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Geographic Isolation in Darwin's Thinking: The Vicissitudes of a Crucial Idea

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I have lately been especially attending to Geograph[ical] Distrib[ution], & [a] most splendid sport it is,—a grand game of chess with the world for a Board.

Charles Darwin to C. J. F. Bunbury, 21 April 1856 (*Natural Selection* [1856-58:526])

The fundamental role that the geographical distribution of species played in Darwin's evolutionary thinking can hardly be overestimated. As Darwin later testified, such evidence provided two of the three main classes of facts that undermined his previously orthodox faith in the permanence of species. In his *Autobiography* he recalled along these lines:

During the voyage of the *Beagle* [1831-36] I had been deeply impressed by discovering in the Pampean formation great fossil animals covered with armour like that on the existing armadillos; secondly, by the manner in which closely allied animals replace one another in proceeding southwards over the Continent; and thirdly, by the South American character of most of the productions of the Galapagos archipelago, and more especially by the manner in which they differ slightly on each island of the group; none of these islands appearing to be very ancient in a geological sense.

It was evident that such facts as these, as well as many others, could be explained on the supposition that species gradually become modified; and the subject haunted me (1958 [1876]: 118-19).[1]

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The great significance of geographical distribution for Darwin's evolutionary argument remained undiminished when, to a largely unprepared scientific world, he finally presented his theory of evolution by natural selection. Indeed, geographical distribution was the only subject to receive two chapters in the *Origin of Species* (1859), and many of Darwin's readers, like Darwin himself, found these discussions the most convincing.

In spite of the great importance that Darwin attached to geographic variation, his thinking on this subject, particularly in relation to geographic isolation in species formation, underwent significant modification during his lifetime. It is the crucial problem of geographic isolation—was such isolation always necessary for the multiplication of species?—that provides the principal focus of this essay. Few problems reflect the changes in Darwin's evolutionary thinking, or the theoretical difficulties that he sought to overcome, as vividly as does this issue of geographic isolation. Yet the nature of the stages through which his thinking passed, together with the precise reasons prompting his vacillations on the subject of isolation, have remained problematic to Darwin scholars. The considerable complexity of the scientific issues, issues that involve not only the problem of geographic isolation, but, more importantly, Darwin's whole concept of species, has not made the historian's task any easier.[2] Finally, as Mayr (1959:221) pointed out two decades ago, "Darwin's contribution to the subject is particularly difficult to evaluate since he was more plagued with doubts on this than on almost any other evolutionary question." And well Darwin might have been perplexed, since the issue was not resolved for more than a half century after his death.

Here I shall consider three general questions concerning Darwin's changing views on isolation as an evolutionary factor. *First,* how, and in what ways, did the evidence of geographical distribution inspire his early (1837–44) evolutionary thinking following his return from the voyage of the *Beagle*? *Second,* why did Darwin, after writing the Essay of 1844, come to believe that species might arise sympatrically (i.e., locally, without spatial segregation)? And *third,* to what extent did Darwin succeed in reconciling his views after 1859 with the criticisms presented on this topic by the German naturalist and explorer Moritz Wagner (1868)?

This essay, which represents part of a more extensive study of Darwin's thinking (see note 1), has a special meaning to me in relation to Ernst Mayr. My interest in Darwin initially grew out of an opportunity to retrace the voyage of the *Beagle* during the summer of 1968. This project, to which Ernst Mayr lent his considerable support, resulted in the making of a series of short films about Darwin's voyage experience (Adams and Sulloway 1970). From this initial interest in Darwin grew both a senior honors thesis on the *Beagle* voyage (Sulloway 1969) and the following essay, an early draft of which was presented to Mayr's graduate course on evolutionary theory in 1971. This course was a learning experience that no one who has shared in it will ever forget. Inasmuch as the topic of my essay is intimately bound up with his researches both as a biologist and as a historian of science (Mayr 1942, 1947, 1959, 1963, 1976), my contribution to this *Festschrift* has inevitably taken the form of a dialogue with him.* I have drawn upon his thinking, published and unpublished, in a liberal fashion, and if I have disagreed with him on certain points, it is only a sign of the inevitable growth of understanding that his own researches, together with the accelerating progress of Darwin studies (Greene 1975), have made possible.

Finally, one cannot help adding that Mayr's historical views on these subjects have changed so greatly over the last twenty years that his students and colleagues often risk finding themselves in a position similar to that which he enjoys recounting about a young associate of Konrad Lorenz's. It seems that the young disciple, after having convincingly demolished a theory proposed by Lorenz many years before, and having excitedly communicated this new insight to Lorenz himself, was abruptly informed: "But I refuted that theory myself years ago!" It is in a profound spirit of admiration for the ever-flexible development of Mayr's own thinking that I venture in this *Festschrift* to publish on a subject that has been so central to his life's work.

The Early Focus of Darwin's Evolutionary Thinking (1837–44): Populations and Their Geographic Isolation

I have already mentioned that Darwin's concept of species is closely linked to his stand on geographic isolation. With the rapid progress of Darwin studies over the last two decades, much new light has been shed upon his species concept. In 1959, prior to the publication of his four

*Indeed, this essay could not be otherwise than a dialogue with Ernst Mayr, since he has coined so many of the relevant technical terms. I may refer in this connection to *sibling species* (introduced as a translation of German and French equivalents), *superspecies* (from Rensch's German term *Artenkreis*), *founder principle, allopatric* speciation, and *sympatric* speciation—all of which will be encountered in this essay. For the clarifying influence of these and other evolutionary terms, historians of science, as well as biologists, must be grateful to Mayr. See also Mayr (1978).

private notebooks on the transmutation of species (1837–39), Ernst Mayr was forced to confess: "I have looked in vain in Darwin's writings for an indication that he ever considered the species as anything but a 'more distinct variety.' Not realizing that the species is a 'reproductively isolated population,' a concept which was definitely familiar to many of his contemporaries (Mayr 1957*a*), Darwin was quite unable to focus on the essential aspects of speciation and on the role of isolation" (1959:222). Since the publication of the transmutation notebooks (de Beer 1960–61, and de Beer et al. 1967), it is possible to argue that Darwin *did* entertain a clearly defined biological species concept during the earliest stages of his evolutionary thinking. It is therefore of interest to account for the later shift in Darwin's views; for Darwin had the modern conception of species within his grasp for at least two full years before he allowed it to slip away in favor of considering the species as just a "more distinct variety." In the present section of this essay I shall review the various intellectual circumstances that temporarily established this biological species concept in Darwin's early thinking. In the section that follows, I shall take up the question of why he abandoned this modern orientation towards species. By referring to the "modern" viewpoints on species and geographic isolation, I should state at the outset that I am not endorsing a Whiggish historiography of science. Rather, I have found it necessary to cite these newer conceptions because they have been important in the occasional misperception of Darwin's own views, and because they also provide a convenient indication of the difficulties he faced.

The Galapagos Experience: Darwin's Ornithological Collections

Darwin's "Journal," a small pocket diary in which he recorded the main details of his life, contains the following famous entry under the year 1837: "In July opened first note book on 'Transmutation of Species'—Had been greatly struck from about Month of previous March on character of S. American fossils—& species on Galapagos Archipelago. These facts origin (especially latter) of all my views" (de Beer 1959:7). What had particularly impressed Darwin about his Galapagos collections was the fact that virtually all the land birds (25 of 26 species), although closely related to South American forms, were endemic not only to the archipelago as a whole, but, in some instances, to specific islands within that group. By March of 1837, John Gould, the British ornithologist who worked upon Darwin's voyage collections, had ascertained that three closely allied species of Galapagos mockingbirds (*Orpheus*) represented one another geographically on different islands within the archipelago, each island possessing *one* form only (Gould 1837*b*). Gould had also named twelve closely related species of finches, which he placed in one entirely new genus (*Geospiza*) and three allied subgenera (Gould 1837*a*). These forms, too, Darwin began to suspect, must replace one another geographically on the different islands within the archipelago.[3] Even a species of gull (*Larus fuliginosus*) was pronounced specifically distinct by Gould, as were two other species from among the eleven waders and water birds!

Not all naturalists, including Darwin, were initially as confident as Gould seemed to be in these remarkable Galapagos designations. As Darwin later recalled in the *Origin*, "Many years ago, when comparing, and seeing others compare, the birds from the separate islands of the Galapagos Archipelago, both one with another, and with those from the American mainland, I was much struck how entirely vague and arbitrary is the distinction between species and varieties" (1859:48; see also *Natural Selection* [1856–58:115]; and 1909 [1844]:82, 197). Nevertheless, Darwin was forced by the bulk of Gould's taxonomic judgments, which were full of many similar surprises regarding Darwin's continental collections, to admit that so-called representative species are far more common in nature than he had previously suspected. Simultaneous taxonomic analysis of Darwin's collection of South American mammalia, particularly the mice, greatly reinforced this general conclusion (see also Herbert 1974:244, 255–56). Staggered by such repeated findings, Darwin surmised that prolonged geographic isolation of populations under slightly differing environmental conditions must be capable of producing new species. The curious bond, in time and in space, as exhibited by the past and present mammalia of the South American continent and, geographically, by the representative species of neighboring districts, was thus reduced by Darwin to one and the same explanation: the organic affinity of common descent.

Within four months of his conversion to the theory of transmutation, Darwin had opened the first of his series of famous notebooks (*B, C, D,* and *E*) on this subject. In notebook *B* (July 1837 to February 1838), Darwin developed the idea of geographic isolation as his basic mechanism of evolutionary change: "According to this view animals on separate islands, ought to become different if kept long enough apart, with slightly differ[ent] circumstances.—Now Galapagos tortoises, mocking birds, Falkland fox, Chiloe fox.—English and Irish Hare.—"

(*B* 7). Also aware that species must remain uniform, owing to continual interbreeding, Darwin surmised that isolation between populations is what allows the "multiplication" of species rather than the uniform phyletic change that would otherwise occur with time (*B* 5, 7, 17, 20–21, 170, and 210, excised). Thus, he asks: "Why are species not formed during ascent of mountain or approach of desert?—because the crossing of species less altered prevents the complete adaptation which would ensue [with isolation]" (*B* 210, excised).

To this law of geographic isolation, Darwin lost no time applying the understanding of geological and climatic changes in the earth's history that he had developed during the five-year *Beagle* voyage, while under the tutelage of Lyell's famous *Principles of Geology* (1830–33). One such model was premised upon the continual elevation and subsidence of large tracts of the earth's surface. "Species formed by subsidence," Darwin inferred. "Java and Sumatra. Rhinoceros. Elevate and join [and if they] keep distinct, two species made; elevation and subsidence continually forming species" (*B* 82). Similarly, with gradual changes in climate, populations would be dispersed and isolated geographically during one period and then rejoined during another: "Speculate on multiplication of species by travelling of Climates & the backward & forward introduction of species" (*B* 202, excised).

