Tennessee River. Likewise, the freshwater drum, *Aplodinotus grunniens*, was known from the Ohio River, whereas Agassiz's "*concinnus*" was from the Tennessee River, and his "*lineatus*" was from the Osage River hundreds of miles away.[39] The differences Agassiz perceived between smallmouth buffalofish from different rivers, and between freshwater drum from different localities, were very slight, but there seems no basis to assume that they were individual differences only. Populations of the same species from two distinct localities are bound to differ slightly, even when the differences are not great enough to warrant subspecific rank today. Of course, the smaller the number of individuals collected from a given locality, the greater the chance that a few individuals not close to the mean for their own locality will be mistaken for a variant population. Agassiz warned time and again that a specimen was not a species, and that extensive series of individuals needed to be gathered before the biologists could hope to properly characterise a species, but he himself, like most of his contemporaries, often ignored this injunction.

In the case of the freshwater drum, of which there is only one species now recognized, Agassiz decided he had a new species, "*concinnus*," on the basis of just two individual specimens sent him by Newman from the Tennessee River. Agassiz ought to have been more cautious, but one reason for his self-confidence must have been that he knew the freshwater drum from fish markets, and had already at least thirty-eight specimens in his collection, from various locations, when the barrel from F. H. Newman of Huntsville arrived.[40] To his eye, this pair of fish had a distinct form, being less elongated, with a steeper profile, and the dorsal fin beginning and ending further forward than in the familiar species. His other new freshwater drum was also based on pickled specimens sent to Cambridge, but this time he had a series of specimens of various sizes, totaling twenty. Besides its form, this fish differed by having faint and variable stripes, so he named it "*lineatus*." But again, the differences were really rather slight, and his specimens few.[41] His problem, I think, was that, as Mayr pointed out, "he based his decision in each case on, shall we say, intuition." He felt that his wide experience gave him a special knack for recognizing species.

He certainly had grounds for feeling that he had an expert's insight into the buffalofish, for they were members of a group that he had known since childhood, that had been the subject of his first contribution to science, and that had presented him with great variety in the Great Lakes. The distinctions he saw between the buffalofish "*taurus*" and "*urus*" are, as in the case of the freshwater drum from two localities, mainly slight differences of form and proportion. But if we look beyond "*urus*" and "*taurus*" to all the other new buffalofish Agassiz described, the story becomes more complicated. In contrast to the freshwater drum, with its single species, there are now recognized not one but three species of buffalofish: the bigmouth, the black, and the smallmouth.

They are similar and easily confused, each species is variable, and their ranges largely overlap. To make matters worse, hybrids between these species do occur in nature.[42] The present century was well under way before the master ichthyologist Carl Hubbs began to disentangle the resulting confusion of nomenclature. And in pointing out the close taxonomic relationship between the smallmouth and the black buffalofish, compared to the bigmouth buffalofish, Hubbs wrote, "Agassiz's differentiation of these genera [now subgenera] in 1855 was clean-cut and decisive, but later authors did not give proper emphasis to the characters he used."[43] In that paper of 1855, Agassiz reported that a Dr. Rauch of Burlington Iowa, had sent him a collection of buffalofish from the Mississippi River. "If there was only one species of Buffalo in those waters the case would be very simple,"[44] but, Agassiz said, he had found three. Hubbs examined Agassiz's specimens (preserved in alcohol for seventy-five years in the Agassiz Museum—the M.C.Z. at Harvard—and still to be found there) and agreed that Agassiz had indeed been separating the smallmouth, from the bigmouth, from the black buffalofish. Agassiz did multiply names of buffalofish on the basis of very slight differences, to be sure, but not at any one locality.[45]

One of Mayr's examples does seem to involve variant individuals at one locality. Agassiz's sunfish "*sanguinolentus*," "*inscriptus*," and "*bombifrons*" were all sent him from the Tennessee River at Huntsville, Alabama. Reeve Bailey, one of the world's experts on sunfish taxonomy, considers all three names to be synonyms of the longear sunfish, *Lepomis megalotis*.[46] Agassiz knew that males and females differ in shape and color in many fish, and he was always on the alert for the changes that accompany growth. He also knew that other, individual variation was sometimes found, but he believed that for every species there were a set of characteristics, to be found by experience, which do not vary. Once familiar with a number of species in a genus, he expected to be able to recognize a new species in that genus easily. Confident in his own skill and experience, Agassiz had his artist, Jacques Burkhardt, draw eight forms of sunfish from the Huntsville collection.[47]

Another of Agassiz's new sunfish, "*pallidus*," demonstrates that he faced other complexities besides individual variability. Reeve Bailey and Carl Hubbs both examined Agassiz's specimen of "*pallidus*" and identified it as a hybrid, the result of a cross between the bluegill and green sunfish. Agassiz knew that hybrids are possible; indeed, like Morton, he insisted that hybridization producing fertile offspring does occur, notably between species of the human genus. But it seems clear that Agassiz, like Morton, believed that crosses between species generally took place under the influence of man. He would not have been expecting to find hybrids in nature.

