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Darwin and the Galapagos

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Charles Darwin's historic visit to the Galapagos Islands in 1835 represents a landmark in the annals of science. But contrary to the legend long surrounding Darwin's famous Galapagos visit, he continued to believe that species were immutable for nearly a year and a half after leaving these islands. This delay in Darwin's evolutionary appreciation of the Galapagos evidence is largely owing to numerous misconceptions that he entertained about the islands, and their unique organic inhabitants, during the *Beagle* voyage. For example, Darwin mistakenly thought that the Galapagos tortoise—adult specimens of which he did not collect for scientific purposes—was not native to these islands. Hence he apparently interpreted reports of island-to-island differences among the tortoises as analogous to changes that are commonly undergone by species removed from their natural habitats. As for Darwin's finches, Darwin initially failed to recognize the closely related nature of the group, mistaking certain species for the forms that they appear, through adaptive radiation, to mimic. Moreover, what locality information he later published for his Galapagos finch specimens was derived almost entirely from the collections of three other *Beagle* shipmates, following his return to England. Even after he became an evolutionist, in March of 1837 (when he discussed his Galapagos birds with the eminent ornithologist John Gould), Darwin's theoretical understanding of evolution in the Galapagos continued to undergo significant developments for almost as many years as it took him to publish the *Origin of Species* (1859). The Darwin–Galapagos legend, with its romantic portrait of Darwin's 'eureka-like' insight into the Galapagos as a microcosmic 'laboratory of evolution', masks the complex nature of scientific discovery, and, thereby, the real nature of Darwin's genius.

KEY WORDS:—Charles Darwin – Galapagos Islands – evolutionary theory – biography.

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THE MYSTIQUE OF THE GALAPAGOS ISLANDS

All remote oceanic islands possess a certain romantic mystique. But Charles Darwin has raised the mystique of the Galapagos Islands to a level that finds virtually no rivals in the history of scientific thought. Both for the biology textbooks and for the history of science, these 'enchanted islands' have become the highly acclaimed symbol of one of the greatest revolutions in Western intellectual thought. Indeed, that this momentous scientific revolution sprang from insights that Charles Darwin garnered during a brief five-week visit to the Galapagos in 1835 has made them into the symbolic equivalent of Newton's famous apple among the great stories of scientific discovery. But unlike Newton's apple, with its fleeting but historic fall, the Galapagos Islands have remained a permanent showcase of the fundamental scientific insights that Charles Darwin first divined. For those who have visited the Galapagos in Darwin's historic wake, there is inevitably a feeling of being on hallowed scientific ground and also of standing intellectually in Darwin's awesome and ever-present shadow. As one Galapagos researcher has recently commented, with a curious mixture of reverence and irritation: "It's like studying art at the Louvre. It's hammered into you—Darwin, Galapagos—Galapagos, Darwin" (cited in Stoppard, 1981:7).

Nevertheless, much of the undeniable mystique that Darwin has given to the Galapagos Islands, while certainly well deserved, is based on a considerable historical misconception. Indeed, the story of Darwin and the Galapagos is shrouded in a series of interrelated myths—myths that are part of a subtle but pervasive politics of science that surrounds all great scientific discoveries. In this essay I will begin by examining the myth of Darwin's Galapagos conversion to the theory of evolution; for it is this myth that forms the very core of the Darwin–Galapagos legend—a legend that tends to obscure both the true nature of Darwin's genius and the important role that these famous islands have indeed played, and continue to play, in the development of evolutionary theory.

The sources of the widespread myth that Darwin was converted 'eureka-like' to the theory of evolution during his Galapagos visit in 1835 are manifold, stemming from certain of Darwin's own autobiographical accounts of his conversion experience, as well as from a century of subsequent biographical writings.[1] Even the scientific evidence—Darwin's *Beagle* collections—also tend to support this view (Lack, 1947:9, 23). But during the last decade or so, Darwin scholars have generally come to the conclusion that Darwin's conversion did not occur during his visit to the Galapagos Islands in 1835; or even, for that matter, during the voyage of the *Beagle* itself.[2] Exactly when the conversion *did* occur has nevertheless remained the subject of doubt. Above all, the real story behind Darwin's conversion—even more important than the timing of that conversion—has not been sufficiently understood; and it is this story,

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[1]See, for example, Darwin, 1859 : 1; 1868, *1* : 9–11; 1958[1876]: 118–19; 1887, *2* : 23, 34; *3* : 159; 1903, *1* : 118–19, 367; F. Darwin, 1888 : 74, 76; 1903, *1* : 37–38, 1909 : xiv; Barlow, 1933 : xiii; 1945 : 262–64; 1963: 204–5, 277; 1967 : 12; Irvine, 1955 : 50; de Beer, 1958 : 5; 1962 : 323; Wichler, 1961 : 85–87; and Huxley, 1966 : 3.

[2]See Himmelfarb, 1959 : 107–23; Smith, 1960 : 392; Gruber & Gruber, 1962 : 200; Sulloway, 1969 : 99–102; 1979 : 26–27; 1982a : 19–20, 22–23; 1982b : 57–58; 1982c; Ghiselin, 1969 : 32–36; Limoges, 1970 : 7–20; and Herbert, 1974 : 249; 1980 : 7–12. Hodge (1983 : 61–63, 104, n.102), however, still holds to the view that Darwin was converted to the theory of evolution during the last year of the *Beagle* voyage. See further note 4.

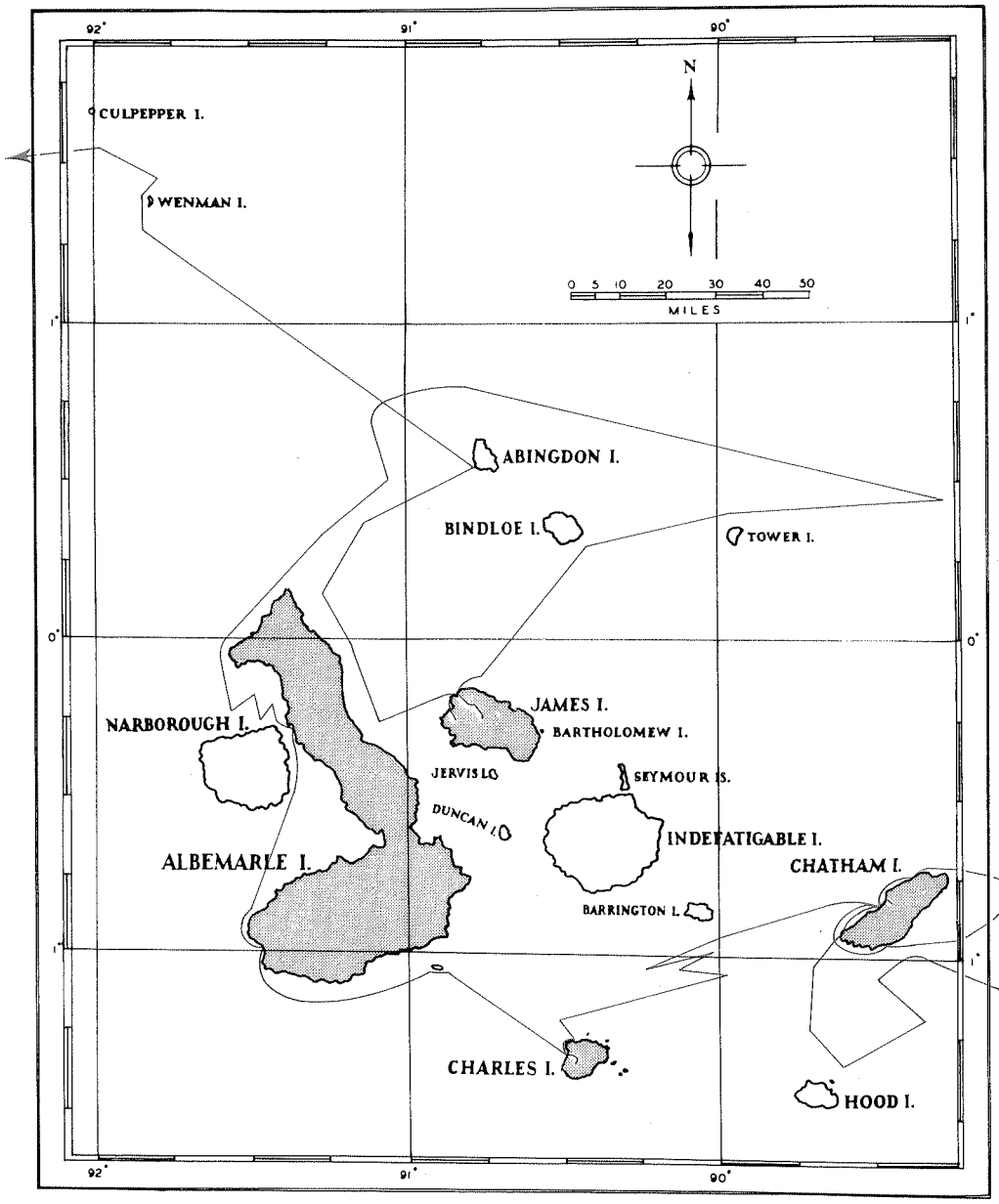

Figure 1. The Galapagos Archipelago. (Adapted from Lack, 1945: Frontispiece.) Of the sixteen principal islands, Darwin visited the four shaded ones, proceeding via the route indicated on the map. Although Darwin glimpsed Hood, a low island, from a fairly close distance (16 September), he did not disembark there. At Chatham, the first island on which Darwin landed, he spent five days collecting and geologizing, mostly on the western side of the island (16–22 September). There he visited four different localities, including a brief landing near Wreck Point on the southwestern tip of the island (16 September); Stephens Bay (17 September); Terrapin Road, near the northern tip of the island (18 September); a possible brief landing at Freshwater Bay, on the southeastern side of the island (20 September); and, after returning once again to Stephens Bay (21–22 September), an area several miles to the northeast that is studded with small volcanic cones (Fig. 2). En route to Charles Island (23 September), which Darwin visited next, he would have had a good glimpse of the southern side of the low but steep-cliffed Barrington Island. On Charles Island, Darwin collected for one day in the area around Post Office Bay (24 September). On 25 and 26 September he visited the highlands, going first by longboat to Black Beach, where he

disentangled from legend, that helps to distinguish Darwin's genius from the intellectual talent of his contemporaries. In what follows I will reconstruct the story of Darwin's conversion from the time of his visit to the Galapagos Islands in the fall of 1835 (Fig. 1) to his decision in July of 1837 to begin the first of a series of notebooks on the transmutation of species. I will also argue that much of Darwin's theoretical understanding of the Galapagos occurred only gradually, during the twenty-two years separating his conversion to the theory of evolution in 1837, from his eventual publication of the *Origin of Species* in 1859.