Darwin was less successful during this early period (prior, that is, to his discovery of natural selection) in explaining the extinction of species. His temporary solution in the spring and summer of 1837 was to adopt Brocchi's view (in Lyell 1830–33, 2:128), which was that species, like individuals, have fixed lifetimes, and that such temporal spans can only be transcended by the rejuvenating effects of evolutionary change. "They die," he speculated, "without they change, . . . it is a *generation* of *species* like a generation of *individuals* . . . . If individual cannot propagate, he has no issue; so with species" (*B* 63–64; see also Gruber 1974:135–36, 165).

Darwin's Biological Species Concept

It was in the context of this dynamic conception of interbreeding populations undergoing isolation through climatic and geological changes that Darwin articulated a biological species concept in his first two transmutation notebooks. Indeed, he seized eagerly upon this conception and made it central to his plans for taxonomic reform within a system whose vagaries he had only so recently experienced. His principal preoccupation was the following: Are evolving species real, and if so, what happens when they meet after having speciated during isolation? Early in the first notebook Darwin maintains: "A species as soon as once formed by separation or change in part of country, repugnance to intermarriage—settles it" (*B* 24; see also *B* 33). Then, in the second notebook, he reaffirms the dynamic, biological reality of species with the words: "As *species* is real thing with regard to contemporaries—fertility must settle it" (*C* 152; see also Ghiselin 1969:91–92). A few pages later, Darwin draws an insightful distinction between sterility (a postmating phenomenon) and other aspects of what, following Dobzhansky (1937), are now termed "isolating mechanisms." Darwin asserts: "My definition of species has nothing to do with hybridity, [but] is simply, an instinctive impulse to keep separate" (*C* 161, excised).

Darwin was fully aware, under such a dynamic conception of species, how crucial the evidence of geographical ranges would be to proper systematic classifications. As he argues at one point in the first notebook:

> ... between species from moderately distant countries there is no test but generation (but [indirect] experience according to each group) whether [they are] good species, and hence the importance naturalists attach to geographical ranges of species.
>
> Definition of species: one that remains at large with constant characters, together with other beings of very near structure.—Hence species may be good ones and differ scarcely in any external character (*B* 212–13).

In this last passage and elsewhere, Darwin recognizes the principle of "sibling species," or forms that are morphologically so close as to be almost indistinguishable, except on the basis of habits. (He mentions the famous case of the English willow wren, a sibling species of the chiff-chaff as well as of the wood wren. See *C* 125; *D* 102; and John Gould [1837*c*, 2:131], whom Darwin cites as his ornithological authority for this example.)

Darwin's proposals for taxonomic reform, announced in the second notebook during the spring of 1838, show how deeply his understanding of the species as a biologically dynamic reality had influenced his thinking at this time. If pronounced geographical races do not meet, he asks, how is one to justify the use of a specific name for each morphological variant? Darwin's solution was to give the *subgenus*, or what today would be called a "superspecies" (Mayr 1931), greater systematic weight in such cases:

Scheme for abolishing specific names & giving subgenera true value—as in Opetiorhync[h]us fuliginosus
(a) Falklands
(b) T. del Fuego differ from
(c) Chiloe
(d) Chile
rupestris—good species
?O[rpheus] modulator + O[rpheus] patagonicus. till neutral ground ascertained call them varieties but two [South American] ostriches good species because [they] interlock (*C* 126; see also Darwin 1841:60–61, 66–69).

Darwin also proposed that species designated only by "analogy" should be specially marked as such. "Analogy to be guide in island species,—each describer giving his test namely [that the isolated forms] differ as much as those (naming them) which are found together [without interbreeding]" (*C* 127, 129). Through these novel taxonomic measures, Darwin thought that many "false species" would be banished from systematics.

Darwin also foresaw such taxonomic reforms as being highly conducive to better observations in the field. "If two species come over to this country['s museums] without range or habits ascertained," he suggested, "put them [down] as (a) (b) until data be given.—This will aid in preventing the chaos,—will point out what to observe,—will aid us in physiology. tell traveller what to observe,—if he knows he has done least part [i.e., only procuring a few specimens],—that he will not have brought home [a] new species until he can show range & habits" (*C* 127). Darwin's far-sighted thoughts about taxonomic reform could be heeded with profit today. As Mayr (1963:499) has recently remarked about this still unresolved dilemma of systematics: "The rigidity of zoological nomenclature forces the taxonomist to record borderline forms either as subspecies or as species. An outsider would never realize how many interesting cases of evolutionary intermediacy are concealed by the seeming definiteness of the species and subspecies designations." For Darwin personally, however, the theoretical revolution he sought to establish in natural history ulimately took precedence over the more practical revolution that he eagerly contemplated in systematics during the late 1830s. The topic was never developed in his subsequent published works.

Isolation and Natural Selection

Although convinced in the transmutation notebooks that isolation was the key to speciation on islands as well as on continents that are divided by major geographical barriers, Darwin was puzzled by the presence of representative species on the large, flat tracts of land characterizing such regions as Patagonian South America. To cite a particularly troublesome instance, during the voyage of the *Beagle,* Darwin had established the existence of a second and smaller species of *Rhea* (or ostrich) inhabiting the southernmost plains of Patagonia. As he also discovered, the range of this second species overlaps with that of the larger and more northerly form at the Rio Negro, across which the ostriches frequently swim. Forty years later he described to Karl Semper his post-voyage doubts about cases like this: "I remember well, long ago, oscillating much; when I thought of the Fauna and Flora of the Galapagos Islands I was all for isolation, when I thought of S. America I doubted much" (*Life and Letters,* 3:160, letter of 26 November 1878). To begin with, Darwin seriously entertained the notion of *per saltum* evolution, as the following passage, jotted down about March 1837, reveals: "Speculate on neutral ground for 2 Ostriches: bigger one encroaches on smaller;—change not progressive; produced at one blow, if one species altered" (*Red Notebook,* p. 127 [Barlow 1945:263]). This same belief in sudden, sympatric speciation is echoed with equal force in the first transmutation notebook (*B* 8-9); and the whole idea fits in admirably with the notion that species, like individuals, are generated suddenly and also suffer eventual death. "In [the] production of varieties," Darwin asked by way of analogy, "is it not per saltum" (*B* 278, about February 1838).

It was Darwin's discovery of a new and gradual mechanism of evolutionary change in September 1838 that apparently put an end to such saltationist speculations. Throughout the spring and summer of 1838 his study of animals under domestication, together with the perfecting techniques of the breeder, had convinced him that improvements in domesticated forms are effected by the "picking" of desired individuals. But how could this principle be applied to a state of nature? In his *Autobiography,* Darwin recalls his solution to this problem:

> . . . fifteen months after I had begun my systematic enquiry, I happened to read for amusement Malthus on *Population* [1798; 1826 ed.], and being well prepared to appreciate the struggle for existence which everywhere goes on from long-continued observation of the habits of animals and plants, it at once struck me that under these circumstances favourable variations would tend to be preserved, and unfavorable ones to be destroyed. The result of this would be the formation of new species. Here, then, I had at last got a theory by which to work . . . (1958 [1876]:120).

In addition to providing him with a mechanism of evolutionary change, Darwin's reading of Malthus completed the revolutionary shift in his thinking about species (in terms of populations rather than "types") that had begun with his conversion to a transmutationist position in March 1837 (Ghiselin 1969:49, 59; Gruber 1974:164 n.; Mayr 1977). Finally, the theory of natural selection plugged the gap in the theory of extinction that had been created by Darwin's abandonment of the species life-span theory (with its alluring parallels to the sudden birth and death of individuals). In the second edition of his *Journal of Researches* (1845: 174–76), Darwin replaced a brief allusion to the notion of species life spans with a discussion of how Malthus's doctrine of population pressure neatly resolves the mystery of extinction.

For roughly a decade following his discovery of natural selection, Darwin placed more stress than ever upon spatial isolation and upon the facts of geographical distribution in explaining the origin of new forms. In his pencil Sketch of 1842 and again in his Essay of 1844, he cited the evolutionary importance of mountain ranges, seas, deserts, rivers, and, for alpine species, the intervening lowlands between mountain peaks. Writing of the speciation process in the Essay of 1844, Darwin asserted as the main prerequisite: "... isolation as perfect as possible of such selected varieties; that is, the preventing of their crossing with other forms; this latter condition applies to all terrestrial animals, to most if not all plants and perhaps even to most (or all) aquatic organisms" (1909 [1844]:183; see also pp. 163, 168, 178, 189–90). To his friend Joseph Hooker, Darwin stated much the same argument in a contemporary letter: "With respect to original creation or production of new forms, I have said that isolation appears the chief element. Hence, with respect to terrestrial productions, a tract of country, which had oftenest within the late geological periods subsided and been converted into islands, and reunited, I should expect to contain [the] most forms" (*Life and Letters,* 2:28, letter of 1844). Past climatic and geological transformations, then, were Darwin's solution in 1844 to the sympatric coexistence of closely allied species.

Such theoretical views illustrate the height of Darwin's endorsement of geographic isolation as a necessary precursor of speciation. Indeed, the Essay of 1844 suggests a certain overreliance upon geographic isolation. Here he did not sufficiently stress the degree of phyletic divergence (and consequent production of new phyletic forms) that can occur independently of the multiplication of species. At this time he assumed that phyletic evolution would soon come to a standstill, once geological or climatic changes had ceased and once organisms had become adapted to their new surroundings (1909 [1844]:189–90, 196). He therefore required continual elevation and subsidence of continental areas in order to create new ecological stations, new and isolated communities of organisms, and hence new potentials for phyletic evolution. Although Darwin's assumptions about the rate of phyletic evolution were in large part correct, he had yet to grasp what he later termed the *principle of divergence* and to see that this principle is constantly promoting phyletic diversification independently of the multiplication of species.

From Geographic to Sympatric Speciation

Why did Darwin, after rejecting the idea of sympatric speciation *per saltum* in the late 1830s, later accept two forms of sympatric speciation premised upon "partial" and "ecological" isolation, respectively?[4] Under the first of these two conceptions, he postulated that geographical races might breed on the confines of their ranges. Occasional intermediate forms, being present within a narrow border territory in comparatively small numbers, would generally be liable to extinction, permitting the establishment of good species without a connecting link (*Origin* [1859:176–77]). Darwin's second and more extreme endorsement of sympatric speciation drew upon the hypothesis of ecological isolation through such behavioral processes as incipient species tending to haunt different stations, to breed at different times, or to pair preferentially with individuals most closely resembling themselves (1859:103).

According to some commentators, Darwin's failure to think clearly about the role of geographic isolation stemmed from his failure to come to terms with the problem of blending inheritance (Romanes 1897, 3:102, 125–27; Vorzimmer 1965; 1970:170–84). This historical interpretation is premised, as we shall see, upon a basic misreading of the *Origin of Species* (1859) and reflects the various difficulties that have long been associated with the proper understanding of Darwin's views on isolation. Mayr (1959; 1976:120–28), who has examined the shift in Darwin's thinking about speciation more thoroughly than anyone else, posits four general circumstances as being responsible for Darwin's error. Mayr's four points bear a brief review.