Newman's Huntsville collections, which Agassiz found so rich in sunfish, drum, and buffalofish, did not supply him with any new kinds of topminnows, but he did use the occasion of publishing his report on that collection to announce, in a footnote, no less than seven new topminnow species, four of them from the same locality! Later workers declared his "*lateralis*" and "*zonatus*" merely synonyms of a name already in existence, *olivaceus*; his five others, "*Nottii*," "*lineolatus*," "*guttatus*," "*dispar*," and "*hieroglyphicus*" were declared duplicate names for the same new topminnow, for which the name "*Nottii*" was chosen. What could be more startling evidence that Agassiz had somehow lost touch with reality? It certainly looked like solid evidence of that when Mayr cited it in 1959. More recently, however, it has been shown that seven different forms corresponding to Agassiz's do exist, distinct enough to be called species.[48] Agassiz did fail miserably in his responsibility as a taxonomist, for even his contemporaries found his terse descriptions of these fish useless, but this is not evidence that he failed in his perceptions.

Agassiz was a specialist on the family to which topminnows belong, the cyprinodonts. He had in 1834 pointed out its distinctness from the minnow family,[49] and in 1851 he had completed a monograph on cyprinodonts.[50] During his stay in Mobile and in New Orleans in the spring of 1853, he paid special attention to the viviparous topminnow *Molliensia latipinna.* "I have had ample opportunity of observing large numbers of this fish," Agassiz wrote, "in the lagoons in the immediate vicinity of these two cities, and not only of ascertaining that they are viviparous . . . but also of tracing the whole development of the embryo from the first stages of the segmentation of the yolk to the hatching of the young, which were freed from the abdominal pouch of the mother in the month of April . . . . I have repeatedly seen them copulate."[51] By the end of 1853 he had over fifteen hundred specimens of topminnow in his collection. Of the seven new species named in that unfortunate footnote, six were based on specimens he had collected himself.[52] Among the characters of his new species are an orange patch, which is to be seen in living individuals only, and silvery sides, which are prone to disappear when specimens are kept in preservatives.[53]

The blackstripe topminnow is now seen to consist of two sibling species, which differ in behavior and chromosome number.[54] Among their few visible differences is the presence or absence of black spots above their bold lateral stripe (see Plate, figs. 10 & 11 versus 12 & 13), which was just Agassiz's distinction between his "*lateralis*" and "*zonatus.*"

The starhead topminnow has long been regarded as a single species and designated *Fundulus nottii,* but recently a close analysis of thousands of specimens has revealed five distinct forms, for which specific status has been claimed. Each of the five occupies a range largely separate from the others, from *Fundulus dispar* along the Mississippi River (where Agassiz found it), to *F. lineolatus* in Florida, Georgia, and the Carolinas (Agassiz received his from Augusta, Georgia). However, there are regions where their ranges overlap. Within thirty miles of Mobile may be found today *F. nottii, F. escambiae,* and *F. blairae.*[55] Differences too fugitive to be useful in identifying museum specimens, such as a slight bluish tinge, enable an expert eye to distinguish these forms in the field with ease.[56] Agassiz's descriptions of his Mobile species "*Nottii,*" "*guttatus,*" and "*hieroglyphicus,*"[57] are perfectly consistent with the possibility that he was describing the forms now called *Fundulus nottii, F. escambiae,* and *F. blairae.*[58]

If the story of Agassiz's topminnows does not mean what Mayr inferred from it, neither should it do Agassiz's reputation as a biologist any credit. He had been a close student of fish since childhood,[59] and there would have been something seriously wrong if he hadn't had "a good eye." But he was supposed to be the great European scientist, not just a clever amateur naturalist. He upbraided his new countrymen in private and in public in a tone of great authority for any deviations from the highest standards of scientific taxonomy, of which he had set a fine example in his *Lake Superior* of 1850. There he had devoted, on the average, nearly three pages of text to every new species. Yet he managed to fit descriptions of twenty new species of topminnow, buffalofish, sunfish, and drum into only four and a half pages of his 1854 article. None of his 1854 species receives a full page, which was his minimum description in 1850. Nor do any of his 1854 descriptions include a fin-ray count, which Baird and Girard carefully reported even in their briefest descriptions. Presumably Agassiz intended to include proper analyses of his new topminnows in the planned monograph of the whole family. He had his artist Auguste Sonrel prepare four beautiful lithographic plates, one of which is reproduced here, reduced in size. But, as so often happened with Agassiz, he never found time to complete the job, and the manuscript and plates lay unpublished at his death, along with scores of other unfinished projects. His hasty