THE *ORNITHOLOGICAL NOTES*

Approximately nine months after leaving the Galapagos Islands, while preparing a separate catalogue for his ornithological specimens, Darwin made the following famous entry as he recopied a portion of his voyage zoology notes dealing with the Galapagos mockingbirds:

> I have specimens from four of the larger Islands. . . . The specimens from Chatham and Albermale [*sic*] Isd appear to be the same; but the other two are different. In each Isld. each kind is *exclusively* found: habits of all are indistinguishable. When I recollect, the fact that from the form of the body, shape of scales & general size, the Spaniards can at once pronounce, from which Island any Tortoise may have been brought. When I see these Islands in sight of each other, & possessed of but a scanty stock of animals, tenanted by these birds, but slightly differing in structure & filling the same place in Nature, I must suspect they are only varieties. The only fact of a similar kind of which I am aware, is the constant asserted difference—between the wolf-like Fox of East & West Falkland Islds.—If there is the slightest foundation for these remarks the zoology of Archipelagoes—will be well worth examining; for such facts [would *inserted*] undermine the stability of Species.[3]
>
> (1963[1836]:262)

This passage, which contains the first explicit hint of the evolutionary views that Darwin was later to expound with such revolutionary consequences, should not be taken, as it sometimes has, as the statement of a confirmed believer in the theory of evolution. Rather, Darwin apparently drew face to face with this possibility, some nine months after leaving the Galapagos, only to reject it on the grounds that the mockingbirds were probably "only varieties".[4] To

[3]The composition of Darwin's *Ornithological Notes*, which has long been the subject of conjecture and divergent opinion, can now be assigned to the thirty-one day period between 18 June and 19 July 1836, while the *Beagle* was sailing from the Cape of Good Hope to St. Helena and Ascension islands (Sulloway, 1982c : 327–37).

[4]Hodge (1983 : 62–63), in contrast to certain other Darwin scholars cited in note 2, believes that Darwin's expression "I must suspect they [the mockingbirds] are only varieties" is a statement *favoring* transmutation, since the formation of local varieties is the first step in the process of transmutation. Even within the creationist system, however, species were widely held to vary at the subspecific level according to local conditions. Hence the only kind of evidence that could ever convincingly shatter the creationist theory was solid proof that local varieties, under certain circumstances, were capable of breaking the immutable 'species barrier'. Darwin's reluctance to accept this conclusion when writing about the Galapagos mockingbirds in mid-1836 is reinforced by the fact that the relevant *Ornithological Notes* passage, drafted nine months after Darwin's zoology diary entry for these birds, has actually backed away from his initial judgment that "This bird. . . is singular from existing as varieties or distinct species in the different Is^{ds}. . ." (DAR 31.2 : MS p. 341; all DAR numbers refer to the Darwin manuscript collection at Cambridge University Library). In short, without the backing of an expert taxonomic opinion, Darwin, in mid-1836, was clearly giving the benefit of the doubt to the prevailing dogma of the fixity of species. Hodge's (1983) differing opinion about this passage is based on his erroneous assumption that Darwin, in 1836, already knew about the highly endemic nature of the Galapagos flora and

understand *why* Darwin was hesitant to see his four Galapagos mockingbird specimens in an evolutionary light, it is necessary to review the impression that various other Galapagos organisms had already made upon him during his five-week visit to these islands.

THE TORTOISES

The reported differences among the various island populations of the Galapagos tortoise are particularly relevant in this connection. Darwin was first informed of the possibility that the numerous islands of the Galapagos group

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(note 4, *contd.*) fauna (see page 45). Darwin, Hodge therefore argues, assumed all these endemic Galapagos forms—including the debatable island "varieties"—had arisen by colonization and subsequent transmutation. Years later, Darwin *did* consider the presence of varieties or "doubtful species" on the different islands of archipelagoes as supporting the theory of evolution (1909[1844]: 160, 187, 197; 1845 : 397; 1859 : 404). But in contrast to his thinking in 1836, when he still did not know whether the Galapagos organisms were endemic or whether the Galapagos mockingbirds, tortoises, or Falkland foxes would be considered by expert systematists as more than local varieties, Darwin had long possessed the decisive "facts" (or rather the sworn judgments of reliable systematists) that were ultimately necessary to "undermine the stability of Species".

What Darwin had in mind when writing the crucial *Ornithological Notes* phrase "*such facts* would undermine the stability of Species" was the common nineteenth-century view that all *constant* forms not united to one another by intermediate morphological links are presumably 'good' species. Since Darwin's day this strictly 'morphological' species concept has been rejected in favor of a more flexible, 'biological' species concept. Darwin, who himself later adopted the biological species concept after he became an evolutionist (see note 13), was clearly aware in mid-1836 that a purely morphological species concept was not apparently suitable to assessing the Galapagos mockingbirds and tortoises unless one was also willing to give up the whole foundations of pre-Darwinian biology.

Once again, Darwin was more inclined to stretch his species concept a bit rather than let four mockingbird specimens, collected from a small and perhaps unrepresentative series of islands within the Galapagos group, overthrow the doctrine of the immutability of species. At present some ornithologists still consider the Galapagos mockingbirds to be a single species (*Nesomimus trifasciatus*) possessing nine insular races (see Davis & Miller, 1960 : 447–48).

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followed a trail to the settlement. On 27 September, after briefly reboarding the *Beagle* at Black Beach, Darwin ascended Saddle Mountain, the highest point on the island. The *Beagle*, leaving Charles Island on the morning of 28 September, subsequently anchored for part of a day in Iguana Cove on the southwestern tip of Albemarle Island (29 September). Darwin, however, disembarked only at Tagus Cove (1 October), mainly exploring the geological terrain a few miles to the south and collecting plants. The *Beagle* then proceeded toward Abingdon Island, where strong currents caused the ship to drift twenty miles to the northwest before favorable winds allowed the vessel to sail within close sight of Tower and Bindloe islands (4–7 October). After passing Bindloe Island, Darwin and three other men were landed on James Island, while the *Beagle* returned to Chatham, Hood, and Charles islands. On James Island Darwin and his companions set up camp for nine days (8–17 October) at Buccaneer Cove, just a few miles north of James Bay. From this base camp Darwin made two trips to the highlands, where he spent three days collecting (9 and 12–13 October). Darwin also took a trip by longboat to James Bay, where he examined the lava flows and the salt mine (11 October). The *Beagle*, after picking up Darwin and his three companions at Buccaneer Cove, surveyed the northeastern side of Albemarle Island (17–18 October). The following day the *Beagle* met up with its surveying yawl at Abingdon Island; and finally, on 20 October, the ship completed its work in the Galapagos Archipelago with a survey of the two northernmost islands (Wenman and Culpepper). Altogether, Darwin spent nineteen days—some only in part—on land in the Galapagos Islands, and another eighteen days on board the *Beagle* during the ship's surveying activities and movements from island to island. Although Darwin landed on only four islands, he had relatively good views of eight of the other twelve main islands of the Galapagos group, including all six of the largest volcanic craters. (I have reconstructed the *Beagle*'s movements from Admiralty survey charts L 945–950, 953–954, 958, and map 1375 [Hydrographic Department, Taunton]. In doing so, I have not included certain minor perturbations in the *Beagle*'s general route.)