1. Darwin's conceptual failure to distinguish between individual variations and subspecies. Darwin, Mayr points out, was repeatedly guilty of confusing individual variations with subspecies, owing to his indiscriminate use of the term "variety" to cover both cases. This important source of confusion is related to Mayr's second observation about Darwin.

2. Darwin's morphological species concept. By 1859, Darwin was defining a species as just "a 'more pronounced variety,'" using a morphological approach as the core of his definition (1859:52, 56, 58–59, 485).* By failing to emphasize the concept of species as "an interbreeding population," he apparently lost sight of the necessity of geographic isolation in the speciation process. Mayr's third point follows logically upon his second.

3. Darwin's failure to distinguish between the multiplication of species and phyletic evolution. Darwin repeatedly referred to the production of "new species" ambiguously within the dual context of speciation and phyletic evolution. According to Mayr, Darwin's confusion of these two evolutionary categories completely clouded the issue of isolation and its crucial role in speciation.

4. Darwin's desire for a single-factor explanation. Darwin, when he did refer to the importance of isolation in the *Origin* (1859:105), tended to vacillate upon the matter, as if isolation were somehow incompatible with his theory of natural selection. (Natural selection is favored by intense selection of large numbers of variations, and hence by a large population, whereas isolation implied to Darwin a smaller population removed from the normal intensity of the struggle for existence.)

Mayr's four points, and Darwin's (1859) confusion with regard to them, are indeed relevant to Darwin's altered views on isolation as an evolutionary mechanism. I do not, however, believe these four points are sufficient to account for Darwin's later thinking on this subject. As is certainly known to Mayr, it is possible to find passages in Darwin's writings where he is fully lucid about these four conceptual distinctions, which elsewhere he confuses or ignores. As is so frequently the case with Darwin, it is the conceptual emphasis rather than a clear-cut oversight that requires explanation here. Especially, one must still ask why Darwin, who at one time held both a "biological" species concept and a correct assessment on the role of isolation, *gave up* these modern viewpoints, apparently changing in the process his whole concept of species. Neglect of this important question also impairs the analyses of Romanes (1897) and Vorzimmer (1970), with their respective (and contrasting) attempts to blame Darwin's error upon his disregard for, and faulty

*I agree, however, with Ghiselin (1969:59, 89–91, 101–02) when he says that Darwin's concept of species was more properly an "evolutionary" one, with occasional lapses into morphological habits of thought. Mayr, in commenting upon an earlier draft of this paper, writes in this connection: "Darwin really had two [species] concepts simultaneously. When he discussed adaptation he was thinking populationally [and hence in 'evolutionary' terms]. When he discussed speciation he was thinking typologically [and hence in 'morphological' terms]." See also Mayr (1963:6).

endorsement of, pre-Mendelian blending inheritance. Why, we would ask, did Darwin suddenly make these "errors" in 1859, when he was fully aware as early as 1837 that unimpeded crossing poses an insurmountable obstacle to the multiplication of species? I would like to supplement Mayr's formal analysis of the problem, which captures what I believe are the telltale "symptoms" rather than the explicit causes of Darwin's reversal, with a more detailed historical approach within which these various conceptual issues may be systematically reappraised.

At least four important historical considerations may be mentioned as having influenced Darwin's thinking on species between 1844 and 1859: (1) his taxonomic work on barnacles (1846–54); (2) tactical considerations in connection with his writing of the *Origin* (1859); (3) his attempt to reconcile his theory with differing organisms (particularly plants) and their diverse patterns of reproduction, mobility, and geographical distribution; and (4) his principle of divergence, formulated in 1852. The first two of these four historical influences relate more directly to Darwin's species concept than to the issues of speciation or geographic isolation per se. In this connection I will argue that his species concept and his position on geographic isolation underwent more independent lines of development after 1844 than has been supposed by Mayr, and that the first topic (species) should not be imputed as such a sufficient cause of the second (isolation). I will also attempt to show that Darwin's position on geographic isolation was considerably more definite and sophisticated than has generally been realized, although frequent misunderstandings of his position have not been without good cause. Foremost among these sources of misunderstanding are the abridgment of his argument in the *Origin* and the repeated ambiguities of terminology and ideas mentioned by Mayr.

Darwin as Taxonomist

In 1846 Darwin took up the study of a peculiar form of barnacle that he had encountered many years before during the *Beagle* voyage. His attempt to elucidate the structure of this unusual species eventually led him to spend eight years on the subject of barnacles. His three monographs on the whole subclass of cirripedes still stand as the definitive treatment of this zoological group.

Darwin's devotion of so much time and energy to the study of barnacles has long remained a puzzle to his biographers, who have frequently treated this episode as a symptom of escapist procrastination.

But as Ghiselin (1969:103–30) points out, barnacles proved to be an extremely instructive subject from an evolutionary point of view, and little of Darwin's time was actually wasted on these pioneering studies. Furthermore, Darwin had been anxious to establish his reputation as a systematist before publishing his heterodox views on the species question, a course of action that his close friend Joseph Hooker had strenuously advised him to follow (*Life and Letters*, 2:31, 39).

That Darwin was prompted by his work on barnacles to see the species as simply a more "well-marked variety" is corroborated by his colorful description to Hooker, in 1853, of the numerous systematic problems that he had encountered during his work: "After describing a set of forms as distinct species, tearing up my MS., and making them one species, tearing that up and making them separate, and then making them one again (which has happened to me), I have gnashed my teeth, cursed species, and asked what sin I had committed to be so punished" (*Life and Letters*, 2:40). In *Natural Selection*—the "big book" interrupted in 1858 by Alfred Russel Wallace's independent formulation of Darwin's theory—Darwin repeats this account of his taxonomic frustrations almost verbatim, adding that "To the naturalist who looks at species as not essentially differing from varieties, . . . the occasional blending by intermedial forms . . . will not be [so] wonderful." (1856–58:103). His relativistic solution to his taxonomic problems found ample reinforcement in the overall strategy of the *Origin of Species*.

Tactical Considerations

Darwin's *Origin of Species* is unique among works of science for being, as he himself expressed it, "one long argument" (1859:459). Indeed, the *Origin* is as much a masterful argument *against* creationism as it is *for* evolution. In this work, Darwin explicitly argues against the creationist theory, comparing its theoretical consequences to that of the evolutionary point of view, on at least twenty-one occasions. The number of implicit arguments against creationism is even more numerous. (For this and other insights about the structure of Darwin's *Origin*, Darwin scholars are indebted to Ernst Mayr's Introduction [1964] and greatly expanded Index to the facsimile edition of Darwin's work.) The structure and goals of Darwin's agrument therefore constitute important determinants of his thinking, and nowhere is this influence more apparent than in his concept of species. Three main tactical considerations are relevant in this connection.

SPECIES AS MERELY "WELL-MARKED VARIETIES." In stressing the arbitrary distinction between species and varieties, Darwin was hoping to convince his colleagues that their taxonomic problems were largely a consequence of the mutability of species. Inasmuch as his creationist peers were largely morphologists and typologists in their species concept, Darwin spoke to them in their own language and tailored his argument so as to exploit the inevitable sense of frustration that virtually all naturalists had at one time or another experienced in their taxonomic work. (See also Ghiselin 1969:82, 93–94.) Darwin was simply echoing the predicament of the typologist when he asserted in the *Origin*: "If a variety were to flourish so as to exceed in numbers the parent species, it would then rank as the species, and the species as the variety; . . . or both might co-exist, and both rank as independent species" (1859:52). As an unfortunate result of this general strategy, he lost sight of his earlier and dynamic conception of species, a conception that had reflected his work as a field naturalist rather than as a systematist and tactician. This conceptual transformation was greatly assisted by his commitment to a second major strategic thesis: the incidental nature of sterility between species.

SPECIES AND STERILITY. Mutual sterility or any other impediment (instinctual, mechanical, or ecological) to interbreeding among closely related organisms is what determines the success of the speciation process after two geographical isolates come into secondary contact. In 1837, Darwin had clearly understood this point, and he had accordingly made it fundamental to his definition of species. Why did he abandon this key insight?

Under the creationist point of view, species were believed to be endowed with a sterility toward all other species in order to prevent complete chaos of life forms in nature (*Origin* [1859]:245). So anxious was Darwin to show that sterility between species was neither absolute nor specially endowed, that he eventually came to underrate its diagnostic importance as an essential criterion of species. The more he examined the experimental literature on this complex subject, the more he felt justified in this belief. Not only had experimental botanists like Joseph Koelreuter (1733–1806) and Karl Friedrich Gaertner (1772–1850) shown that sterility graduates insensibly between varieties and species, but there were other botanists who were willing to place in separate genera forms that later proved fertile together in breeding experiments (*Origin* [1859]:251–53). It was "begging the question," Darwin remarked in the Essay of 1844, to call such divergent but mutually fertile forms varieties, as Gaertner and Koelreuter regularly did, based upon their creationist's "sterility test" of species (1909 [1844]:98; 1859:246–47).[5] By the time he wrote the *Origin,* Darwin had demoted the test of sterility from the most important to a "secondary" consideration (after "trueness or the absence of variability") in his definition of species. (See *Natural Selection* [1856–58:225]; cf. the Essay of 1844 [1909:96].) Such views also harmonized better with his basic belief that "there is no fundamental distinction between species and varieties" (1859:278).

Yet Darwin (1859:245), unlike Romanes (1886, 1897), Gulick (1888), Wallace (1889), and numerous other Darwinians, fully understood that natural selection does not promote sterility, but only an aversion to crossing once a certain amount of sterility has already been incidentally acquired. In short, Darwin's insight into the secondary nature of sterility was ahead of his time, like so many of his ideas, but this insight nevertheless reinforced his mistaken conviction that species do not differ essentially from varieties.

LOVE VERSUS STRIFE: OR WHAT HAPPENS WHEN TWO GEOGRAPHIC RACES MEET? Time and time again in the *Origin,* just as one thinks Darwin is about to discuss the issue of crossing between geographic races and to reaffirm in this connection a biological species concept, he instead asks which form will triumph over the other in the struggle for existence. A passage from his *Natural Selection* conveys this logic most explicitly: "Such [isolated] forms are often called by naturalists representative or geographical species, races or varieties: they are maiden knights who have not fought with each other the great battle for life or death. But, whenever . . . they meet, & come into competition, if one has the slightest advantage over the other, that other will decrease in numbers or be quite swept away" (1856–58:227; see also *Origin,* 1859: 177). Mutual competition, not sexual attraction, dominated Darwin's argument in the *Origin.*[6] For a book whose novelty and revolutionary message resided in the theory of natural selection, Darwin's preoccupation with struggle was hardly surprising.

Each of the above three tactical considerations—Darwin's morphological species definition, his stand on sterility, and his preoccupation with competition among geographic races—are already manifest in his Sketch of 1842 and Essay of 1844. By the time he wrote *Natural Selection* (1856–58), his tactical orientation had become more formalized still. Above all, the severe abridgment of his big book into the *Origin of Species* greatly enhanced his tactical concerns by placing a further premium on logical rigor.