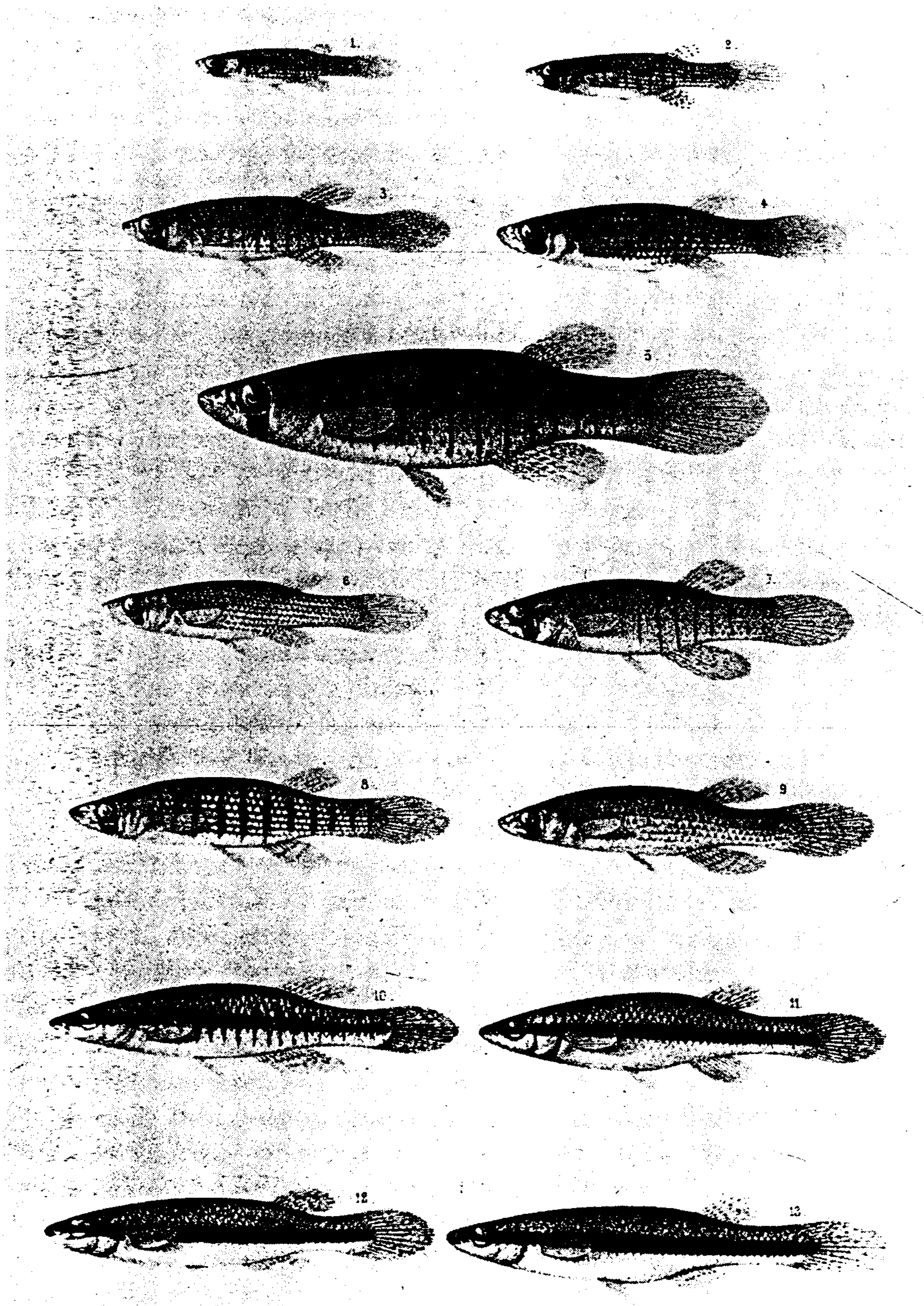

Plate I. Lithograph of topminnows made by Auguste Sonrel for Louis Agassiz about 1854 (Garman, "Cyprinodonts," *Mem. M. C. Z.* 1895, vol. 19, no. 1, pl. 10) descriptions, exemplifying the careless species-mongering he deplored, quickly dropped out of use, or, indeed, were never applied to any but his original specimens, even in his own museum.[60]