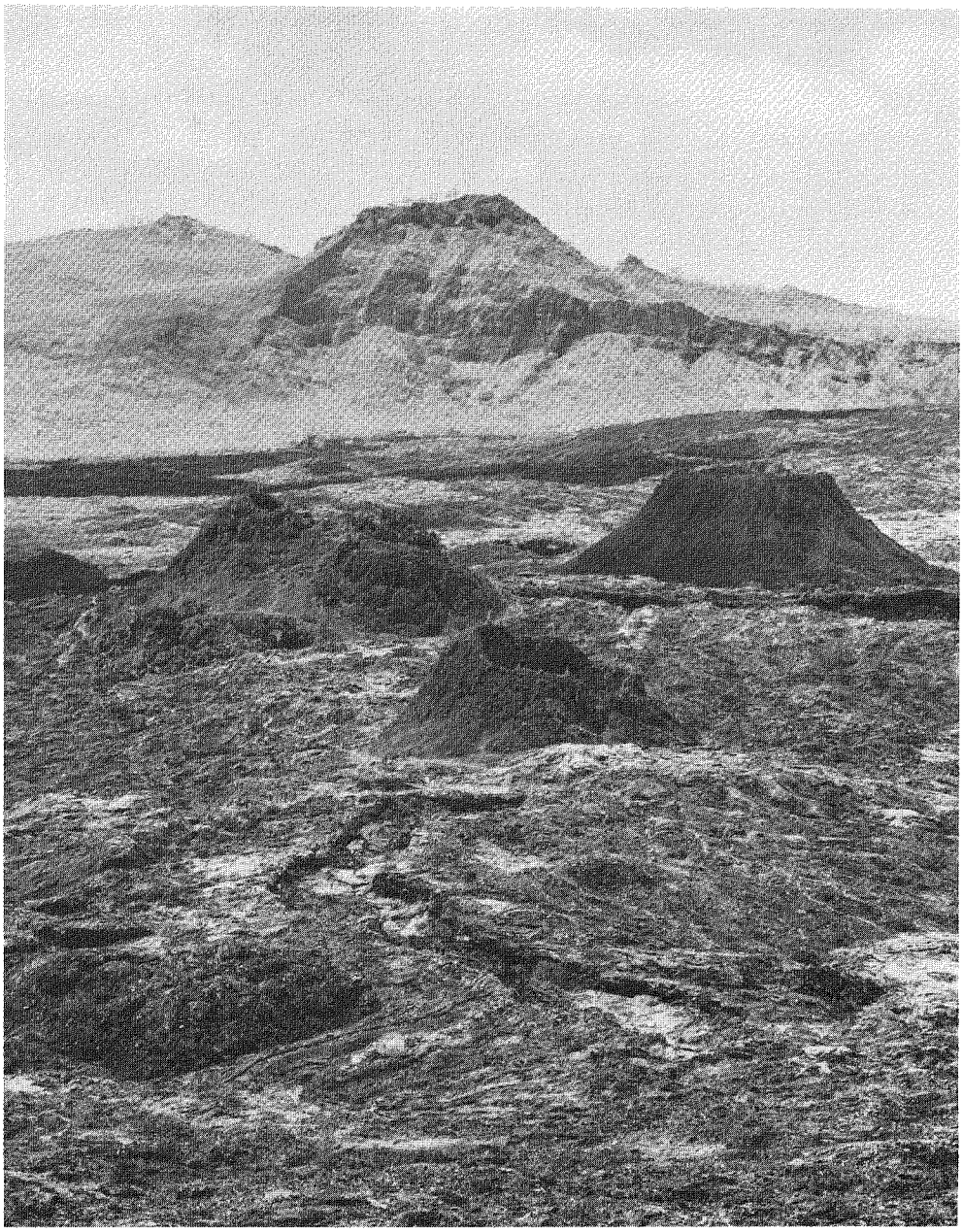

Figure 2. The heavily cratered region northeast of Stephens Bay that Darwin visited on 21 September 1835. In his *Journal of Researches* Darwin described this area as "part of the island where some black cones—the former chimneys of the subterranean heated fluids—were extraordinarily numerous. From one small eminence, I counted sixty of these truncated hillocks, which were all surmounted by a more or less perfect crater. . . . From their regular form, they gave the country a *workshop* appearance, which strongly reminded me of those parts of Staffordshire where the great iron-foundaries are most numerous" (1839:455). Photographed by the author on Chatham Island.

might be tenanted by slightly different forms when Nicholas O. Lawson, the vice-governor of the islands, told Darwin that "the tortoises differed from the different islands, and that he could with certainty tell from which islands any one was brought" (1845:394). "I did not for some time," Darwin later asserted, "pay sufficient attention to this statement, and I had already partially mingled together the collections from two of the islands. I never dreamed that islands, about fifty or sixty miles apart, and most of them in sight of each other, formed of precisely the same rocks, placed under a quite similar climate, rising to a nearly equal height, would have been differently tenanted. . . . [B]ut I ought, perhaps, to be thankful that I obtained sufficient materials to establish this most remarkable fact in the distribution of organic beings" (1845:394). What Darwin did not go on to relate in his *Journal* account of this episode, however, are the various reasons that caused him initially to disregard the vice-governor's comments.

The key to Darwin's oversight lies in the specific name—*Testudo indicus*—by which the Galapagos tortoise was known at the time. In the 1830s two different species of giant land tortoise, one now known to have come from the Aldabra Islands in the Indian Ocean and the other from the Galapagos, had been confused under this name. This error in systematics had in turn encouraged the mistaken belief that the Galapagos form of giant tortoise was not actually native to these islands but had been transported there by buccaneers and, earlier, by the oceangoing peoples of the Pacific islands. Captain Robert FitzRoy reiterated this view in his own published account of the *Beagle* voyage. There he emphasized that virtually no animal was more suited for extensive oceanic transport, since the giant land tortoise was easily caught and good to eat, and required little food or water for long periods (1839:505). FitzRoy also cited the views of the buccaneer William Dampier, who claimed to have seen another variety of this species in Madagascar and elsewhere in the Indian Ocean (1729:102). Like Dampier, FitzRoy had no doubt that the Galapagos form of tortoise was a mere variety of this other race, slightly altered by removal to its new environment.

It was this widespread confusion regarding the original habitat of the Galapagos tortoise that apparently caused Darwin, like FitzRoy, to dismiss the reported island differences as a phenomenon readily explained by the changes in form that customarily accompany an animal's introduction into a new and dissimilar country. Since *Testudo indicus* was already known to be a single species, Darwin seems to have concluded that the differences found on the various islands of the Galapagos were merely varietal peculiarities somehow dependent upon the harsh and by no means identical conditions of each island.[5]

Darwin's attitude toward the reported differences among the tortoises was

[5]Although Darwin later stressed in his *Journal of Researches* (1845 : 394, 397) how similar all the islands of the Galapagos were, he was fully aware at the time of his visit that these islands varied considerably in size, height, terrain, availability of fresh water, and degree of vegetation. For example, in a voyage specimen catalogue he referred to Chatham Island as "a dry Isld" compared with some of the other islands (Porter, 1980 : 87). Moreover, Darwin knew that such geographic and climatic differences were occasionally associated with local variations of an apparently subspecific nature among the organic inhabitants of the islands. In his voyage *Diary* he recorded that "those [plants] of the same species" attained a much greater size on James Island than elsewhere in the archipelago (1933 : 340). Similarly, he noted that marine iguanas grew to a larger size on Albemarle Island than on other islands he had visited (DAR 31.2 : MS p. 333). At the time, none of these observations prompted any particular surprise or evolutionary speculations on Darwin's part.

reinforced by one other circumstance that has gone unrecognized in connection with his visit to the Galapagos. The first island that Darwin visited, and the place where he saw his first tortoise, was Chatham Island (Fig. 3). From there the *Beagle* proceeded to Charles Island, where the vice-governor was residing. The Charles Island tortoise, like the nearby Hood Island variety, has its shell turned up in front like a Spanish saddle. This is an adaptation found on the smaller and drier islands, allowing the tortoise to stretch its neck much higher in search of food (Fig. 4). At the time of the *Beagle*'s visit to Charles Island, this distinctive saddleback tortoise was nearly extinct, and apparently no live ones were seen by Darwin or FitzRoy. Nevertheless, Darwin did have at least one opportunity to observe the unusual Charles Island form of tortoise shell. Carapaces were readily visible at the settlement, where they were being used as flower pots (FitzRoy, 1839:492). Unfortunately, neither Darwin nor FitzRoy thought it important to procure a specimen for scientific purposes, or even to record the form of the shell as compared with the Chatham Island form. Within about ten years of the *Beagle*'s visit, the Charles Island tortoise became extinct, and herpetologists had to wait nearly a century to find remains of this subspecies in a lava cave (Broom, 1929).

From Charles Island Darwin proceeded to Tagus Cove on Albemarle Island, where he spent only part of a day on shore (1 October) and did not see any tortoises. Then on 8 October, Darwin, his servant, and three other men were left on James Island for nine days in order to collect specimens from this large and central location. In the highlands on James Island Darwin saw many tortoises. As luck would have it, the James Island tortoise is fairly similar to the Chatham Island race, the only other form that Darwin had personally seen (Fig. 5). Both have a carapace that is relatively dome-shaped, the other of the two morphological extremes found in the archipelago. Darwin, noticing no real difference based on his memories of the Chatham Island tortoise, probably concluded that whatever distinguishing features there were could not be all that pronounced. In fact, herpetologists can by no means tell at a glance what island any Galapagos tortoise is from, and the vice-governor's claim was something of an exaggeration. For example, of the more than fifty tortoises that zoos have recently repatriated to the Galapagos in order to assist in the tortoise-rearing and conservation program, only one has thus far been identified by island.

Darwin had one last opportunity, after his departure from James Island, to follow up the vice-governor's claims about the tortoises. FitzRoy, returning to Chatham Island for fresh water while Darwin was collecting specimens on James, had taken on thirty large tortoises to be stored in the ship's hold as a supply of fresh meat during the *Beagle*'s cruise across the Pacific (1839:498). But Darwin and his *Beagle* shipmates gradually ate their way through the evidence that eventually, in the form of hearsay, was to revolutionize the biological sciences. Regrettably, not one of the thirty Chatham Island carapaces reached England, having all been thrown overboard with the other inedible remains.

Two small tortoises, evidently kept as pets by Darwin and his servant, did survive the *Beagle* voyage. When Darwin, back in England, finally realized the necessity for having an expert compare the various forms of tortoise, these, together with two specimens that FitzRoy had procured for the British Museum, were his only remaining sources of evidence. Although the four tortoises were from three different islands (Hood, Charles, and James), those brought home by

Figure 3. The Chatham Island tortoise (*Geochelone elephantopus chathamensis*), a relatively dome-shaped form. Photographed by the author in the interior of northwestern Chatham Island, near where Darwin did most of his collecting and geological observations. Three days after a hunting party had brought eighteen live tortoises on board the *Beagle*, Darwin went for an extensive geological walk (21 September), during which he first saw Galapagos tortoises in the wild. He later described this episode in his *Journal of Researches:* "The day was glowing hot, and scrambling over the rough surface and through intricate thickets, was very fatiguing; but I was well repaid by the strange Cyclopean scene. As I was walking along I met two large tortoises. . . . These huge reptiles, surrounded by the black lava, the leafless shrubs, and large cacti, seemed to my fancy like some antediluvian animals" (1845 : 374–75).

Figure 4. The Hood Island tortoise (*Geochelone elephantopus hoodensis*), an extreme saddleback form of tortoise similar to the now-extinct Charles Island race (*G. elephantopus galapagoensis*). Photographed by the author at the Charles Darwin Research Station, Isla Santa Cruz.

Darwin and his servant were too young to allow any meaningful scientific comparison (1839:465).