Thus far I have dealt with two of the four major historical influences upon Darwin's post-1844 thinking about species: his taxonomic work with barnacles and his intellectual development as a tactician. Both influences, by transforming his definition of species, turned his attention away from reproductive isolation as a formal criterion of species. By themselves, however, these two influences did not prompt Darwin to endorse a sympatric theory of speciation. Rather, it was the next two influences that were most directly responsible for his change of heart on this topic.

The Diversity of Life Forms

As a theory, sympatric speciation seems most plausible for hermaphroditic, parthenogenic, and asexual forms, as well as for organisms that do not disperse themselves widely within a given habitat (Dobzhansky 1951:205; Ghiselin 1969:147–48). In the Essay of 1844, Darwin had barely raised this issue of the differences between organisms. By 1859 he was much more fully aware of these special conditions and of the need to present a theory of speciation that would encompass them all. In the *Origin,* Darwin argued that among organisms that do not unite for each birth, and likewise among organisms that wander little but reproduce at a very rapid rate, a new variety might arise and spread without spatial isolation (1859:103).[7] On the other hand, among organisms that unite for each birth and are highly mobile, he believed that spatial isolation would be virtually indispensable for speciation. "Hence in animals of this nature," he asserted in the *Origin*, "for instance in birds, varieties will generally be confined to separate countries; and this I believe [altered to 'find' in the 6th edition] to be the case" (1859:103; see also p. 48; and *Natural Selection,* pp. 138, 241, 255–56). Darwin's mature views on geographic isolation are, therefore, closely tied to the particular organism he has in mind whenever he makes a statement on this subject. Much of the confusion about his theory of speciation derives from a failure to appreciate this important point.

Particularly in the case of plants, which, unbeknown to Darwin, speciate by the special genetic mechanism of *polyploidy* (a sudden increase in chromosome number), he felt that speciation might well be possible without major geographic isolation. He may not have understood the unique genetic mechanism allowing sympatric speciation in plants, but under the botanical tutelage of Joseph Hooker, H. C. Watson, Alphonse de Candolle, and various other contemporary botanists, he was fully aware of the negative, as well as positive, evidence that plants presented for the theory of geographic isolation. (Approximately one-third of all flowering plants have originated sympatrically by polyploidy, and the rate is much higher for certain botanical forms within this group. See Stebbins 1950:300–01.) Darwin, who after 1844 drew heavily upon plants for his evidence concerning both variation and geographical distribution, was clearly bothered by such recalcitrant botanical facts. Writing about this subject in an unused fragment from *Natural Selection,* he asked himself: "No doubt here comes in the question of how far isolation is necessary, 'I shd' have thought more necessary than [botanical] facts seem to show it" (p. 582; fragment dated November 1854).

To appreciate the full extent of Darwin's dilemma, one must also consider what botanists themselves had to say on this perplexing issue. Foremost among these was Alphonse de Candolle (1806–93), the Swiss naturalist whose masterful two-volume *Géographie botanique raisonnée* appeared in 1855, just four years before the *Origin of Species.* Like Darwin in his Essay of 1844, de Candolle insisted repeatedly that isolation was the major source of new botanical forms. What is more, de Candolle accounted for many of these new forms—namely, the "representative species" that replace each other geographically—by the heterodox notion of transformation (1855, 2:1093, 1098)! But de Candolle also maintained that many closely related species were to be found intermingled in nature, and these species, which he considered more "real" than representative forms, he attributed to special creation.* Such forms were clear evidence, he believed along with his complimentary reviewer Joseph Hooker (1856:153), that time and isolation could not have given rise to all species (1855, 2:1098, 1122–23).

Darwin was very impressed by such botanical arguments, and he later endorsed de Candolle's views on isolation, together with Joseph Hooker's "excellent remarks" about them, in *Natural Selection.* After extolling the evolutionary virtues of isolation, Darwin warned in this connection:

*Thomas Wollaston (1856) upheld an identical point of view about the origin of species in a volume dedicated to Charles Darwin, "Whose researches, in various parts of the world, have added so much to our knowledge of Zoological geography" (p. iii). From his study of insects in the Madeira Islands, Wollaston was "driven to acknowledge that isolation *does,* in nearly every instance, in the course of time, affect, more or less sensibly, external insect form" (1856:91). By this principle, Wollaston accounted for numerous representative species on the separate islands of the Madeira group. Regarding *real* species and the doctrine of transmutation, he nevertheless remarked: "It does indeed appear strange that naturalists, who have combined great synthetic qualities with a profound knowledge of minutiæ and detail, should ever have upheld so monstrous a doctrine as that of the transmission of one species into another. . . . The whole theory is full of inconsistencies from beginning to end; and from whatever point we view it, it is equally unsound" (1856:186, 188).

"It must not, however, be supposed that isolation is at all necessary for the production of new forms" (1856–58:254). Clearly, to convince such friendly experts as de Candolle and Hooker that real, nonisolated species had originated by natural means, Darwin was obliged to account for the seeming fact of sympatric speciation in plants. Darwin's solution was intimately associated with his principle of divergence.

The Principle of Divergence

In his *Autobiography,* Darwin describes how the principle of divergence finally came to him one day, in 1852, as he was riding in a carriage:

> But at that time [1844] I overlooked one problem of great importance; and it is astonishing to me, except on the principle of Columbus and his egg, how I could have overlooked it and its solution. This problem is the tendency in organic beings descended from the same stock to diverge in character as they become modified. That they have diverged greatly is obvious from the manner in which species of all kinds can be classed under genera, genera under families, families under suborders, and so forth. . . . The solution, as I believe, is that the modified offspring of all dominant and increasing forms tend to become adapted to many and highly diversified places in the economy of nature (1958 [1876]:120–21).

In the *Origin,* almost half the chapter on natural selection is devoted to this crucial principle and to the "divergence of character" that it explains. As Darwin conceived of it, evolutionary divergence results from natural selection's tendency to favor the most divergent varieties, species, genera, and other higher groups, that is to say, those forms that are in least competition with one another. Divergent varieties, he reasoned, should tend to exterminate their parent forms on the model of unconscious selection (a process by which the breeder gradually improves his domesticated stock by breeding from the best, and neglecting the most undesirable, individuals in each generation). This principle allowed Darwin to explain the continued phyletic evolution of "new species" without recourse to the constant geological and climatic changes that he had called upon in the Essay of 1844. So important did he consider this component of his evolutionary thinking that he described it, along with the theory of natural selection, as the "keystone" of his *Origin of Species* (*More Letters,* 1:109; Darwin to Hooker, 8 June 1858).

Applied to the problem of speciation, Darwin's principle of divergence greatly enhanced his attention to ecological aspects of isolation, and particularly to the question of how a botanical genus could evolve so many local species and varieties. His logic can be seen most clearly in *Natural Selection,* where his prime illustration of the principle is that of a genus of plants. Darwin compares his hypothetical genus along a gradient of moisture preference, with species *A* occupying the wettest habitat and species *M* preferring the driest habitat (see Fig. 1). Divergent species *A* might develop several varieties (a^1, d^1, and l^1), he argues, each of which displays a differing preference for moisture. Over many thousands of generations, the divergent species *A* might flourish at the expense of other species, and its three varieties, diverging still further, might become distinct species in their own right (1856–58:242–43). A^{10}, for example, might become semiaquatic, while l^{10} might succeed in supplanting *B* within a drier habitat. Here, then, was Darwin's solution to the problem of geographical distribution, largely peculiar to plants, that had been brought to his attention by de Candolle, Hooker, and other botanists.

On the surface, Darwin's reasoning appears to endorse the doctrine of sympatric speciation, but in *Natural Selection* his treatment of the subject clearly distinguishes local phyletic evolution from speciation through geographic separation. In a small and homogeneous locality, divergent varieties would tend to supplant their parent forms, promoting phyletic evolution and gradual divergence relative to other species (1856–58:239–40). Species *M,* living in an increasingly drier habitat, is Darwin's major example of this phyletic process. By contrast, in a large and heterogeneous area possessing various open ecological niches, the principle of divergence would promote numerous local varieties, in time creating the appearance of a subgenus with many fine species (or what today would be called a polytypic species). But for such varieties, even among plants, to attain *reproductive* isolation, Darwin definitely insisted upon the need for isolation: "On the hypothesis that sterility at last supervenes between varieties formed by nature, & called by us species, there will obviously not be the least difficulty [under the theory of natural selection], where this has happened in keeping such varieties for ever distinct: But on this hypothesis it may be very important that two varieties during the early formation until converted into species should be kept isolated or kept apart" (1856–58:260).* Only in separate localities,

*This passage is noteworthy, demonstrating that Darwin had not totally lost sight either of the biological nature of species or of the paramount importance of spatial isolation for the multiplication of such mutually sterile species. But the issue of reproductive isolation was simply no longer Darwin's dominant concern in 1859. As he well knew, many botanists were willing to recognize as separate species, forms that were experimentally interfertile. What Darwin is saying here is that if reproductive isolation is one's criterion of species integrity, then spatial isolation is particularly crucial to the speciation process.

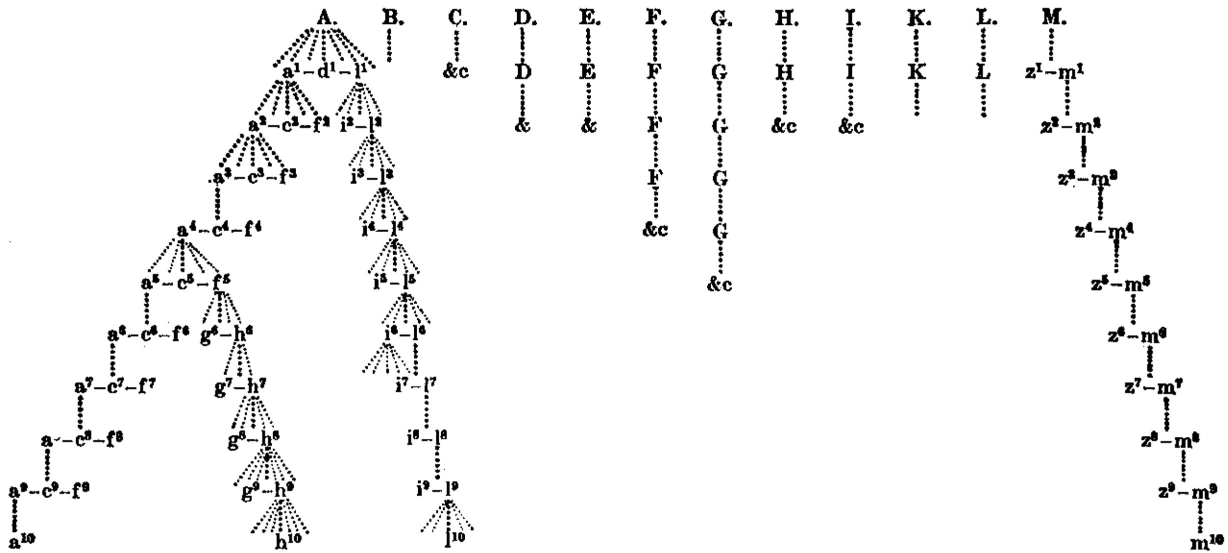

Fig. 1. Darwin's principle of divergence, illustrated with reference to a genus of plants (*Natural Selection*[1856–58:236]).

then, would true speciation generally occur. For self-fertilizing forms like plants, these localities might be relatively close, lacking the formal geographical barriers required for speciation among birds or mammals (1856–58:238, 240, 242, 255–56). Such neighboring localities would nevertheless have to present distinctly different ecological terrains (for example, the wet and dry habitats mentioned in connection with Darwin's diagram).[8]

PARTIAL ISOLATION. For continental areas, Darwin's theory of "partial isolation" was integral to his concept of divergent evolution, and this theory immediately follows his discussion of that concept in *Natural Selection* (1856–58:264–70). To explain cases of representative species found within continuous continental regions, Darwin contended that such adjoining districts are generally not continuous ecologically. As physical conditions (heat or moisture, for instance) graduate, certain species will decrease in numbers, finally becoming rare. Other species, ecologically dependent upon those becoming rare, will also suffer restrictions in their ranges. More adaptable competitors in neighboring districts will further delimit the distribution of each species. In short, physical conditions may graduate, but *biotic* ones do not. As a consequence, each district will tend to present relatively discrete constellations of species.