Conclusion

Why did Agassiz oppose Darwin's theory of evolution in 1860, and continue to oppose it until his death in 1873? His religious beliefs, scarcely Christian and certainly at odds with contemporary reverence for scripture, did not stand in the way, for, as Mayr pointed out, other naturalists as devout as Agassiz did make the shift. Neither did his belief that the ultimate cause of organic form is not material make evolution inconceivable, for that same cause operates in embryology, and, as Mayr showed, embryonic development was a congenial model of organic transformation for many other thinkers. Agassiz was a leading proponent of the idea that embryonic forms may usefully be compared to fossils (thus opening the way for his students to eulogize him later as a founder of their own evolutionary views), and he insisted in his last article that the word "evolution" properly referred to the development of an individual. An idea of descent with modification, though far from Darwin's, modeled on embryological development was attractive to many of Agassiz's contemporaries. He could perfectly well imagine such a process of transformation, but he saw no evidence of it actually having taken place.

Agassiz did insist that it was logically impossible for types to be modified, but these "types" were just the four main branches of the animal kingdom. Darwin made allowance for this view by suggesting "that animals have descended from at most only four or five progenitors," life "having been originally breathed into *a few* forms or into one."[61] Within each of the types, endless differences of structure and detail could exist. Agassiz's "typological thinking" had but slight affinity to Plato's or Aristotle's, and however impossible the modification of an *eidos* might have been in their systems, there was, as far as I can see, no logical impediment to the alteration of a species in Agassiz's. Rather, the obstacle he cited was the principle of heredity. The phenomenon that tiny bits of tissue can mature, sometimes after complex metamorphoses, into organisms resembling their parents, had in Agassiz's day no reasonable physical explanation. The little known of the laws of inheritance at that time did at least establish that neither a replica of one parent nor an exact combination of the two is produced, and that injuries or accidental peculiarities tend not to be passed on. It was as if the developing embryo could receive guidance from the whole species, not just the immediate parents. Thus, the hereditary force, whatever it may be, was observed to operate conservatively. Furthermore, the fossil record showed that it acted constantly over vast reaches of time.

Even species that resemble one another in all but the most trivial details are seen to maintain their particular distinctness generation after generation, often for millions of years. It takes a very determined and sympathetic searcher to find any transformation in nature comparable to the appearance of domestic breeds, and such forms are not regarded as species. No wonder that Agassiz felt the fixity of species to be an observed fact questioned only by philosophers or the uninformed. Yet important as this fact was to Agassiz, it was less profound and significant than another discovery of post-Linnaean biological science: that species are related to one another in a natural hierarchy of groups and subgroups. After years of experience in the collecting field, laboratory, and museum, Agassiz produced an original explanation of these facts. His synthetic "Essay" of 1857 declared that each level of classification, from branch and class down to genus and species, was a different category of intelligent analysis. It never occurred to him that the imprint of mind, which he believed he had inductively discovered and not assumed in nature, was merely the projection of his own.

The factors that dominated Agassiz's hostility to Darwinism were not logical but psychological. His early rejection of evolutionary speculations became part of his self-image as a careful scientist. Once he had published his own interpretation, at the age of fifty, no one who knew him personally expected him to welcome the idea of evolution, in whatever dress that theory might next appear. Edward Lurie's sympathetic biography softens but does not conceal what a difficult man Agassiz was, for his friends, colleagues, and students. Brimming with child-like enthusiasm for the wonders of nature one day, he would display on the next an authoritarian deafness to reason. Careless of the needs of others, he found himself entangled in an incredible series of bitter disputes with assistants, students, and peers throughout his career. His self-importance wearied his most loyal supporters, though he assured them his ambitions were all for science and not for himself. He seemed constitutionally unable to entertain honest doubts of his own judgment and too proud to admit his own errors. Some of his friends wished he would give Darwinism a fair hearing, for the sake of his reputation, but none of them were surprised when he did not. By 1859, Agassiz was committed to a system of ideas very different from Darwin's. The dogmatism of that commitment is clear to us because we no longer agree with his ideas. But it was his dogmatism, not his ideas, that was unscientific.