It was also upon his return to England that Darwin was told by Thomas Bell and other herpetologists that, in their opinion, the Galapagos tortoise was almost certainly native to that archipelago and, furthermore, that at least two species were endemic there. Once informed of this opinion, Darwin soon realized the evolutionary significance of the Galapagos tortoise evidence. But it was not

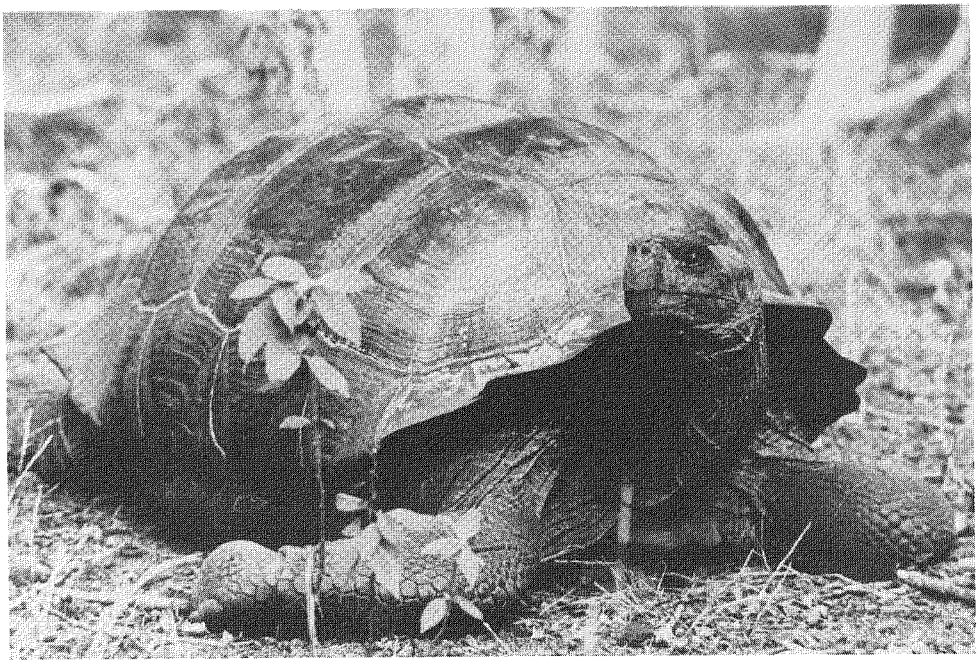

Figure 5. The James Island tortoise (*Geochelone elephantopus darwini*), a dome-shaped form. Photographed by the author in the intermediate zone, three miles southeast of the salt mine on James Island.

until the second edition of his *Journal of Researches* (1845:394) that he was finally able to describe the different dome-shaped and saddleback carapaces based on Captain David Porter's informative report thirty years earlier (1815, *1*:215). So it took Darwin nearly a decade to resupply the scientific evidence that he had initially allowed to slip through his fingers when he visited the Galapagos Islands in 1835.

DARWIN'S FINCHES

Analogous to the legendary roles assigned to the Galapagos tortoises and mockingbirds, it has widely been claimed that Darwin's finches played a key role in converting Darwin to the theory of evolution.[6] According to David Lack (1947:23), Darwin began to separate his finches by island shortly after hearing the vice-governor's testimony on Charles Island that the tortoises from the different islands could be differentiated. Lack based his assertion on certain of Darwin's own statements about his collecting procedures, as well as on the fact that many of Darwin's type specimens at the British Museum (Natural History) are labeled as coming from James Island, the last of the four islands Darwin visited. Still, Lack himself had doubts about the accuracy of a number of

[6]See, for example, Swarth, 1931 : 10; Huxley, 1954 : 6; 1960 : 9; Eibl-Eibesfeldt, 1961 : 18; Eiseley, 1961 : 172–73; de Beer, 1963 : 132; Peterson, 1963 : 11–12; Moody, 1970 : 303; Leigh, 1971 : 136; Thornton, 1971 : 12, 161–62; Grzimek, 1973 : 359; Gruber & Barrett, 1974 : 130; Dorst, 1974, *2* : 252; Silverstein, 1974 : 505; Dobzhansky *et al.*, 1977 : 12; Kimball, 1978 : 587; and Ruse, 1979: 164; 1982 : 24, 115.

Darwin's localities—including specimens from the one island (James) where Lack believed Darwin had carefully segregated all of his finch specimens. Contrary to the impression Darwin may have given Lack and others, he derived virtually all of his locality information for the Galapagos finches by borrowing, after his return to England, the carefully labeled collections of three other *Beagle* shipmates (Sulloway, 1982a; 1982b). This circumstance has nevertheless served, in a highly ironic manner, to reinforce the myth that Darwin's conversion to the theory of evolution occurred during his visit to the Galapagos. Curators at the British Museum naturally assumed that Darwin's published locality information had come from his *own* finch specimens. Hence, whenever Darwin, in the *Zoology of the Voyage of H.M.S. Beagle* (1841), indicated that a species had come from one island only, the curators subsequently entered that island on the labels of Darwin's type specimens. As time went on, it increasingly appeared that Darwin must have appreciated the evolutionary significance of his Galapagos finches while he was still in the archipelago, if he had gone to the trouble of segregating most of his specimens by island.

On the other hand, this circular derivation of the localities of Darwin's types largely accounts for the taxonomic nightmare these specimens have caused later ornithologists (e.g., Swarth, 1931; and Lack, 1945; 1947). The dubious localities entered on many of Darwin's type specimens even gave rise to vigorous debates about whether certain subspecies of Darwin's finches had evolved since his visit to these islands! Fortunately, clarification of the borrowed nature of Darwin's localities has resolved these debates, together with certain related problems concerning the systematics and geographic distribution of two now-extinct subspecies of Darwin's finches.

Elsewhere I have identified and described in detail the four separate *Beagle* collections of Galapagos specimens and, through caliper measurements or manuscript evidence, have been able to supply an accurate island locality for almost every *Beagle* specimen of Darwin's finches (Sulloway, 1982b). From these measurements and manuscript records—especially Captain FitzRoy's meticulously kept catalogue of his own official voyage collection—it is now evident that *Geospiza magnirostris magnirostris*, the extinct and unusually large-billed subspecies of the large ground finch, was once endemic to two islands—Chatham and Charles.[7] This extinct form was never present, as some ornithologists have believed, on James Island or any of the other northern islands of the Galapagos group. Of additional ornithological interest, John Gould's (1837a) "*G. nebulosa*" is indeed, as David Lack (1947:23) strongly suspected, an extinct and unusually large-billed form of the sharp-beaked ground finch (*G. difficilis*) once endemic to Charles Island. Besides the two surviving *Beagle* specimens, I have recently located a third and virtually identical specimen, collected on Charles Island in 1852 during the voyage of the Swedish frigate *Eugenie*. Steadman (1982) has also found six fossil specimens of

[7]At least 90 percent of the *Beagle* specimens of *Geospiza magnirostris magnirostris* are distinguishable from *G. magnirostris strenua*, thus more than satisfying David Lack's criterion of subspecific status (1947 : 17). David Steadman (1981) has recently found fossilized remains of *G. magnirostris magnirostris* on Charles Island, where, prior to its extinction, it was by far the most common species of Darwin's finches in the arid zone. If suitable paleontological sites can be found on Chatham Island, fossilized remains of this subspecies should also be encountered there.

this large-billed subspecies on Charles Island. In the light of these facts, the name *nebulosa* (Gould, 1837a) has valid priority over the name *difficilis* (Sharpe, 1888) and accordingly should be restored as the official name of this taxon (Sulloway, 1982b:69–70).[8]

The imprecise nature of many of Darwin's Galapagos finch localities is a large part of the reason why Darwin, contrary to the legend, never mentioned these birds in the *Origin of Species* (1859).[9] For without more accurate and extensive locality information, it was simply not possible to put these finches forward as a convincing example of speciation through geographic isolation. The two cases of geographic replacement among the finches that Darwin tentatively argued for in his *Journal of Researches* (1845:395) are, in fact, spurious, being based on inaccurate locality records and insufficient collecting. It is no wonder, then, that Darwin was so excited and relieved in 1845 when he finally learned the results of Joseph Hooker's rigorous demonstration of geographic representation in Darwin's several hundred species of Galapagos plants. To Hooker he responded in July of that year, "I cannot tell you how delighted and astonished I am at the results of your examination; how wonderfully they support my assertion on the differences in the animals of the different islands, *about which I have always been fearful*" (1887, *2*:22; italics added).[10] Darwin's subsequent decision not to use the Galapagos finches to bolster his evolutionary argument in the *Origin* proved well advised. After Drs. Kinberg and Habel brought back extensive collections of birds from the Galapagos in the 1850s and 1860s, Osbert Salvin was forced to comment that "Mr. Darwin's views as to the exceedingly restricted range of many of the species must be considerably modified" (1876:461). By then, however, Darwin's evolutionary views, and his generalized claims about the Galapagos, had won the day, owing largely to Joseph Hooker's indisputable botanical evidence.

As for the claim that Darwin was immediately impressed by the morphology of the finches as a classic case of adaptive evolutionary radiation, nothing could

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[8]The international code of zoological nomenclature states that the name of the first described subspecies shall be the specific name of all subsequently described subspecies of the same species-group. The convention of disallowing otherwise valid names that have not been used for more than fifty years is not applicable in this instance, since *G. nebulosa* is by no means a forgotten or overlooked name. The name has been used by Lack (1945, 1947, 1969) and other ornithologists, throughout the last three decades, when referring to the Charles Island subspecies of the sharp-beaked ground finch; and it has also been proclaimed by Paynter & Storer (1970 : 162) to be the obligatory name of this taxon should Lack's views be confirmed and accepted. Similarly, clarification of the long-disputed localities of the *Beagle* specimens of *G. magnirostris magnirostris* and *G. magnirostris strenua* has now legitimated beyond any doubt the tentative trinomials proposed by Lack (1947, 1969) and Paynter & Storer (1970 : 161n.). See further Sulloway (1982b: 68, n.53).

[9]The following authors, for example, have mistakenly assumed that Darwin honored the Galapagos finches with a prominent place in the *Origin*: Lack, 1945: 4; Gillsäter, 1968 : 85; and Ruse, 1982 : 115. See also Williamson (1983 : 566), who perpetrates a slightly modified version of this myth (Sulloway, 1983). The various island forms of the Galapagos tortoise are also not mentioned in the *Origin*, presumably because Darwin remained rightfully doubtful about whether the different populations could really be considered separate species. Today the eleven living and four extinct forms of the Galapagos tortoise are considered, just as Darwin himself suspected, to be subspecies of a single species (*Geochelone elephantopus*). See Thornton (1971 : 115).