Applying this idea to the speciation process, Darwin envisioned that two geographic races, each adapted to neighboring districts within a large continental area, would both become rare toward the borders of their ranges. Intermediate or hybrid forms, when they occasionally existed, would tend to be rarer still and thus liable to extinction under adverse conditions. In this matter, natural selection would easily overcome the occasional effects of intercrossing (1856–58:269; 1859:176–77).

Although scientific hindsight allows one to question Darwin's partial isolation scheme (at least as having general applicability),[9] his conception of the ecological abruptness of distribution patterns was an important one. As Mayr (1947) and Dobzhansky (1951:205), among others, have pointed out, extremely small distances—sometimes on the order of fifty yards—may differentiate one species from another in the field. Such abrupt patterns make it difficult to decide precisely what is "isolation," or when speciation qualifies as a sympatric rather than an allopatric process. In Darwin's mind at least, partial isolation between contiguous geographical races could be surprisingly complete, owing to generally unappreciated ecological considerations.

BEHAVIORAL ISOLATION. It was doubtless Darwin's attention to ecological considerations in the divergence process that prompted him to endorse one final form of speciation that was, unlike his other models in the *Origin,* a undeniably sympatric process. There he argues at one point: "Even in the case of slow-breeding animals, which unite for each birth, we must not overrate the effects of intercrosses in retarding natural selection; for I can bring a considerable catalogue of facts, showing that within the same area, varieties of the same animal can long remain distinct, from haunting different stations, from breeding at slightly different seasons, or from varieties of the same kind preferring to pair together" (1859:103). In *Natural Selection* (1856–58), where this argument is expanded upon, Darwin sets forth his supporting evidence, which consists largely of cases of secondary overlap between good species that had developed their ecological differences during a prior period of isolation (pp. 257–59). In other words, he misinterpreted the relevant data. (I am indebted to Ernst Mayr for this observation. See also Mayr 1963:370.) It is in this restricted sense of behavioral and ecological isolation that Darwin *did* endorse in 1859 the limited possibility of sympatric speciation.

Misconceptions about Darwin's Origin Argument

At least two major misconceptions have arisen concerning Darwin's views on speciation. Both misconceptions stem from the way he presented his views in the *Origin of Species* (1859), although Darwin himself is not solely at fault for being misunderstood. In each instance, the confusion derives from his principle of divergence.

THE TWO MEANINGS OF "ISOLATION." The principle of divergence greatly reinforced Darwin's belief that evolution on continents, where populations are large and competition is severe, would tend to proceed faster than on isolated islands. Those floras and faunas evolving in large, ecologically complex continental areas would tend to be dominant, and after spreading and diverging, would generally succeed in eradicating more isolated forms. On this theoretical basis, he argued, one could explain why the marsupials of Australia have yielded before the more dominant placental mammals characteristic of the Euro-Asiatic region (1859:106; see also p. 390 for Darwin's comments on the vulnerability of island species).

It should be borne in mind that Darwin is using the term "isolation" here in a distinctly different sense from its customary one. In its more usual usage, "isolation" is simply a relative term referring to the geographic separation that enables speciation. A more absolute meaning, however, is denoted by his second application of the word, namely, that of being removed from large continental areas. Solitary, mid-oceanic island such as St. Helena are "isolated" in this second sense, and for this reason, Darwin thought, such spots might be expected to exhibit a slower rate of evolution. (Adaptive radiation into vacant niches, as has occured, for example, among his finches in the Galapagos Islands, he recognized as an important exception to this rule. See *Natural Selection,* p. 261.)

The confusion arises in Darwin's writings when one comes across passages like the following, which has repeatedly been cited, without the last and clarifying clause, as evidence that he underestimated the importance of isolation in the speciation process: "Although I do not doubt that isolation [in the absolute sense of the term] is of considerable importance in the production of new species, on the whole I am inclined to believe that largeness of area is of more importance, more especially in the production of species, which will prove capable of enduring for a long period, and of spreading widely" (1859:105).* Darwin's meaning in this passage is made more explicit in *Natural Selection,* where he states: "I do not doubt that over the world far more species have been produced in continuous [that is, continental] than in isolated areas. But I believe that in relation to the area far more species have been manufactured in, for instance, isolated islands than in continuous mainland" (1856-58:254; see also p. 261). Darwin goes on to mention the remarkable case of the Galapagos Islands, with 25 of its 26 land birds being endemic to that archipelago (p. 257). But he then adds that highly isolated localities, being relatively few in number and not favorably

*Darwin's critic Moritz Wagner (1883:348 n.), Ernst Mayr (1959:222-23), and Peter Vorzimmer (1970:170) have all cited this sentence (without the final clause "more especially . . . spreading widely" and without ellipses marking their deletion) as an indictment of Darwin's faulty views on isolation. More recently, however, Mayr (1965) has shown that an important element of unrecognized truth lurks in Darwin's counterintuitive pronouncements about "largeness of area." The frequency of endemic island species, Mayr has statistically demonstrated, is directly proportional to island size, even in islands exceeding 5,000 square kilometers. The most plausible inference from this fact is that extinction rates are inversely proportional to population size (and hence to genetic variability). Thus, once a new species has arisen in isolation, largeness of area is indeed important, as Darwin surmised, in the evolution of new species "which will prove capable of enduring for a long time, and of spreading widely." Darwin may not have understood the full details of this complex issue, but he was rightly aware that isolation, at least when it implies smallness of area or remoteness from potential colonizing sources, can be a double-edged sword in the evolutionary process (*Origin* [1859]:105). See also MacArthur and Wilson (1963; and 1967: 17-18, 173-74).

located for diffusing their new forms back to continents, will not have played an important part in "the manufacturing of species" that succeed in becoming dominant (p. 261). Finally, he concludes his discussion by arguing that the ideal situation for the production of new and dominant forms would be a large tract of land temporarily converted into a group of islands like "the great Malay archipelago" (p. 273). Clearly Darwin believed in the importance of isolation, but he saw this factor as operating in two separate ways. To understand his pronouncements on this subject, one must constantly ask oneself what form of isolation (absolute or relative) he has in mind.

THE ABRIDGMENT OF DARWIN'S ARGUMENT IN THE ORIGIN. Darwin's principle of divergence is easily confused with a theory of sympatric speciation as a result of certain abridgments that occurred when *Natural Selection* was condensed into the *Origin of Species.* The example of a plant specializing in wet and dry terrains was dropped, and his argument was presented wholly abstractly without reference to spatial isolation and its crucial role in speciation. In addition, his elaboration of this scheme as a theory of speciation through partial isolation (which discussion had immediately followed the principle of divergence in *Natural Selection*) was transposed to the next chapter in the *Origin of Species.* There, under the heading "On the absence or rarity of transitional varieties," the theory of partial isolation was used to explain why so few intermediate forms are generally observed between species. Unfortunately, these organizational changes in Darwin's argument were highly misleading for the topic of divergence, which has long struck his readers as an out-and-out endorsement of sympatric speciation. (Wagner [1868], no doubt, thought this, as did Gulick [1888:204–05], Romanes [1897: 25–26, 109], and Ortmann [1906:72]. See also the relevant references to sympatric speciation in Mayr's [1964] Index to the facsimile edition of the *Origin.*) Combined with the confusion over Darwin's views on isolation (in its two differing senses), this further source of misunderstanding has effectively masked the high degree to which he actually did consider isolation an essential concomitant of speciation.

Darwin's Views (1859) on Isolation: A Summary

Given the four major influences upon Darwin's concepts of species and speciation after 1844—his taxonomic work on barnacles, tactical considerations in connection with composition of the *Origin*, the problem of differing life forms (especially plants), and the principle of divergence—it is surprising that he emphasized geographic isolation as much as he did in the *Origin of Species* (1859). In that work, and especially in *Natural Selection* (1856-58), Darwin insisted that the ideal conditions for the multiplication of species were the continued elevation and subsidence of a large continental mass, so as to create temporary archipelagoes (*Origin,* pp. 107-08, 174; *Natural Selection,* pp. 273-74). Although the *Origin of Species* may give the impression that Darwin "de-emphasized" spatial isolation compared to his earlier views (Ghiselin 1969:147-48), it is possible to argue that he understood isolation in a much more sophisticated sense in 1859, and that his views on the subject constituted a considerable intellectual advance from those presented in the Essay of 1844. Especially through his principle of divergence, he recognized that speciation would be dependent upon ecological, as well as geographical, barriers and that this evolutionary process might be possible for certain nonmobile or hermaphroditic forms, such as plants, without the extensive spatial isolation he had originally thought necessary. Not only did this heightened, ecological understanding of isolation harmonize better with the facts of geographical distribution (for which plants had always been an exception), but it strengthened Darwin's argument for transmutation among precisely those problematic species—namely, the commingled ones—that were considered most aboriginal by creationists like de Candolle.

As for sympatric speciation, Darwin did admit this as a limited possibility in 1859, especially among higher forms for which sexual and habitat preferences might come into play, and among forms that do not pair for each birth. But sympatric speciation was not a major aspect of Darwin's theory on this subject, and he treated this mechanism as largely incidental to his theories of complete and partial isolation (see *Natural Selection,* p. 266, where he provides a clear rank order of these evolutionary influences). Finally, without *some* form of isolation—whether complete, partial, or behavioral—Darwin fully understood, and repeatedly insisted, that speciation would be impossible (*Origin,* pp. 103, 356; *Natural Selection,* pp. 241, 255-56). From the modern standpoint, his only error was to confuse behavioral isolation, which is secondary and derivative as an evolutionary phenomenon, with geographic isolation, which is always primary.

If Darwin's position on isolation, in spite of its considerable complexity, comes through clearly in *Natural Selection,* the same cannot be said about his treatment of this question in the *Origin of Species.* There, his ideas on this subject became so condensed as to be misleading, a point that relates to his later controversy with Moritz Wagner, as well as to the historical misinterpretations that have long surrounded this debate.