NOTES

**Acknowledgements.* The opportunity to honor Ernst Mayr, whose campaign to raise the status of taxonomy has been the foundation of my own interest in the history of biology, stimulated my conception and research of this essay. It is characteristic of Dr. Mayr, that his prompt replies to all my inquiries contained not only warm words of encouragement, but concrete and helpful suggestions. The research for this paper was done mostly in the Museum of Comparative Zoology, which Dr. Mayr directed through a crucial period of its history. I am indebted for endless favors to the present Director, Alfred W. Crompton; to the staff of the M. C. Z., including Ann Blum, Ruth Hill, and others in the incredibly rich Library; Robert Schoknecht, Karsten Hartel, William Fink, and Karel Liem of the Fish Department; members of the Mollusk Department, and many others. My ichthyological inquiries were greeted with generous cooperation by Robert L. Butler, Labbish N. Chao, William Childers, E. J. Crossman, William Eschmeyer, J. S. Nelson, Luis R. Rivas, and Stanley Weitzman; I am especially grateful to Reeve M. Bailey and E. O. Wiley for the considerable time they devoted to my queries. Jacques Berger, William Coleman, Bruce Sinclair, and Richard I. Johnson read my manuscript and kindly gave me constructive suggestions on style, some of which I have adopted and all of which I was very glad to have.

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I am deeply indebted to those scholars upon whose labor I have built, especially Elmer Charles Herber, Edward Lurie, and William Stanton.

1. Ernst Mayr, "Agassiz, Darwin, and evolution," *Harvard Library Bulletin* 13 (1959): 165–94; also in Mayr, *Evolution and the Diversity of Life: Selected Essays* (Cambridge, 1976), pp. 251–76. My page citations will be to the reprinted essay.

2. Ibid., p. 258.

3. Elizabeth Cary Agassiz, *Louis Agassiz: His Life and Correspondence* (Boston, 1886), 1:144–45.

4. Ibid., 1:150–52.

5. Edward Lurie, *Louis Agassiz: A Life in Science* (Chicago, 1960), pp. 59, 254; Mayr, "Agassiz, Darwin, and evolution," p. 253.

6. In his chart of the human races, Agassiz chose as the type of the European a picture of Cuvier (J. C. Nott and G. R. Gliddon, *Types of Mankind* [Philadelphia, 1854], p. lxxvii).

7. E. C. Agassiz, *Agassiz: His Life and Correspondence,* 1:383.

8. Jules Marcou, *Life, Letters and Works of Louis Agassiz* (New York, 1896), 1:285; 2:28–29. This episode has been fully described by Edward Lurie ("Louis Agassiz and the races of man," *Isis* 45 [1954]:227–42); and by William Stanton, *The Leopard's Spots: Scientific Attitudes Toward Race in America* (Chicago, 1960).

9. So Morton and his contemporaries believed, but Stephen J. Gould has recently argued that Morton's measurements do not support his claims ("Morton's ranking of races by cranial capacity," *Science* 200 [1978]:503–09).

10. The Agassiz letters cited by Stanton and Lurie are quoted more fully by S. J. Gould, "This view of life: Flaws in the Victorian veil," *Natural History* 87(1978):16–26.

11. Stanton, *Leopard's Spots*, p. 141.

12. Louis Agassiz, "Sketch of the Natural Provinces of the Animal World and Their Relation to the Different Types of Man, in *Types of Mankind*, by J. C. Nott and G. R. Gliddon (Philadelphia, 1854), pp. lviii-lxxvi; lxxii.

13. Louis Agassiz, "Fishes of Lake Superior Compared with Those of the other Great Canadian Lakes," in his *Lake Superior* (Boston, 1850), pp. 292, 370.

14. *Correspondence between Spencer Fullerton Baird and Louis Agassiz—Two Pioneer American Naturalists*, ed. E. C. Herber (Smithsonian Institution, Washington, 1963), pp. 73, 94.

15. Mary P. Winsor, *Starfish, Jellyfish, and the Order of Life* (Yale, 1976).

16. He included as well "all the variations to which they are liable" (*Essay*, p. 178). This phrase refers, I think, to the belief, common among nineteenth-century naturalists, that the tendency to vary is strong in some species and slight in others and that the pattern of variability is inherent in each species; domestic breeders had been so successful, for example, because they were working with very "plastic" species.

17. Louis Agassiz, "Essay on Classification," in *Contributions to the Natural History of the United States of America* (Boston, 1857), 1:3-232; my citations are to the recent reprint (ed. E. Lurie, Harvard University Press, 1962), pp. 178-79.

18. Ibid., p. 176.

19. *Correspondence between Baird and Agassiz*, pp. 134, 126.

20. The many important differences between living organisms and molecules of water may make some biologists unhappy with my analogy, for the process of speciation is now receiving much attention. My analogy serves to underline the difference between random individual variation and the shift in mean character of an entire population. There is, of course, more going on biologically than just that shift (a species may vary greatly over different parts of its range without ever breaking up into two species or altering the mean of the whole), for the pressure of natural selection may favor rapid speciation on one hand, and the conservation of specific distinctions on the other.

21. *Correspondence between Baird and Agassiz*., p. 130.