[10]Darwin's comment that he had "always been fearful" about his previous claims with regard to the differences between the animals on the various islands of the Galapagos group clearly shows that he believed *specific*, not *varietal*, distinctions were necessary to support the doctrine of the mutability of species. Darwin's 1845 remark to Hooker therefore reinforces the interpretation I have given earlier concerning Darwin's *Ornithological Notes* (1963[1836] : 262) passage about the "varieties" of the Galapagos mockingbirds. See note 4.

be further from the truth.[11] While in the Galapagos Islands Darwin was more impressed by the apparent differences than by the similarities among these unusual finch species. At the time, he actually believed he was dealing with a highly diverse group having at least three or four separate subfamilies. For example, Darwin identified the cactus finch in his voyage notes as an "Icterus", a genus in the family of the orioles and blackbirds; and he mistook the warbler finch for a "Wren" or warbler. In fact, Darwin correctly identified *as finches* only six of the thirteen species—less than half the present total—and he placed these six species in two separate groups of large-beaked and small-beaked Fringillidae. Thus, it was only after his return to England, when the eminent ornithologist John Gould astutely recognized the close affinities of this bird group, that Darwin's finches became Darwin's *finches* in the sense that we now comprehend.

Furthermore, with the exception of the cactus and warbler finches, Darwin had failed to observe any differences in diet among the various species, mistakenly believing that their food consumption was largely identical (1841:99–100). For this reason he could never argue in the *Origin* that the different beaks were necessarily adaptive and hence produced by natural selection. Ornithologists continued to discount the adaptive nature of the beak differences in Darwin's finches for nearly a century.

It was in the wake of Darwin's failure to appreciate the evolutionary significance of the tortoises and the finches that he was also inclined to reject such an interpretation for the mockingbirds and hence to suspect, in the *Ornithological Notes* (1963[1836]) passage I have already cited, that these birds must be "only varieties". This brings me to another more general point. What was crucial to Darwin's eventual decision to accept the mutability of species was not really the mockingbirds or any other single group of Galapagos organisms. Rather, his appreciation of the mockingbirds required his concomitant appreciation of the Galapagos evidence as a whole. This was not possible, however, until he had been freed of the many misconceptions he had entertained about these unusual organisms during his brief visit to these islands.

DARWIN'S CONVERSION

Darwin's conversion to the theory of evolution can, I believe, be dated with considerable certainty to the second week of March 1837, nearly a year and a half after Darwin had departed from the Galapagos Islands, and five months following his return to England (Sulloway, 1982c). What finally catalyzed Darwin's conversion was a meeting he had at the Zoological Society of London with John Gould, the society's eminent ornithologist and taxidermist.

At Cambridge University Library there exists a piece of paper on which Darwin, in a somewhat hurried hand, recorded the various taxonomic conclusions that Gould had already reached by early March regarding Darwin's Galapagos birds (Figs 6, 7). On this same sheet Darwin later added various memoranda that clearly indicate the revolutionary new direction his thoughts

[11] Most of the authorities cited in note 6 make this claim, sometimes emphasizing, in addition, how impressed Darwin must have been by the habits of the tool-using 'woodpecker' finch (*Camarhynchus pallidus*). In actual fact, Darwin never saw this species, which was first collected in 1868, nine years after Darwin published the *Origin of Species*. The earliest report of the woodpecker finch's remarkable tool-using behavior had to wait another fifty years (Gifford, 1919:256).

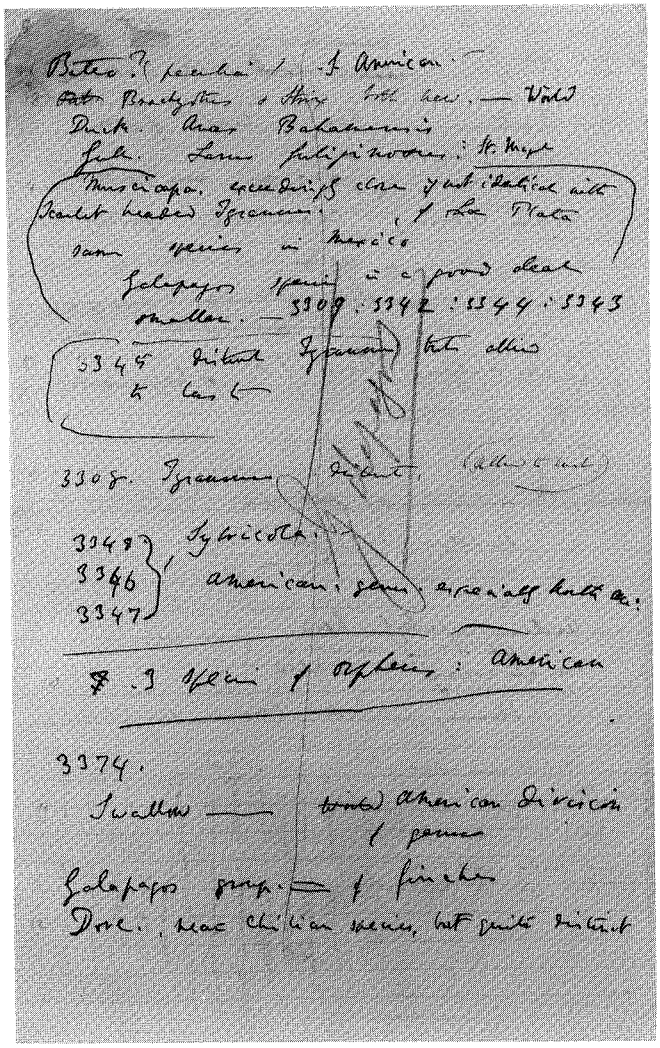

Figure 6. Darwin's manuscript record of John Gould's Galapagos species designations (*front*). (Courtesy of the Syndics of Cambridge University Library.)

began to take following his meeting with Gould. The meeting, and the document recording what was discussed, can be dated to within a six-day period, namely, 7 to 12 March, immediately after Darwin had moved from Cambridge to London in order to be near the various systematists who were working on his *Beagle* collections.[12] The document (Fig. 6) begins with a listing

[12]As early as 4 January 1837, when Darwin delivered his collection of birds and mammals to the Zoological Society, he had evidently discussed his Galapagos birds in general terms with Gould. In a letter of 9 January 1837 to William Jardine, John Stevens Henslow reported that "Darwin has just returned from a visit to London & tells me that Gould pronounces all his Galapagos animals to be so entirely novel & curious that he will undertake an express work to illustrate them" (Jardine letters, Royal Scottish Museum, Edinburgh). It was not until March 1837, however, that Darwin learned the full details of Gould's taxonomic judgments, as recorded on Darwin's handwritten "Galapagos" sheet (Figs 6, 7). I have discussed the dating of this document (DAR 29.3 : 27), as well as the timing of Darwin's conversion, more fully in Sulloway (1982c).

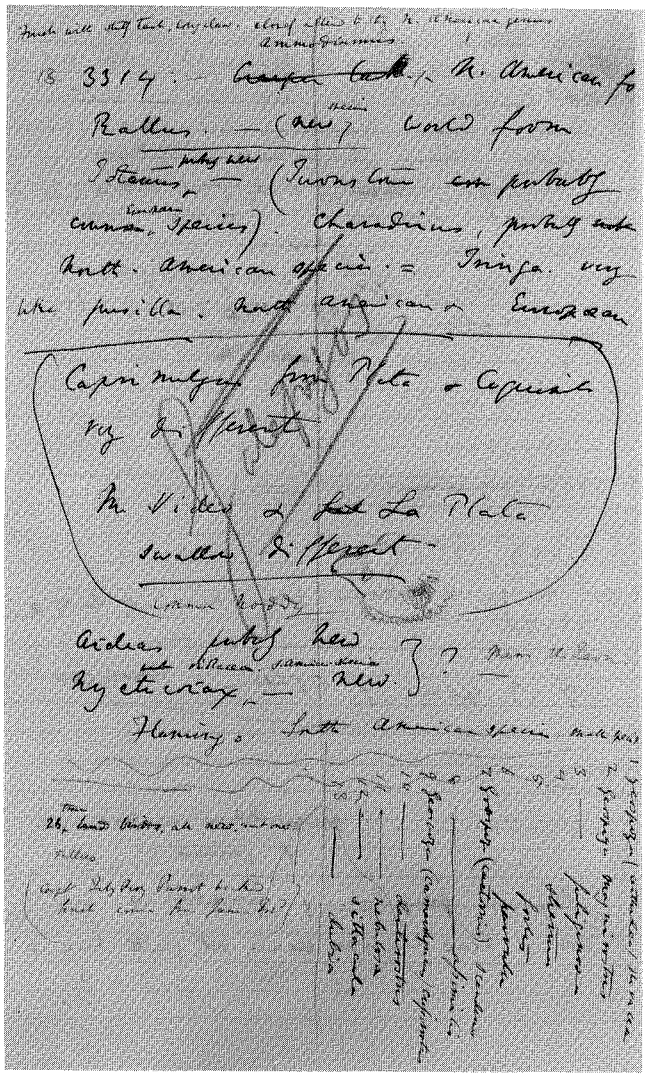

Figure 7. Darwin's manuscript record of John Gould's Galapagos species designations (*back*). (Courtesy of the Syndics of Cambridge University Library.)

of the Galapagos land birds in almost precisely the same order, and with the same commentaries about their American continental alliances, as in Darwin's *Journal* (1839:461–62). The oral nature of Darwin's discussion with Gould is indicated by Darwin's omission, within the list of finches, of the silent '*p*' in his spelling of the name *psittacula* (Fig. 7). As Gould began to tell Darwin about the Galapagos birds, I believe that Darwin, whose interests were undoubtedly aroused by Gould's remarks, asked for a sheet of paper on which to record the details of their discussion. Since someone, perhaps Gould, had already made a pencil sketch of a small animal on one side of the sheet, Darwin began writing on the unused side, proceeding later to the used side of the sheet, eventually writing over the drawing.

From the very first entry on the list—"Buteo?"—it is clear that Darwin was in for a surprise during his meeting with Gould. In his voyage ornithological notes, Darwin had previously classified the Galapagos hawk among the caracaras or Polybori owing to the bird's unusual tameness and carrion-feeding habits (1963[1836]:238, 262). During a 24 January meeting of the London Zoological Society, John Gould—not knowing of Darwin's voyage observations about the bird's behavior—had rightly assigned this new species to the Buteos; and Gould's assignment is why Darwin, who was initially unpersuaded, entered a question mark after Gould's judgment. Based, however, on Darwin's testimony about this hawk's habits, Gould subsequently convinced himself that the species shared various morphological characters with both the Buteos *and* the Polybori (1837b). Not long afterwards, in his first notebook on the transmutation of species, Darwin correctly recognized this Galapagos species as a case of convergent behavioral evolution. Thus he wrote of the "principle of animal having come to island where it could increase, but there were causes to induce great change, like the Buzzard [*Buteo*] which has changed into Caracara at the Galapagos" (de Beer *et al.*, 1967: *B* 55e). Later, in the second edition of the *Journal of Researches*, Darwin hinted publicly at his evolutionary interpretation of this unusual species when he remarked that "it might be fancied that a bird originally a buzzard, had been induced here to undertake the office of the carrion-feeding Polybori of the American continent" (1845:380).