Darwin and Wagner

In 1868 Darwin received a sixty-two-page essay from the German naturalist and explorer Moritz Wagner (1813–87). In this essay, which was entitled "The Darwinian Theory and the Migration Law of Organisms," Wagner insisted that migration and an ensuing geographic isolation of new colonies from the main population were prerequisites for speciation. Wagner's ideas on this subject were the outgrowth of thirty years' thought about patterns of geographical distribution. Between 1836 and the late 1850s, Wagner had traveled extensively in North Africa, Asia, and the Americas, collecting specimens and observing the habits and ranges of indigenous organisms. As early as 1841 he had shown that distinct but closely related species of insects are often separated by mountain ranges, deserts, and even small rivers (1841, 3:199–210). Like Darwin, Wagner had been much struck by such facts of species distribution. But it was only after reading Darwin's *Origin of Species* (1859) that Wagner became fully awakened to the evolutionary significance of such evidence as documented by Darwin in his two chapters on this subject (Wagner 1889:33–35, 45, 358). Wagner saw his own observations, together with his steadfast emphasis upon geographic isolation, as filling an important gap in Darwin's theory of the origin of species. Writing in the Preface to his 1868 paper, he maintained in a generally pro-Darwinian spirit: "The migration of organisms and their formation of colonies is, according to my conviction, the necessary condition of natural selection. It confirms the same, does away with the most essential objections that have been raised against it, and makes the whole natural process of species formation much clearer and more understandable than it has been up to now" (1868:vii). Two years later, Wagner renamed his doctrine "the separation theory" (*die Separationstheorie*), by which designation it became generally known in the debate that ensued.

Darwin entered into friendly correspondence with Wagner in 1868, and for the remainder of Darwin's life he, Wagner, and a number of Darwin's German supporters (Weismann, Haeckel, Schleiden, Seidlitz, and Semper, among others) conducted a lively and increasingly divergent exchange of views on the subject of isolation.[10] To the German explorer's views, Darwin responded warmly in his first letter:

That a naturalist who has travelled into so many and such distant regions, and who has studied animals of so many classes, should, to a considerable extent, agree with me, is, I can assure you, the highest gratification of which I am capable. ... Although I saw the effects of isolation in the case of islands and mountain-ranges, and knew of a few instances of rivers, yet the greater number of your facts were quite unknown to me. I now see that from want of knowledge I did not make nearly sufficient use of the views which you advocate ... (*Life and Letters*, 3:157–58).

The following year Darwin altered the text at one point in the *Origin* (5th edition) in order to reflect Wagner's views on isolation. He nevertheless concluded: "But from reasons already assigned, I can by no means agree with this naturalist, that migration and isolation are necessary elements for the formation of new species" (1869:120). By 1872, Darwin had acquired an even more skeptical opinion of Wagner's argument, as he conveyed to August Weismann with the words: "In the first part of your essay [Weismann 1872], I thought that you wasted (to use an English expression) too much powder and shot on M. Wagner; but I changed my opinion when I saw how admirably you treated the whole case" (*Life and Letters,* 3:156, letter of 5 April 1872). Three years later, across the front of Wagner's 1875 paper on the separation theory, Darwin inscribed his final judgment "Most Wretched Rubbish" (Vorzimmer 1970:182).

Darwin's debate with Wagner has frequently been cast in the form of a hero/antihero opposition in which Wagner emerges historically as an unsung hero and Darwin appears as a slightly obtuse antihero whose surprising failure to endorse Wagner's position retarded the progress of evolutionary theory. Thus, David Starr Jordan could complain two decades after Wagner's death that Wagner's "epoch-making work" had been "almost universally ignored" by the subsequent scientific generation (1905:545, 554). Peter Vorzimmer, who does not hesitate to call Darwin's position on isolation "a result of shortsightedness," says of the unappreciated Wagner that he "hit upon the [Darwinian] theory's greatest weaknesses" (1970:159, 184–85). It is ironic and strange, Vorzimmer concludes, that "the Darwin of the Galapagos Archipelago should feel so strongly about demonstrating speciation by natural selection, specifically *excluding* isolation as a vital condition" (1970:184). Ernst Mayr has also lent his support to the hero/antihero impression that one receives from recent discussions of Darwin's debate with Wagner. Wagner is said to have advanced "radical and novel" ideas that met with misunderstanding criticism (1947:270; 1959). Summarily dismissed by Darwin and by such combative followers as August Weismann (1872), who persisted, with Darwin, in endorsing a "single-factor" theory of evolution, Wagner had to wait seventy-five years for the final vindication of his position through the work of Rensch (1933), Dobzhansky (1937), Huxley (1942), and Mayr (1940, 1942) himself.* Wagner's own reflections about his fate, voiced in a letter to his friend Karl von Scherzer, provide personal confirmation of the tragic neglect that characterized the reception of his ideas. Three years before his death, in words that remind one of Gregor Mendel's famous pronouncement "My time will come!," Wagner prophesied that he would one day be vindicated by posterity (Wagner 1889:3). Wagner's last efforts, interrupted by his death in 1887, were directed at presenting his final answer to the Darwinians. The posthumous publication of his collected essays, edited with commentaries by his nephew and namesake, was the closest that Wagner ever came to a final synthesis of his views.

The Debate Reassessed

In spite of the considerable kernel of historical truth inherent in the traditional assessment of the Darwin/Wagner debate, the customary interpretation summarized above is unsatisfactory in many important respects. One cannot deny, of course, that Wagner's ideas and observations entailed much that was only properly appreciated long after his death. Nor should one minimize the fact that critics like August Weismann (1872) displayed a singular lack of understanding in their "refutations" of Wagner's ideas. (As Mayr [1959] has shown, Weismann consistently confused the evidence of polymorphism with the concept of geographic races and, on this erroneous basis, dismissed Wagner's

*Between 1959 and 1963 Mayr's historical interpretation of Wagner's theory and its reception underwent a significant change. In *Animal Species and Evolution*, Mayr comments: "When Moritz Wagner proclaimed in 1868 that geographic isolation was a necessary prerequisite for species formation, he failed to submit any real proof. Worse than that, some of his early explanations were so obviously absurd that they endangered his thesis as a whole and were in part responsible for its cool reception. Although he gave a much sounder interpretation of his thesis in a revised edition of his work (1889), the theory of geographic speciation was still more than 50 years ahead of a rational genetic interpretation" (1963:516). Also, compare Mayr (1976:124) with Mayr (1959:224). The present section of this article expands upon this reassessment, which Mayr has not developed in any historical detail. I disagree only with his claim that Wagner's (1889) collected essays, published posthumously, offered "a much sounder interpretation of his thesis." It is the later essays that are the most fanatical and scientifically naive. Vorzimmer's assessment of the Darwin/Wagner debate has drawn exclusively upon Mayr's 1959 article, a circumstance that may in part explain the survival of the hero/antihero dimension in Vorzimmer's recent analysis.

claims about geographic isolation.) Yet the fate of Wagner's separation theory was sealed far more by his own extremist conception of isolation than by his contemporaries' closed-minded rejection of this idea. As I shall argue, Wagner was indeed his own worst enemy.

At the same time, one is appalled by the intellectual portrait of Darwin that has been conjured up by certain commentators in order to explain his supposed obtuseness on the issue of isolation. According to Romanes (1897:107) and Vorzimmer (1970:251), Darwin had become a tired old man, frustrated and confused "on the eve of his retirement," and was no longer able to think clearly about such difficult problems. Convenient as this historical explanation may be, it is premised upon a long-standing myth that Darwin was somehow beaten into a state of submission and mental impotence by the many critics of his *Origin of Species*. As Ghiselin (1973:163) rightly remarks, "Darwin never retired," and those who have taken at face value Darwin's statements about preferring to work at "easier subjects" in his old age have mistaken modesty in a man who was still in his sixties, for mental enfeeblement. Finally, Darwin in no way capitulated to Wagner's own views, as both Romanes (1897:107) and Vorzimmer (1970:181, 183) would have us believe. In his communications with Wagner, Darwin's position on geographic isolation remained largely the same as it had been in the first edition of the *Origin of Species*. To rectify these various misapprehensions concerning his attitude towards Wagner, we must first review the debate more closely so as to clarify what their disagreement was really about.

Wagner on Natural Selection

Not only did Wagner believe that spatial isolation was necessary for the formation of new species, but he also insisted that natural selection could not act without the migration and complete isolation of a few colonists from the main population (1868:42–44, 50–51). Under this view, phyletic change was considered impossible in large, continuous populations, where individual differences would always be blended together and lost through free intercrossing. "Organisms that never leave their ancient area of distribution," Wagner asserted, "will undergo just as little change as certain other organisms to whom nature has granted a far too extensive means of transportal [for isolation ever to occur]" (1868:42–43). By means of this argument, Wagner believed he could account for two of the most serious objections to Darwin's theory: (1) why the mummified forms of crocodiles and birds found in Egyptian tombs had undergone no change during the last four thousands years (namely, because these species had failed to migrate from the Nile valley); and (2) why certain simple forms, such as infusoria, foraminifera, algae, and lichens, had not progressed above their present level of organization (because such forms are too cosmopolitan ever to become isolated).

To overcome what he saw as the insurmountable problem of blending inheritance in large populations, Wagner proposed that the evolution of new forms occurs only when a pregnant female, or at most a few individuals, manage to colonize a wholly new territory well isolated from the main distribution. These few migrants bring with them the stamp of their own individuality, which, no longer subject to the leveling effects of free intercrossing, provides an immediate basis for a constant new form (1870*b*:104–07; 1875:288, 291). (Wagner has adumbrated here the notion that Ernst Mayr [1942:237] later termed the "founder principle" in explaining the reduced variability and evolutionary discontinuity of peripheral populations established by a few individuals.) These incipient species, Wagner contended, undergo further divergence from the parent population through the combined influences of changed nutrition, altered climate, and other peculiarities of the new environment. When an isolated colony has at last achieved a sizable population, evolution once again comes to a halt. Finally, owing to the extremely small size of the speciating population, few intermediate links, especially within the fossil record, were to be expected under Wagner's ingenious theory (1870*b*:105–06).*

It was Wagner's failure to understand the role of natural selection

*Wagner's shrewd explanation of gaps in the fossil record has a modern ring to it, and it was Ernst Mayr (1954) who greatly helped to revive this interpretation in connection with his novel theory of "genetic revolutions in founder populations" (not to be confused with Mayr's earlier "founder principle"). According to this notion, which Mayr (1976:188) has described as "perhaps the most original theory I have ever proposed," the selective value of genes is related to their total genetic background. A small founder population in a peripherally isolated area brings with it only a limited portion of the genetic background of the species. Thus a genetic revolution may ensue, proceeding with a chain reaction pattern, as overall gene frequencies respond to the change in each gene's selective value. This theory accounts for the drastic evolutionary changes that are observed in peripheral isolates, as well as for the absence of intermediate links connecting new forms within the fossil record. One cannot help suspecting, from a historiographical point of view, that Mayr's early (pre-1963) depiction of Wagner's tragic neglect (see above, pp. 50–51) reflects an intellectual feeling of "kindred spirit" with a man whose radical scientific ideas indeed were, in many important respects, well ahead of their time. It is not without interest in this connection that Mayr's own theory was "almost universally ignored" in the early years following its publication (Mayr 1976:188).

in phyletic evolution that prompted Darwin's first set of objections to the "migration theory" in 1868. After praising the many new facts presented by Wagner, and acknowledging the several difficulties his theory appeared to solve, Darwin countered: "But I must still believe that in many large areas all the individuals of the same species have been slowly modified, in the same manner, for instance, as the English race-horse has been improved, that is by the continued selection of the fleetest individuals, without any separation. But I admit that by this [phyletic] process two or more new species could hardly be found within the same limited area; some degree of separation, if not indispensable, would be highly advantageous; and here your facts and views will be of great value . . ." (*Life and Letters,* 3:158). In other words, Darwin was saying, Wagner's migration theory left no room for the gradual phyletic evolution of "new species" on the model of unconscious selection as practiced by the breeder.