22. Agassiz, *Contributions*, 1:445.

23. This is my amateur opinion, based on a comparison of Agassiz's species descriptions with the corresponding description of subspecies in Carl H. Ernst and Roger W. Barbour, *Turtles of the United States* (University Press of Kentucky, 1972).

24. Agassiz, *Essay*, p. 180.

25. Ibid., pp. 49-53.

26. Agassiz, *Contributions*, 1:445.

27. Ibid., 1:294 fn., 1:445 fn.; *Correspondence between Baird and Agassiz*, p. 106.

28. Agassiz, *Essay*, p. 145.

29. Baden Powell, *Essays on the Spirit of the Inductive Philosophy, the Unity of Worlds, and the Philosophy of Creation* (London, 1855), p. 412.

30. Agassiz, *Essay*, p. 59, fn.; other replies to Powell, pp. 11, 15, 74-75.

31. Powell, *Essays*, p. 142.

32. E. C. Agassiz, *Agassiz: His Life and Correspondence*, 1:153.

33. Agassiz, *Essay*, p. 12.

34. Agassiz's repetition, in the spring of 1860, of the ideas of his "Essay" has recently been documented by the indefatigable Ralph W. Dexter, "Historical aspects of Louis Agassiz's lecture on the nature of species," *Bios*, 48(1977):12-19.

35. Mayr, *Agassiz, Darwin, and Evolution*, p. 258. Mayr, an ornithologist, thanked the ichthyologist Reeve M. Bailey for his information.

36. A quantitative study of one subfamily of fishes suggests to me that he may not have been an extreme splitter by the standards of his own day (Bruce B. Collette, "The taxonomic history of the Darters (Percidae: Etheostomatine," *Copeia* [1967]:814-19). I am grateful to Karsten Hartel of the M. C. Z. for pointing this article out to me.

37. Leonard Huxley, *Life and Letters of Sir Joseph Dalton Hooker* (London, 1918) 1:190, 366-74, 439-43, 467-70.

38. Proper taxonomic practice would require me to always include the name or abbreviation of the genus with the species name, but I am afraid the tangle of changes the generic names went through would hopelessly confuse my readers, while to "correct" these to the modern genus would be inaccurate historically. For instance, Rafinesque had replaced his own earlier name *Aplodinotus* with the more appropriate name *Amblodon*, and Agassiz followed Rafinesque in calling the common freshwater drum *Amblodon grunniens*. Agassiz himself changed the names of his smallmouth buffalofish from *Carpoides taurus* and *C. urus* to *Bubalichthys taurus* and *B. urus*, while he carefully kept them out of the genus *Ictiobus* (the black and bigmouth buffaloes), in which the smallmouth are included today. Therefore, I beg the indulgence of biologists for my usage: Agassiz's buffalofish "*taurus*," Agassiz's sunfish "*inscriptus*," and so on.

39. Louis Agassiz, "Notice of a collection of fishes from the southern bend of the Tennessee River, in the state of Alabama." *American Journal of Science* (1854), ser. 2, 17(50):297-308, 353-65.

40. The Catalogue of the Fish Department of the Museum of Comparative Zoology records the specimens received, who collected them, the place and date of collection, and who donated them to the Museum. My statements about specimens in Agassiz's possession in 1854 are, therefore, conservative, for they include only those preserved and deposited in the M.C.Z. about 1861. The catalogue entry for one of his freshwater drums is "N.Y. market, 1847."

41. Great care should be exercised before concluding that since no subspecies are recognized by modern taxonomists, Agassiz's distinctions were the product of his imagination. Reports of morphological differences among freshwater drum led to a study (Louis A. Krumholz and Harold S. Cavanah, "Comparative morphometry of freshwater drum from two midwestern localities," *Trans. Amer. Fish. Soc.* (1968), 4:429-41) that found that Lake Winnebago drum were measurably deeper-bodied, at all lengths, than Ohio River drum. In the markets of Detroit and Chicago, which receive both lake and river fish, freshwater drum is sold for two different prices, according to the texture of flesh (Robert L. Butler, "The Status of the Freshwater Drum *Aplodinotus grunniens* Rafinesque, in the Commercial Fishery of the Upper Mississippi River," thesis, University of Minnesota, 1962, pp. 120-24). Butler reports that "hard flesh" fish grow more slowly and have a high, sharp back (personal communication). Butler, Krumholz, Cavanah, and Chao believe that these differences in flesh and form are direct effects of the environment and, therefore, of no value to the taxonomist. I am indebted to Dr. Chao for sending me a portion of his "Basis for classifying West Atlantic Sciaenidae," in press, and to Dr. Butler for sending me portions of his unpublished thesis.