As John Gould continued to discuss the various land birds recorded on Darwin's March 1837 "Galapagos" sheet, he emphasized that virtually all of the land birds were endemic to the Galapagos, although clearly of American character. This was a fact that Darwin, who had not visited the coast of South America north of Lima, could not have fully appreciated without access, like Gould, to large museum collections. Darwin, who was evidently very impressed by this information, made a special note of it at the bottom of the verso side of the sheet ("26 true land birds, all new except one"). Even several of the waders and waterbirds were new, Gould also informed Darwin—something that likewise surprised Darwin, and to which he later called special attention in his *Journal of Researches* (1839:461). Equally startling was the conclusion, backed by Gould's expert authority, that some of the Galapagos species (namely, the mockingbirds) indeed replaced one another geographically on the different islands of the Galapagos group. It was facts such as these, Darwin had already acknowledged eight months earlier, that, if ever confirmed, "would undermine the stability of Species". Finally, Gould must surely have piqued Darwin's interests when he informed him that his Galapagos "Wren" and "Icterus" were actually finches, and that the whole group constituted a unique and unusual genus of thirteen species (*Geospiza*), comprising three separate but closely related subgenera (*Cactornis*, *Camarhynchus*, and *Certhidea*).

Darwin was frankly stunned by Gould's various taxonomic conclusions. On the one hand, Gould's judgments convinced him beyond a doubt that transmutation must be responsible for the presence of similar but distinct species on the different islands of the Galapagos group. The supposedly immutable 'species barrier' had finally been broken, at least in Darwin's own mind. At the same time Darwin was prompted by Gould and other systematists who examined and discussed Darwin's Galapagos species at the London Zoological Society, to realize just how little agreement there was, even among experts, as to

what constitutes a 'species'. It was this experience that Darwin apparently had in mind when he later wrote in the *Origin of Species:* "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).[13]

It was also in reference to the crucial changes in his thinking that occurred in the spring of 1837 that Darwin subsequently wrote in a pocket "Journal": "In July [1837] opened first notebook on 'Transmutation of Species'—Had been greatly struck from about Month of previous March on character of S. American fossils—and species on Galapagos Archipelago. These facts origin (especially latter) of all my views" (de Beer, 1959:7). Darwin's reference in this passage to the "character of S. American fossils" is clearly an allusion to Richard Owen's recent paleontological findings about Darwin's collections, communicated to Darwin in mid-February 1837. By that date, Owen had assertained that Darwin's fossil Mammalia were virtually all extinct prototypes of the smaller, present-day forms that now characterize this continent (llamas, sloths, armadillos, and so forth). But this information about the close bond between the living and the extinct fauna of the South American continent had apparently not, on its own, been sufficient to convince Darwin of the mutability of species—although he may have had growing suspicions in this direction; hence Darwin's later insistence in his pocket "Journal" that it was "especially" the Galapagos facts, fully clarified by Gould three weeks later, that had provided the "origin. . . of all my views".

Consistent with this historical interpretation, Darwin's first evolutionary entry in another pocket notebook—the *Red Notebook*, which precedes the transmutation series—can be dated to about 15 March. This date is within a few days of Darwin's meeting with John Gould and is also the day after he and Gould had delivered papers on the two species of South American rheas that replace each other geographically in Patagonia (Darwin, 1837; Gould, 1837c). Ironically, Darwin had actually been eating (and had almost finished consuming) his only specimen of the southern form of rhea, when he had suddenly recalled, in 1834, what the gauchos and indians had previously told him about the existence of a *second* species of rhea in South America. Darwin managed to salvage most of the bones and some feathers for Gould's later examination; and this half-eaten specimen became the type of the species, which Gould named *Rhea darwini* in honor of Darwin's energetic labors in natural history. In his *Red Notebook* Darwin now pondered whether the model of speciation by geographic isolation would suffice for such cases of continental speciation, thus beginning a long chain of evolutionary deliberations that were never to cease (Darwin, 1980[1836–37]:127–28).

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[13]Soon after accepting the transmutation of species, Darwin adopted a biological species concept (based on the criterion of actually or potentially interbreeding populations) as a means of reconciling the 'reality' of species with their sometimes 'arbitrary' classification by different naturalists. In the late 1840s and early 1850s Darwin gave up this biological species concept in favor of a predominantly morphological concept—one that defined species as "only strongly marked and permanent varieties" (1859:469). This view was in many ways a 'tactical' species concept, aimed at convincing numerous frustrated systematists that species distinctions *are* arbitrary and hence that systematic work could never succeed in discovering the true 'essence' of each and every species (1859:48). See further Kottler (1978) and Sulloway (1979).

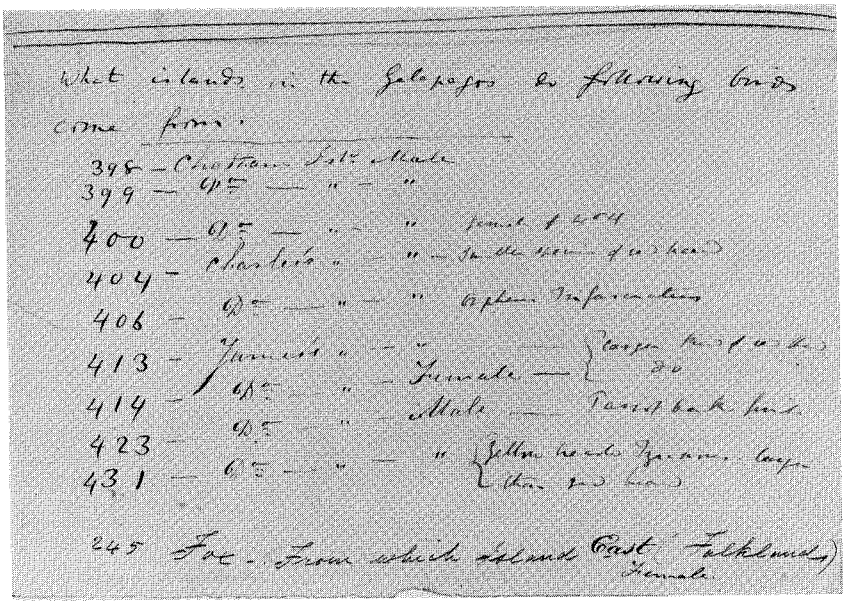

Figure 8. Darwin's request for information regarding the localities of Captain FitzRoy's Galapagos birds, with replies in the hand of an unidentified amanuensis. A second unidentified amanuensis, who is known to have worked for Darwin after the *Beagle* voyage, addressed the last question on the list, which was in turn answered by the first amanuensis. Additional memoranda, later added by Darwin, appear at the right of most of the entries. (Courtesy of the Syndics of Cambridge University Library.)

By mid-March of 1837, then, Darwin had finally come to accept the evolutionary implications inherent in his Galapagos collections; and he wasted little time in extending this evolutionary point of view to include patterns of geographic distribution among numerous other South American species, as well as the evidence of the fossil record. The *Red Notebook*, in which Darwin recorded most of these early evolutionary speculations, was completed by the end of June 1837 and was followed by a series of six notebooks on the transmutation of species (1837–42) and two additional notebooks devoted to man, mind, and comparative psychology (1838–39).[14] Although Darwin's famous Galapagos finches are not mentioned either in the *Red Notebook* or in any of the transmutation notebooks, it must have been during the spring of 1837 that Darwin realized what a great mistake he had previously made during his Galapagos visit when he had failed to separate his finches by island. This conclusion is borne out by two of the memoranda on Darwin's "Galapagos" list: "Capt Fitz Roy['s] Parrot beaked finch comes from James Isl[d]", and "No specimens [*or* 'species'?] from James Island". This second observation, written in pencil and later erased, apparently refers to *Camarhynchus crassirostris* or to *Geospiza nebulosa* among the list of finches (Fig. 7). Darwin subsequently sought to rectify his failure to label his own Galapagos finch specimens by island, by collecting every scrap of available locality information from the accurately labeled collections of three other *Beagle* shipmates (Figs 8, 9), including that

[14]See Gruber & Barrett (1974) and Kohn, Smith & Stauffer (1982 : 419).

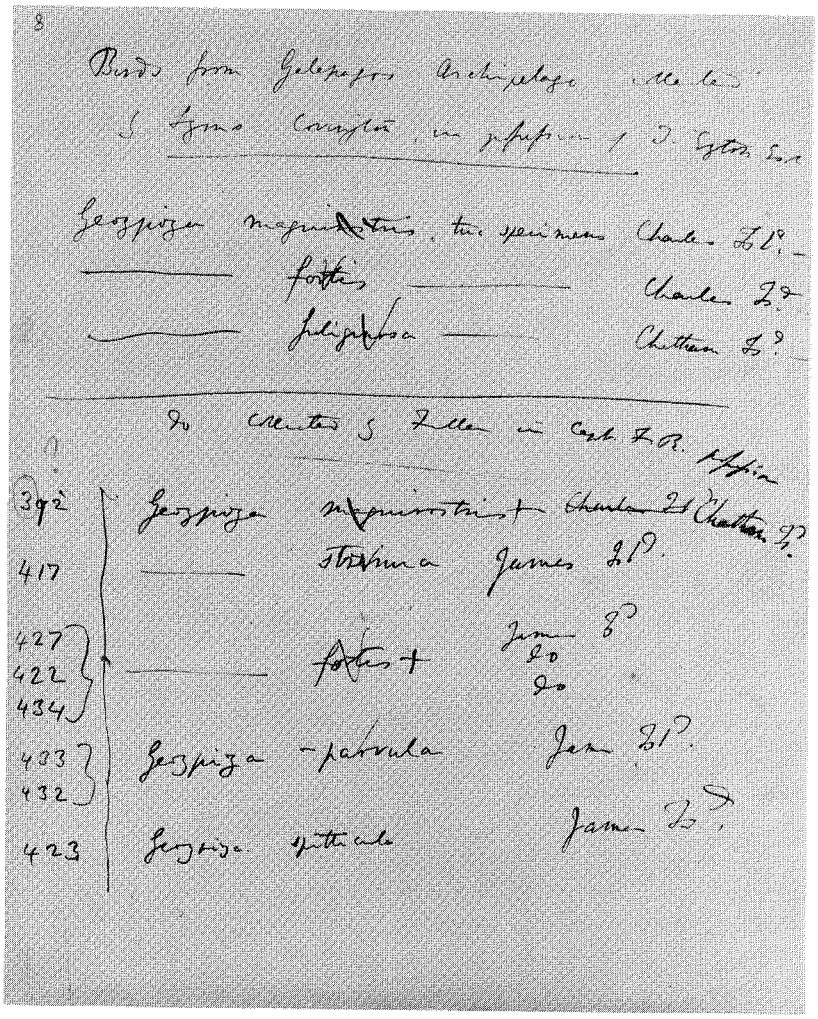

Figure 9. Darwin's notes on the island localities of his servant Covington's and another shipmate's Galapagos finches. (Courtesy of the Syndics of Cambridge University Library.)