Wagner continued to disagree with Darwin's logic, and in subsequent publications he became more and more hostile to the concept of natural selection. By 1870 he was referring to Darwin's doctrine as "superfluous" in the light of his own separation theory. He also bluntly insisted that Darwin's evolutionary mechanism reflected "a profound error" in Darwin's thinking about the whole problem (1870*a*:434 n.; 1870*b*:101–02).[11] Three years later Wagner was publicizing his critique of Darwinian theory under such titles as "The Error of Darwinism" (1873), an attitude that stimulated August Weismann's equally polemical reply "To the Defense" (1873). Again and again Wagner claimed in these later publications that natural selection could only act in a *conservative* manner, eliminating anomalous forms from an already adapted population. Wagner did, however, retain a limited place within his own theory for Darwin's broader concept of the struggle for existence. Induced by this pervasive life-and-death struggle, peculiar forms—mutations—migrate to new environments where they are better able to survive and to escape the iron hand of conservative selection (1875:287; 1880:406).

In his later publications, Wagner also proposed a novel theory of variation that harks back to certain views briefly held by Darwin in the late 1830s. Wagner's ideas on this subject were designed to account for certain evolutionary phenomena not covered by his separation theory. Just like individuals, Wagner proclaimed, species have fixed lifetimes. Without the invigorating influence of migration and isolation, every species must eventually die. During its youth, a species is liable to considerable variation, just as a young organism is more plastic in its form than an older one. By means of this theory of species lifetimes Wagner believed he could account for the various continental forms that are occasionally encountered in an unchanged condition on isolated oceanic islands. Such identical forms, he argued, are colonists from a nonvarying mainland species in the twilight of its life span. Finally, Wagner saw his theory of species lifetimes, together with the origin of new forms through isolation, as neatly corroborated by Ernst Haeckel's famous biogenetic law. The ontogenetic separation of the plastic offspring from its parent, Wagner maintained, is recapitulating the phylogenetic "birth" of new species following geographic separation of a few individuals from the parent form (1875:291–93, 301; 1880:407).

Wagner's Lamarckian Theory of Adaptation

Wagner's inability to comprehend the creative side of natural selection was closely linked to his predilection for a Lamarckian interpretation of evolutionary phenomena.[12] At the heart of Wagner's conception of evolution was the constant striving of every organism for the means of survival and reproduction. Organisms are continually migrating, Wagner believed, in order to improve their chances for survival. He based an unconvincing and even fantastic theory of adaptation upon this principle. For example, he argued that polar bears and other predominantly white organisms from the poles are descended from albino individuals that migrated towards snow-covered areas in order to enhance their chances of survival (1875:294–95; 1880:421). The numerous cases of adaptive mimicry in nature received a similar explanation from Wagner. The mimic, a product of individual, preadaptive variation, seeks out a new and more suitable habitat through migration. How much easier it was to believe that migration, not the improbable process of natural selection, was responsible for such phenomena (1875:287–88; 1880:408). Still other adaptations were thought by Wagner to derive from the act of migration itself, which inevitably brings the organism into contact with new conditions of life, climate, food, and so forth, inducing hereditary changes whose adaptiveness could always be insured by further migration to the proper environment.

It is this last aspect of Wagner's migration theory—his far-fetched explanation of adaptation—that must be borne in mind when considering Darwin's sharp reversal of opinion after 1870 concerning the overall value of Wagner's publications. His "strongest objection" to the separation theory, Darwin informed Wagner in 1876, was precisely that "it does not explain the manifold adaptations in structure in every organic being—for instance in a Picus [woodpecker] for climbing trees and catching insects—or in a Strix [owl] for catching animals at night, and so on *ad infinitum.* No theory is in the least satisfactory to me unless it clearly explains such adaptations" (*Life and Letters*, 3:158–59). Darwin's deprecatory comment "Most Wretched Rubbish" was inscribed on Wagner's 1875 pamphlet in precisely this context (Vorzimmer 1970: 182).

Wagner's Failure to Understand Darwin

Although Wagner was hardly alone in his failure to grasp Darwin's views on isolation, it is clear that he was battling a highly distorted version of Darwin's thinking on this subject. In Wagner's own case, more than just the complexity of Darwin's arguments, the ambiguities of his terminology, or the abridgment of his logic in the *Origin* was involved. I have not succeeded in gaining a clear picture of Wagner's personality, but the following considerations appear relevant to Wagner's extremist theoretical views, as well as to their cool reception by his contemporaries.

Working for most of his scientific life under the shadow of his elder brother Rudolph, a renowned physiologist of strongly anti-Darwinian persuasions, Moritz Wagner found his scientific career suddenly transformed by the new conception of nature announced by Darwin. Whereas, brother Rudolph saw the *Origin of Species* as "a great dream" (*einen grossartigen Traum*) and reveled in its numerous refutations, Moritz Wagner was an early and enthusiastic convert to the Darwinian cause (1889:38, 277). Four years after his brother's death, Wagner (1868) issued the first of his theoretical papers, while still under the general influence of Darwin's views. Increasingly convinced, however, that he had discovered a fundamental flaw in Darwin's reasoning, Wagner soon came to believe that he, not Darwin or Lamarck, had finally solved the problem of the origin of species.[13] Then, when he found himself uniformly rejected by his countrymen as "anti-Darwinian," Wagner assumed the identity of a persecuted martyr in his disputes with Darwin's various German supporters. The year prior to his death he was comparing his scientific fate to that of Copernicus and Lamarck before him (1889:280).

Wagner's single-minded conviction that he, not Darwin, had discovered the true mechanism of organic evolution is reflected by his astonishing failure to acknowledge Darwin's views on isolation, insofar as they agreed with his own. Almost never in his publications did Wagner refer to specific passages or arguments in Darwin's *Origin of Species,* in order to compare their respective theories. Yet he drew liberally upon Darwin's findings, often without the slightest acknowledgment. In one article, Wagner devotes eleven pages to showing how the flora and fauna of the Galapagos Archipelago provide a definitive refutation of Darwin's theories! Yet Darwin, who is briefly mentioned for having visited this archipelago, is nowhere credited as the person who first emphasized the evolutionary importance of such data (1875:325–33, 340–41; see also 1880:436–37). In another publication, Wagner (1868:15) does credit Darwin for recognizing that the different islands in the Galapagos possess different species, but he then cites a metaphorical and unrepresentative passage from Darwin's *Journal of Researches* (1845), in order to show that Darwin had yet to appreciate such facts in an evolutionary light even a decade after visiting this archipelago! Elsewhere, Wagner (1889:475–77) credits John Gould, the creationist taxonomist who worked out Darwin's Galapagos birds in the 1830s, for Darwin's own evolutionary interpretations of the Galapagos case—once again without mentioning Darwin's name! Finally, when Wagner did cite Darwin's views on isolation in order to compare them with his own, he picked the one passage from the *Origin of Species* (omitting the last and crucial clause) where Darwin had brought up the disadvantages of isolation, considered in an "absolute" as opposed to a "relative" sense (1883:348 n.). With Wagner as one's source, one would never have dreamed how much importance Darwin himself placed upon geographic isolation in the multiplication of species.

It was for reasons such as these that Darwin, in 1876, once again protested politely to Wagner:

> I think that you misunderstand my views on isolation. I believe that all the individuals of a species can be slowly modified within the same district, in nearly the same manner as man effects by what I have called the process of unconscious selection. . . . I do not believe that one species will give birth to two or more new species, as long as they are mingled together within the same district. Nevertheless I cannot doubt that many new species have been simultaneously developed [through partial isolation] within the same large continental area; and in my 'Origin of Species' I endeavored to explain how two new species might be developed, although they met and intermingled on the *borders* of their range. It would have been a strange fact if I had overlooked the importance of isolation, seeing that it was such cases as that of the Galapagos Archipelago, which chiefly led me to study the origin of species (*Life and Letters,* 3:159).

Similarly, two years later Darwin expressed himself to Karl Semper concerning his position in the debate with Wagner: "There are two different classes of cases, as it appears to me, viz. those in which a species becomes slowly modified in the same country (of which I cannot doubt there are innumerable instances) and those cases in which a species splits into two or three or more new species; and in the latter case, I should think nearly perfect separation would greatly aid in their 'specification,' to coin a new word" (*Life and Letters,* 3:160, letter of 26 November 1878). Wagner, whose separation theory was formulated in zealous opposition to Darwin's own ideas on evolution, was never able to acknowledge how close their thinking really was on the issue of speciation. (See also Karl Semper's [1881:290-92] comments to this effect.) In the midst of this considerable rivalry of ideas, the issue of sympatric speciation through behavioral isolation, upon which Darwin had placed least weight, was unfortunately lost sight of during the debate.[14]

Conclusion

As we have seen, Wagner's separation theory was hardly synonymous with the modern theory of geographic speciation. Rather, his doctrine involved a fanatical devotion to an almost mystical conception of the organism's adaptive transformations through migration and isolation. In contrast to Darwin, Wagner was also highly select in his evidence (he largely ignored the problematical subject of plants, which had played such an important role in Darwin's own thinking). In many respects, Wagner's position—involving no plausible theory of adaptation, a denial of phyletic evolution, the notion of species lifetimes, and an excessive reliance upon Lamarckian principles in explaining migration, isolation, variation, and evolution—seems like a throwback to certain of Darwin's earliest speculations (1837-38) on the origin of species. Wagner, then, was "right" for the wrong reasons, and Darwin, who has long been seen as having "missed the boat," was far more insightful on the issue of isolation than he has generally received credit for being. Indeed, it is only because Darwin himself has been so misunderstood on the issue of isolation that Wagner's bizarre theories could appear "epoch-making" to later observers like D. S. Jordan (1904:554). Above all, it was Darwin who, more than anyone else, realized how insoluble the debate over speciation was in his own lifetime, owing to the complexity of the theoretical issues and the lack of compelling data from the field. To August Weismann, he lamented about this extremely intricate question in 1872: "I thought much about isolation when I wrote Chapter IV. [of the

Origin] on the circumstances favourable to Natural Selection. No doubt there remains an immense deal of work to do on 'Artbildung' [species formation]. I have only opened a path for others to enter, and in the course of time to make a broad and clear high-road" (*More Letters,* 2: 95–96).