42. Carl L. Hubbs, Laura C. Hubbs, and Raymond E. Johnson, "Hybridization in Nature between Species of Catastomid Fishes." *Contributions of the Laboratory of Vertebrate Biology of the University of Michigan at Ann Arbor, 1943*, no. 22, pp. 1-76; Donald W. Johnson and W. L. Minckley, "Ichthyological notes: Natural hybridization in buffalofishes genus *Ictiobus*," *Copeia* 1(1969): 198-200; Johnson and Minckley, "Variability in Arizona buffalofishes," *Copeia* 1(1972):12-17; Milton B. Trautman, *The Fishes of Ohio with Illustrated Keys* (Ohio State University Press, 1957), p. 231.

43. Carl L. Hubbs, "Materials for a Revision of the Catostomid Fishes of Eastern North America," Misc. Publ. Mus. Zool. Univ. Mich. 1930, no. 20, pp. 1-47.

44. Louis Agassiz, "Synopsis of the Ichthyological Fauna of the Pacific Slope of North America, chiefly from the collections made by the United States Exploring Expedition, under command of Capt. C. Wilkes, with recent additions and comparisons with Eastern types," *American Journal of Science*, ser. 2, 19 (1855):71-99, 215-31.

45. Ernst Mayr has often used the phenomenon of "sibling species" as an illustration of the difference between a purely morphological definition of species and the biological species concept. Species that resemble one another are usually found not to have much overlap in range, but sometimes extremely similar, "sibling" species share the same range. If attention were paid only to the appearance of specimens, they would all be regarded as one species, but when their reproductive behavior is noticed, the presence of two distinct

breeding networks satisfies the biologist that they are two species. In practice, the term "sibling species" is reserved for pairs of species that have fooled the experts, or still require an expert to identify them. The three buffalofish might not be called sibling species today, because both expert and fisherman can recognize them, but historically the question takes on an extra twist, because expert knowledge changes. Reeve Bailey tells me that where all three buffaloes occur together, "fishermen readily distinguish them, at least the adults," but Trautman thinks that few fishermen before 1925 were capable of distinguishing the black buffalofish from the smallmouth (Milton B. Trautman, *The Fishes of Ohio with Illustrated Keys* [Ohio State University, 1957], pp. 223, 227). Part of the reason ichthyologists have had problems, Bailey explains, is that they usually have small specimens and the young ones are much more similar to one another than the adults are.

It is very easy for the modern taxonomist to think of biological species concept as modern and the morphological approach as old-fashioned, though Mayr has pointed to naturalists of the past who seem in this respect more modern than some in our own day. In this regard the oldest published notice of the black buffalofish as distinct from the smallmouth, though useless taxonomically, is very interesting. Rafinesque wrote in 1820, "I have not seen this fish. Mr. Audubon describes it as a peculiar species, found in the Mississippi and the lower part of the Ohio [where the smallmouth was the "common" buffalo], being *entirely similar* to the common Buffalo-fish, but larger, weighing sometimes upwards of fifty pounds, and *living in separate shoals* [schools]." (Italics mine. Constantine Samuel Rafinesque, *Ichthyologia Ohiensis: or natural history of the fishes inhabiting the River Ohio and its Tributary Streams*, reprinted by R. E. Call, Cleveland, 1899, p. 113.) It was the thoughtful and thorough scholarship of Carl Hubbs which led me to see this interesting aspect of Rafinesque's much-maligned description.

46. Reeve M. Bailey, "A Systematic Revision of the Centrachid Fishes, with a Discussion of Their Distribution, Variations, and Probable Interrelationships," Ph.D. dissertation, Univ. Michigan, Ann Arbor 1938; I have not seen this work, but Dr. Bailey has explained to me by letter that his identification of Agassiz's "*sanguinolentus*" and "*bombifrons*" are based on Agassiz's descriptions, since the specimens to which Agassiz applied those names have not been located.

47. The Catalogue of the Fish Department of the Museum of Comparative Zoology shows only one specimen for some of Agassiz's new sunfish species. It also shows many hundreds of specimens of many sunfish species from various localities in his collection by the end of 1853, which again suggests that Agassiz could have felt that he knew what to expect in the way of ordinary variability or specific characters in the sunfish. The catalogue tells us which specimens Burkhardt drew, but I have been so far unable to find those drawings.