of his own servant.[15] Darwin also tried to reconstruct, from memory, the localities of some of his own Galapagos finches (Fig. 10); but it is evident from bill and wing measurements of these specimens that, in at least two instances, he guessed incorrectly (Sulloway, 1982b:64).[16] Unfortunately, this dubious locality speculation—"?Chatham Isd??"—for eight of his thirty-one finch specimens later became the basis for the official British Museum tags; and over the years Darwin's own question marks were dropped from most of these tags as the British Museum substituted various new labels for Darwin's originals. Still, Darwin, by collating locality information derived from the four separate *Beagle* collections of Galapagos finches (1841:100–106), was ultimately able to supply

[15]DAR 29.3 : 26, 30.

[16]See Darwin's voyage catalogue of specimens ("Printed Numbers No[s] 1426 . . . 3342", Down House, Downe, Kent).

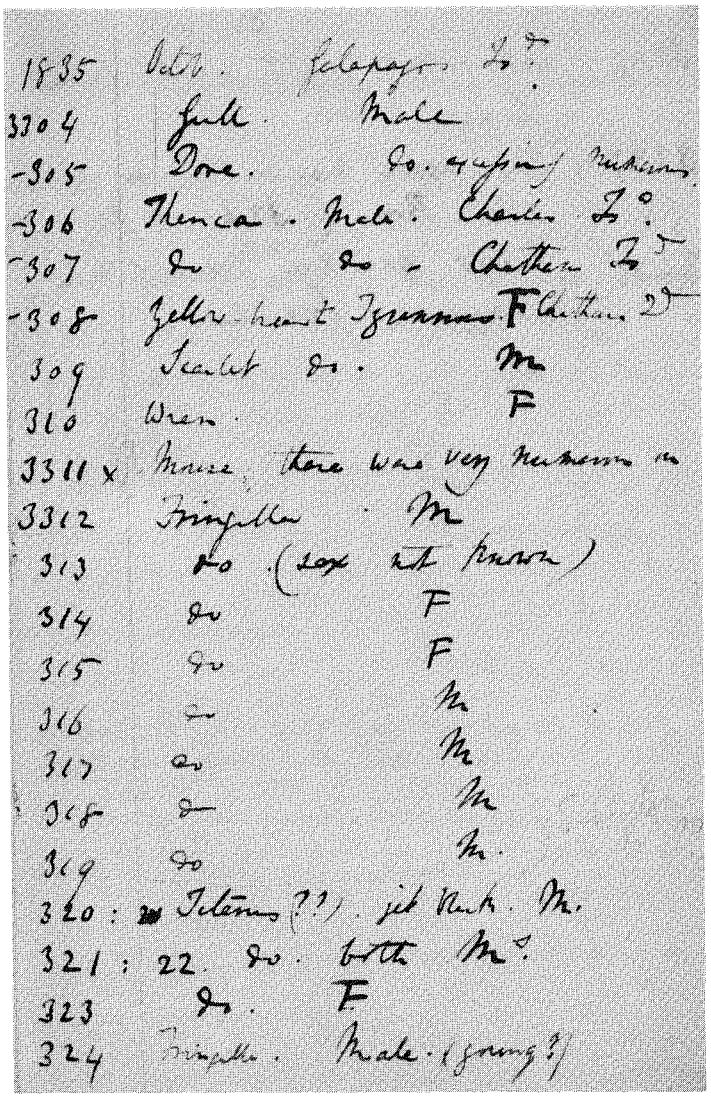

Figure 10. A page from Darwin's voyage specimen catalogue, recording some of the ornithological specimens collected in the Galapagos Archipelago. Specimen no. 3310 (*Certhidea olivacea*, mistakenly thought to be a "Wren") and nos. 3312–24 are Darwin's finches. Under the first eight "Fringilla", Darwin later drew a faint line in pencil and added the conjecture "?Chatham Is^{d}??" Because Darwin apparently remembered having first seen the largest-billed species of Galapagos finches (*Geospiza magnirostris magnirostris*) on Chatham Island and also remembered collecting specimens of the cactus finch—"Icterus (??)" = *G. scandens*—on James Island, he later guessed that the first eight "Fringilla" (mostly specimens of *G. magnirostris magnirostris*) must have come from Chatham. One must appreciate, however, that Darwin's entire cataloguing operation was done on the way to Tahiti, and that all of his finch specimens had already been thoroughly intermixed. What Darwin proceeded to do, then, was to catalogue his finches by general form rather than by island, beginning with the largest-billed birds. It is for this reason that he later confused two specimens of *G. magnirostris strenua*, collected on James Island, with specimens of *G. magnirostris magnirostris*, collected either on Chatham or Charles Island. (Courtesy of Down House and the Royal College of Surgeons of England.)

geographic distribution data for all but two of the thirteen species named by Gould.

FURTHER DEVELOPMENTS IN DARWIN'S UNDERSTANDING OF THE GALAPAGOS ISLANDS (1837–1859)

In the first edition of Darwin's *Journal of Researches*, the text of which was completed in June of 1837 and sent to the printer in August, he aptly referred to the Galapagos Archipelago as "a little world within itself" and commented on how "very remarkable" its organic productions were (1839:454). But he limited himself to a detailed description of the islands and the various species he had collected there, making no statement about the heterodox evolutionary conclusions he had privately drawn from such evidence. In the second edition of his *Journal* (1845)—emboldened in part by Joseph Hooker's (1846, 1847a) findings of extensive island endemism among Darwin's Galapagos plants (Fig. 11)[17]—Darwin revised and greatly expanded, by nearly fifty percent, the text of his chapter on the Galapagos Islands. The finches of the Galapagos, four different species of which Darwin had illustrated in this second edition, were discussed more fully than in the first edition; and Darwin even hinted at his evolutionary interpretation of their closely allied nature when he remarked: "Seeing this gradation and diversity of structure in one small, intimately related group of birds, one might really fancy that from an original paucity of birds in this archipelago, one species had been taken and modified for different ends" (1845:380). Darwin also intimated, in several other veiled passages, the evolutionary conclusions that might be drawn from the Galapagos evidence.[18] It was in one of these interpolated passages that Darwin made perhaps his most famous pronouncement about the bearing of the Galapagos Islands on the question of the origin of species:

> The archipelago is a little world within itself, or rather a satellite attached to America, whence it has derived a few stray colonists, and has received the general character of its indigenous productions. Considering the small size of these islands, we feel the more astonished at the number of their aboriginal beings, and at their confined range. Seeing every height crowned with its crater, and the boundaries of most of the lava-streams still distinct, we are led to believe that within a period geologically recent the unbroken ocean was here spread out. Hence both in space and time, we seem to be brought somewhat near to that great fact—that mystery of mysteries—the first appearance of new beings on this earth. (1845:377–78)

[17] Although not published until 1846 and 1847, the general results of Hooker's first two major papers on the plants of the Galapagos Islands were communicated to Darwin in early 1845, in time to be included in the second edition of Darwin's *Journal of Researches* (1845 : 395–97). George Robert Waterhouse's (1845) analysis of the 29 coleopterous insects collected by Darwin in the Galapagos also became available in time to be included in the second edition of the *Journal*. Of the 14 insects for which Darwin had supplied an island locality, Waterhouse found that each was confined to a single island. (Darwin was later able to provide island localities for some, but not all, of his coleoptera as an incidental result of having recorded habitat information in his zoology notes for certain of the specimens.)

[18] Perhaps the two most significant changes that were made in the second edition of Darwin's *Journal* were his great expansion of the Galapagos chapter (the text of the book as a whole had to be cut by about five percent) and the change that Darwin made in the book's title (he reversed the positions of the words "Geology" and "Natural History", to read *Journal of Researches into the Natural History and Geology of the Countries Visited during the Voyage of H.M.S. Beagle round the World . . .*). For further discussion of the changes between the first and second editions of Darwin's *Journal of Researches*, see Gruber (1981 : 259–99).

GALAPAGOS ARCHIPELAGO.

Name of Island.	Total No. of Species.	No. of Species found in other parts of the world.	No. of Species confined to the Galapagos Archipelago	No. confined to the one Island.	No. of Species confined to the Galapagos Archipelago, but found on more than the one Island.
James Island .	71	33	38	30	8
Albemarle Island	46	18	26	22	4
Chatham Island.	32	16	16	12	4
Charles Island .	68	39 (or 29, if the probably imported plants be subtracted)	29	21	8

Figure 11. Darwin's tabular presentation of Joseph Hooker's analysis of the flora of the Galapagos Islands. Darwin was particularly impressed by the frequency with which many endemic Galapagos genera, such as *Scalesia* and *Euphorbia*, are also endemic as distinct species on the separate islands (1845:396).

Darwin's publication of his solution to this "mystery of mysteries" had to wait another fourteen years, in part because Darwin himself still had not come to terms with certain unresolved issues in connection with his general theoretical argument. And the Galapagos case was an important part of the problem.