The subsequent history of the debate over geographic speciation has been documented by Mayr (1959; 1963:481–88), who has shown how de Vries's mutation theory fueled the cause of sympatric speciation after 1900, and how the theory of geographic speciation continued to survive in the work of field naturalists and systematists like Henry Seebohn (1888), Karl Jordan (1896), David Starr Jordan (1906), Erwin Stresemann (1919), and many others. (See D. S. Jordan [1905] for a survey of turn-of-the-century viewpoints on this subject.) It was perhaps Mayr (1947) who, more than anyone else, finally put this issue to rest when he forced the proponents of sympatric speciation to retreat to a few exceptional instances under which the normal pattern of geographic speciation may possibly be violated.[15]

The ultimate resolution of the problem reflects a well-known lesson in the progress of scientific knowledge. For over a century, no amount of confirming evidence, convincing as it may have seemed to some observers, succeeded in establishing geographic isolation as the sole method of speciation among higher organisms—in spite of the widespread conviction among field naturalists that this *must* be so. Agreement came only when it was possible to refute the numerous theoretical schemes positing ecological and behavioral isolation as effective mechanisms of speciation. This proved a surprisingly difficult task that necessitated considerable progress in field studies and in population genetics during the half century following Darwin's death. It was in the context of these new discoveries, characteristic of the "modern synthesis" in evolutionary theory, that Mayr's penetrating critique of various models of sympatric speciation succeeded where other such attempts had failed. More recently, Mayr (1976:144) has reflected upon his role in this controversy: "It seemed to me [in 1947] that the best strategy was to state the case against sympatric speciation as uncompromisingly as possible in order to provoke refutation if such was possible. I specifically enumerated all the conditions that had to be met to permit the occurrence of sympatric speciation. My strategy was successful. The vague claims of sympatric speciation were henceforth replaced by well worked-out, fully documented cases." (Of these exceptions, only one—that of sympatric speciation through host specialization—has generally been admitted as a viable possibility. See Mayr 1970:261–73.)

Finally, it is a curious and instructive historical fact that Ernst Mayr, who was initially trained as an ornithologist and who as a young naturalist-explorer in New Guinea and the Solomon Islands was exposed, like Darwin, Wallace, and Wagner, to the compelling evolutionary consequences of geographic isolation, should have done so much to complete the scientific revolution that grew out of Darwin's own ornithological collections from the voyage of the *Beagle.* For this reason, it is all the more befitting that the extreme importance of the individual, as championed by Darwin and Wagner in such different ways, has been reunited by Ernst Mayr with the biological species concept that Darwin allowed to slip through his grasp.

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NOTES

*Dedicated to Ernst Mayr on his seventy-fifth birthday.

1. For similar statements concerning the influence of these three classes of facts, see Darwin (1859:1; 1868:9-11; and *More Letters,* 1:118-19). In a longer draft of this essay, the remainder of which is to be published elsewhere, I have treated Darwin's voyage experience in more detail and have shown that he was not actually converted to the evolutionary viewpoint until after his return to England. (See also Sulloway 1969, Gruber 1974, Grinnell 1974, and Herbert 1974.) Darwin's curiously delayed conversion was intimately associated with the innumerable clarifications and corrections that various systematists effected in his taxonomic understanding of his voyage collections during February and March of 1837.

2. Vorzimmer's (1965; 1970:21, 47, 135, 159-85, 284) discussions of this issue, for instance, are vitiated by a repeated confusion of the concept of speciation (or the multiplication of species) with that of phyletic evolution. Such an indiscriminate transposition of concepts and terms makes Vorzimmer's treatment of the historical problem highly self-contradictory and difficult to follow. See also Ghiselin (1973:157), who corrects Vorzimmer on this and other points.

3. Gould originally named only twelve species in the *Geospiza* group, as the manuscript Minutes of the London Zoological Society (meeting of 10 January 1837) plainly show. By 10 May the number had increased to fourteen species. When the Minutes were finally published, Gould had revised this number down to thirteen. These facts are extremely relevant to Darwin's comment, cited below in the text, on "how entirely vague and arbitrary" the taxonomic decisions about his Galapagos birds seemed to him at the time. Throughout this discussion I have used Gould's specific names for Darwin's birds. Some of these have been replaced by alternative designations. For example, the mockingbird genus *Orpheus* is now known as *Mimus* in the case of South American species and as *Nesomimus* for the Galapagos forms.

4. For a discussion of models of "partial" and "ecological" isolation, together with a refutation of their feasibility in promoting speciation, see Mayr (1947). That Darwin supported the possibility of speciation without any form of isolation is an erroneous belief

that will be treated below. Romanes (1897:103–04, 109), among others, has labored under this misapprehension.

5. It would seem that Darwin lost sight of the distinction between sterility as a fundamental criterion among species in nature and sterility as a more dubious criterion, as he himself felt, under artificial laboratory conditions. Nor did the extremely complex nature of the problem (especially with plants), and the often contradictory results of different hybridizers, help him in reaching a proper judgment on this subject (1859:250).

6. Darwin (1859:87–90), of course, discussed the importance of sexual selection in the *Origin,* but here he was concerned with differential reproduction among individuals of the same general form and geographic race.

7. Even under the second of these circumstances, Darwin did not usually have sympatric speciation in mind, believing only that such local varieties might arise in sufficient numbers to exterminate their parental forms. This process is clearly one of phyletic evolution, not the multiplication of species.

8. There is a partial flaw in Darwin's argument that was long ago noted by Romanes (1886:385–87; 1897:125–27). If geographic races are isolated from one another, then the selective pressure for divergence is greatly reduced. It is therefore not possible to attribute geographic speciation to divergence, as Darwin attempts to do here. (Under conditions of "partial isolation," however, some pressure toward divergence might logically be called upon. See below, in the text.) What is important in this context is that Darwin recognized the necessity of geographic isolation for speciation, even though he was less correct in believing that divergence between varieties would always assist this process. His botanical speculations about microgeographic isolation stemming from differing ecological conditions are only partly borne out by more recent studies. Stebbins (1950:204–08) reports a number of striking cases of closely related sympatric species that are isolated ecologically through soil and moisture differences. Hybridization occurs on an occasional basis in these genera, sometimes producing highly fertile offspring. Yet ecological isolation has generally ensured that these species remain distinct from one another. Except for cases of polyploidy, however, these forms appear to have evolved during prior geographic isolation, only subsequently coming into secondary contact.

9. Darwin's theory of partial isolation bears resemblance to the phenomenon of "circular overlap," in which intergrading subspecies form a loop or ring, the terminal ends of which meet and exhibit successful speciation (Mayr 1963:507–12). The principal difference between Darwin's theory and cases of ring speciation is the amount of geographical distance involved between the populations attaining reproductive isolation.

10. For a more complete list of Wagner's supporters and opponents, see Wagner (1889: 20–21, 44–45, 98–99, 274, and 276–79). For a list of Wagner's scientific publications, see Wagner (1889:25 n., and 100).

11. Wagner's opposition to Darwin's theories may be traced in large part to his erroneous belief in "blending inheritance." In contradistinction to Vorzimmer's (1970) repeated claims, it is a myth that Darwin believed that *all* individual variation was lost through blending. Darwin's theory of pangenesis (1868, 2:357–404) provided for quasi-Mendelian particulate inheritance in the form of "gemmules." Some gemmules become hybridized or otherwise altered during each generation; other gemmules, however, do not, and they may exist unaltered for thousands of generations, later manifesting themselves as "reversions." Moreover, Darwin (1868, 2:401) explicitly argued that some characters show particular antagonism to blending. It is ironic that Darwin's supposed belief in blending inheritance has caused Vorzimmer to castigate him for his intellectual "shortsightedness" and ad hoc assumptions, while Wagner, with his fanatical endorsement of the same hereditary fallacy, is portrayed by Vorzimmer as one of Darwin's most insightful critics! The time is ripe for a major historical reappraisal of Darwin's theory of inheritance and its role in his disputes with his critics.

12. It is perhaps significant, as Dobzhansky (1951:204) suggests, that virtually all the major supporters of geographic speciation prior to 1930 drew heavily upon Lamarckian

assumptions. (In the course of time, differing environments were supposed by such Neo-Lamarckians to produce permanent geographic races.) Of the supporters named by Dobzhansky (Wagner, Karl Jordan, David Starr Jordan, P. Semenov-Tian-Shansky, and Bernhard Rensch), Wagner was by far the most Lamarckian of them all.

13. Wagner (1883) later acknowledged the priority of Leopold von Buch (1774–1853), who had insisted as early as 1825, in his monograph on the flora and fauna of the Canary Islands, that "[isolated] varieties become constant and turn into separate species. Later they may again reach the range of other varieties which have changed in a like manner, and the two will now no longer cross and thus they behave as 'two very different species'" (p. 133; trans. Mayr 1963:483). Darwin also acknowledged von Buch's priority in his Historical Sketch added to the third (1861) edition of the *Origin of Species.* See also Darwin's transmutation notebooks (de Beer 1960–61: *B* 158, *D* 69).

14. Vorzimmer (1965:154–55; 1970:173–74) claims that Darwin, under combined pressure from Fleeming Jenkin and Moritz Wagner, changed his mind about sympatric speciation through behavioral (and ecological) isolation. But Darwin never deleted his discussion of this subject from the *Origin*, and he certainly had the opportunity to do so in the fifth (1869) and sixth (1872) editions of that work. Still, one may ask, as Vorzimmer does, why Darwin never raised this issue in his letters to Wagner. It would appear that Darwin, who saw himself in general agreement with Wagner on the problem of speciation, and who knew how far apart they were on the problems of phyletic evolution and adaptation, considered this behavioral aspect of the matter to be of little importance in their real disagreement. Nevertheless, I suspect that Darwin indeed had such behavioral modes of isolation in mind when he wrote to Wagner in 1868, "But I admit that by this [phyletic] process two or more species could hardly be found within the same limited area; some degree of separation, *if not indispensable,* would be highly advantageous" (*Life and Letters* 3:158; italics added).

15. Plants, of course, remain as major an exception today as they were in Darwin's day, although the unusual genetic reason for this status—polyploidy—is now understood. In all other respects, plants obey the principle of geographic speciation (Stebbins 1950:238). It is worth noting that when D. S. Jordan (1905) insisted upon the necessity of geographic isolation for speciation, he was supported by zoologists, but not by botanists. See the lively correspondence that ensued in *Science* 22 (1905):710–12 (F. E. Lloyd); 836–38 (Leroy Abrams); 23 (1906):34 (Edward W. Berry); 71–72 (E. A. Ortmann); 433–34 (John T. Gulick); and 506–07 (O. F. Cook). Similarly, Romanes (1897:76–77) drew upon the botanist Carl Nägeli for his general conclusion that "closely allied species are most frequently found in intimate association with one another, not, that is to say, in any way isolated by means of physical barriers."