48. Jerram L. Brown, "Geographic variation in Southeastern populations of the cyprinodont fish *Fundulus notti* (Agassiz)," *American Midland Naturalist* 59(2) (1958): 477–88; Luis R. Rivas, "The taxonomic status of the cyprinodontid fishes *Fundulus notti* and *F. lineolatus*," *Copeia* (1966):353–54; E. O. Wiley, "The Phylogeny and Systematics of the *Fundulus nottii* Species Group" (Teleostei: Cyprinodontidae), *Occasional Papers of the Museum of Natural History of the University of Kansas*, 1977, no. 66:1–31. A geographic form that is distinct enough may be ranked as a subspecies or full species. The decision as to which is appropriate in a given case depends largely on what happens where the ranges of the two forms overlap. The question becomes, do they behave like sibling species, or do they interbreed freely? The decision as to specific rank becomes a matter of opinion when interbreeding occurs too commonly for them to be clearly sibling species, but not often enough to form an intermediate population. (Ernst Mayr, E. Gordon Linsley, and Robert L. Usinger, *Methods and Principles of Systematic Zoology* [New York, 1953], pp. 101–104.) Differences of opinion of just that kind exist now for the topminnows. There seems to be universal agreement, however, that the various forms under discussion do reflect measurable genetic differences among populations.

49. But he was not alone in doing so; see Samuel Garman, 'The Cyprinodonts," *Memoirs of the Museum of Comparative Zoology at Harvard College* 19(1) (1895):1-179.

50. *Baird-Agassiz Correspondence,* pp. 45, 46, 77. The cyprinodont manuscript seems to be lost. The plates, however, were finally published, forty years after they were made, in Garman's "Cyprinodonts."

51. Louis Agassiz, "Discovery of viviparous fish in Louisiana, by Dr. Dowler," *American Journal of Science,* ser. 2 (29) (1855):136.

52. I do not base this claim entirely on the Catalogue of the Fish Department of the M.C.Z., which does seem to show this, but also on the fact that Agassiz was always very careful to mention in his publications the names of people who supplied him with material, and he insisted upon it as a museum policy, because he saw it as a way of encouraging collectors. In his topminnow footnote, only "*lineolatus*" is credited entirely to another collector.

53. E. O. Wiley, personal communication.

54. Jamie E. Thomerson, "A comparative biosystematic study of *Fundulus notatus* and *Fundulus olivaceus* (Pisces: Cyprinodontidae)," *Tulane Studies in Zoology* 13 (1) (1966): 29-47; Marvin C. Braasch and Philip W. Smith, "Relationships of the topminnows *Fundulus notatus* and *Fundulus olivaceus* in the Upper Mississippi River Valley," *Copeia* (1965):46-53.

55. Wiley, "Systematics of *Fundulus.*" Although Agassiz collected large numbers of topminnows in Mobile, he had "only isolated specimens" of some of his new species (*Correspondence between Baird and Agassiz,* p. 63). Many jars of this collection were discarded from the M.C.Z. years ago, and only *F. nottii* have so far been found among the remainder. *F. nottii* is common and *F. blairae* has been found in the immediate vicinity of Mobile; *F. escambiae* has been collected about thirty miles eastward of Mobile, in Baldwin County.

56. E. O. Wiley, personal communication.

57. When Agassiz arrived in Mobile in April 1853, George R. Gliddon and Dr. Josiah C. Nott were deeply engaged in putting together a volume to honor the late Dr. Samuel G. Morton of Philadelphia, the man whose definition of species Agassiz had so admired. It was Nott's suggestion that the races of mankind were really species, which Morton and Agassiz had taken up and developed. Gliddon, former vice-consul in Cairo and, like Agassiz, once a Lowell lecturer, was "living in a shanty in the woods" (Stanton, *Leopard's Spots,* p. 162) in Baldwin County (Nott and Gliddon, *Types of Mankind,* p. xi). Agassiz very much shared the feelings of these two men that narrow-minded religious dogmas had threatened, and were still threatening, the progress of scientific truth. Agassiz agreed to contribute to their work, published in 1854 as *Types of Mankind.* Dr. Nott was with Agassiz when one form of starhead topminnow was collected, which Agassiz named *Nottii* in his honor. Gliddon was working on the archaeological portion of the book, including a "history of the art of writing," which would help to demonstrate the antiquity of humankind and multiple origin of human culture. Is it possible that discussions with Gliddon inspired Agassiz to name another one of his new topminnows "*hieroglyphicus*"?

58. This opinion, with which Dr. Wiley agrees, does not affect the taxonomic status of the more recent names, because Agassiz's poor descriptions make it impossible to be certain about what he was seeing.

59. E. C. Agassiz, *Agassiz, His Life and Correspondence,* p. 3.

60. D. S. Jordan and A. W. Brayton, "On the distribution of the fishes of the Allesherry region of South Carolina, Georgia, and Tenn.," *Bull. U.S. Nat. Museum* 12(1878):7-95; see pp. 31, 48.

61. Charles Darwin, *On the Origin of Species* (London, 1859; facsimile, Harvard University Press, 1964), pp. 484, 490.