In particular, even when Darwin was making revisions for the second edition of his *Journal*, he had yet to appreciate the full significance of Joseph Hooker's botanical findings for explaining geographic speciation on the different islands of the Galapagos group. Thus he still maintained in 1845 that "neither the nature of the soil, nor height of the land, nor climate, nor the general character of the associated beings, and therefore their action on one another, can differ much in the different islands" (1845:397). Isolation, by implication, was the major cause of evolutionary change.[19] It was not until two years later, while reading Hooker's third major publication on the Galapagos flora (1847b), that Darwin finally grasped the full nature and significance of floral diversity between islands; namely, that this diversity is not just due to geographic speciation but is also caused by the frequent presence of plants on each island—random colonists—belonging to totally different genera and even families. In the margin of the relevant portion of Hooker's paper (1847b:239), Darwin wrote: "so the Flora of [the] different isl$^{d[s]}$ must be very different independently of representation".[20] This insight was to prove crucial to Darwin's subsequent

[19]This was the same position that Darwin had taken on the role of isolation in his Essay of 1844 (1909[1844]:163, 168, 183, 189–90). See Sulloway (1979:32–49) and Ospovat (1981:193–200) for further discussion of Darwin's changing views on the role of geographic isolation in the speciation process.

[20]Darwin Reprint Collection, quarto item no. 36, Cambridge University Library. Curiously, Darwin had anticipated this insight on purely theoretical grounds as early as 1838, when he remarked in his second notebook on the transmutation of species: "N.B. (Isl^{ds} springing up [would be] more likely to have different species than those sinking. because arrival of any one plant might make condition[s] in any one isl^{d} different).—" (de Beer *et al.*, 1967: *C* 25e). Darwin again mentioned this idea in his Essay of 1844, although without altogether realizing its implications (1909[1844]: 187). It took Hooker's concrete and, even to Darwin, striking botanical evidence to allow this important insight to come to full fruition in 1847.

thinking about evolution in the Galapagos Islands. In fact, this idea contributed to a major shift in Darwin's evolutionary theorizing, a shift that eventually led to a significant new emphasis upon ecological factors as part of what Darwin later termed the "principle of divergence".[21]

Twelve years later (and twenty-four years after his brief visit to the Galapagos), Darwin's efforts to reconstruct the biological world within a comprehensive evolutionary framework culminated in the publication of the *Origin of Species* (1859)—"the book that shook the world" (Mayr, 1964:vii). In the *Origin,* Darwin devoted just 1.1 percent of the text to discussing the Galapagos Islands, barely more attention than he gave to New Zealand or the Madeiras. Pigeons, in comparison, merited three times as much text! As part of other supporting examples drawing upon oceanic islands, Darwin's Galapagos remarks were made in a number of different contexts—such as the organic bond of affinity between islands and the nearest mainland, the absence of certain classes of organisms on remote oceanic islands, and the high rate of species endemism on such islands. Perhaps more surprising than the seemingly minimal use Darwin made of the Galapagos case is that fully two-thirds of his Galapagos remarks were inspired by, and directly based on, Hooker's various botanical analyses of the islands' flora (1846, 1847a, 1847b). Why, Darwin asked in his chapter on geographical distribution, should islands "within sight of each other, having the same geological nature, the same height, climate, etc." be tenanted by different but closely related species? Could not these differences be seen, in fact, as an argument against his theory? To this issue, Darwin responded:

> This [problem] long appeared to me a great difficulty: but it arises in chief part from the deeply-seated error of considering the physical conditions of a country as the most important for its inhabitants; whereas it cannot, I think, be disputed that the nature of the other inhabitants, with which each has to compete, is at least as important, and generally a far more important element of success. (1859:400–401)

Darwin employed this reasoning about the extensive biotic, and especially botanical, differences between the islands of the Galapagos to explain not only why natural selection would favor different varieties (or species) on the different islands but also why some forms, once established, would be able to exclude

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[21] Ironically, Darwin's increased attention to ecological considerations in speciation—prompted as it was by Hooker's Galapagos publications—later led him to de-emphasize the role of isolation in the multiplication of species. Thus, while Darwin continued to believe that isolation was a primary factor in the evolution of island species, he mistakenly came to believe that speciation could occasionally occur on continents through partial (geographic) or ecological isolation (1859:103, 176–77). One consideration that apparently influenced Darwin's change in views was Hooker's finding that some plant genera, like *Scalesia,* possess more than one species on the different islands of the Galapagos group. In 1845 Darwin admitted to Hooker that such facts were "hostile" to his theory, and he wrote in a contemporary memorandum: "Several species of same genus w^{d} be apt to arise on same isl^{d} in proportion as that isl^{d} was badly placed for new colonists—for then they often w^{d} have to fill separate functions." Similarly, Darwin wrote at this time, "I must give up my crossing notions & advantage of Paucity of individuals. I must stick to new conditions & especially new groupings of organic beings" (DAR 205.4:19). Darwin seems subsequently to have reconciled this problem for the Galapagos biota by realizing that the large number of islands in the group would allow repeated interisland colonizations by species having achieved reproductive isolation on another island. To Hooker's 1847 observation that the Galapagos possessed 1.7 species per genus, compared with 1.0 species per genus for Keeling Island, Darwin responded in the margin of Hooker's paper: "But why so [many species] created. I can account for [this]. I think number of is$^{ld[s]}$ comes into play" (Hooker, 1847b: 247). See further Sulloway (1979:44–45) and Ospovat (1981:193–200).

other closely related forms from successfully colonizing neighboring islands. Thus Darwin correctly recognized that interisland colonizations within the Galapagos are not just a matter of chance, or of the distance between islands, but rather are dependent on major ecological considerations as well. He therefore correctly anticipated the theoretical view that both ecological conditions and interspecific competition are ultimately responsible for the patterns of geographic distribution observed among various Galapagos organisms. It is only in the last twenty years that Darwin's *Origin* insight—after considerable controversy—has been fully accepted (Grant 1981b), although Darwin himself is not always recognized as the first proponent of this view.[22]

CONCLUSION: THE DARWIN–GALAPAGOS LEGEND

The publication of the *Origin of Species* not only revolutionized the biological sciences, but it also made Darwin into a celebrated intellectual hero—a man thoroughly worthy of scientific deification and hence destined to become the subject of legend. And because myths and legends, above all else, gravitate toward the problem of origins, Darwin's discoveries increasingly became enshrouded by the typical misconceptions of reconstructed 'heroic' history. Accordingly, the true story of Darwin's conversion to the theory of evolution is a far cry from the Darwin–Galapagos legend that has arisen in the wake of Darwin's scientific triumph, and that adorns so many of the biology textbooks today.[23] In fact, the legend, which is composed of three major component myths, tends to obscure precisely what it pretends to explain, namely, the nature of scientific insight.

The first of these component myths is that of Darwin's 'eureka-like' conversion during his visit to the Galapagos Islands in 1835. It may appeal to our romantic conception of scientific discovery to imagine the lone voyager suddenly throwing off the shackles of creationist thinking when finally confronted, in the Galapagos, with a microcosmic paradigm of evolution in action. But this myth, for all of its inherent allure, is both wrong and misleading. What this myth especially tends to obscure is the fascinating question 'Why Darwin?' That is to say, why was it that Darwin, and no one else, was converted by evidence that was widely known to many other contemporary naturalists—naturalists who, like Richard Owen and John Gould, were often far superior to Darwin in their experience and abilities as systematists? The answer to this question is closely associated with the real nature of Darwin's genius as a scientist. Repeatedly the far-seeing amateur among specialized experts, Darwin exhibited his unique intellectual caliber in the pattern of 'gifted individualism'

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[22]Grant (1981b : 660), for example, has mistakenly assumed that Darwin thought the habitats of the various islands in the Galapagos group were the same and, moreover, that Darwin considered interisland colonizations to be basically random. It is true that Darwin, in his Essay of 1844, believed colonizations, both of oceanic archipelagoes like the Galapagos and of the separate islands within such archipelagoes, to be largely random (1909[1844] : 185, 187; see also Sulloway, 1982a : 34). By the time he wrote the *Origin*, however, Darwin had completely changed his mind on this issue, primarily as a result of his greater appreciation of the extensive biotic differences among the various islands of the Galapagos group (1859 : 399–403). In this respect Darwin anticipated Bowman's (1961) views, although he did not, like Bowman, believe that large-scale adaptive radiation could proceed without subsequent interspecific competition (1859 : 111–30).

[23]See notes 1, 6 and 11.

that manifested itself in the process of his conversion. While other naturalists stood by and calmly rationalized the Galapagos evidence in creationist terms, Darwin—virtually alone—took up the heterodox challenge offered by that evidence.[24] Expressed another way, the Galapagos did not make Darwin; if anything, Darwin, through his superior abilities as a thinker and a theoretician, made the Galapagos; and, in doing so, he elevated these islands to the legendary status they have today.

The second of the three component myths associated with Darwin and the Galapagos is the myth that these islands provided him, at an early stage, with a basic paradigm for his theory of evolution by geographic isolation and natural selection. As I have shown in the case of Darwin's finches, nothing could be further from the truth; and the same conclusion applies to Darwin's Galapagos observations as a whole, which were only slowly incorporated into his final theory. Thus the *Origin of Species* was ultimately the product of twenty-two years of thinking and further research (1837–59), not the five weeks that Darwin spent in the Galapagos Islands or even the five years that he spent accompanying H.M.S. *Beagle* around the world. True, the Galapagos certainly provided Darwin with some crucial hints; but Darwin's full understanding of both evolution and the Galapagos case required almost as long as it took him to publish the *Origin of Species*. Moreover, much of Darwin's evolutionary argument, as finally presented in the *Origin*, had to be constructed from alternative sources, owing to Darwin's failure to appreciate, and to collect, the necessary Galapagos evidence in 1835. Other scientists have been collecting that 'necessary' Galapagos evidence ever since, which leads me to the third of the three component myths encompassing the Darwin–Galapagos legend.

This third and last myth involves the notion that Darwin singlehandedly discovered almost everything there is to know about evolution in the Galapagos—or at least everything of *basic* importance—and hence that subsequent research in these islands has merely been a sort of Kuhnian (1962) mopping-up operation characteristic of 'normal', postrevolutionary science. This myth, promulgated in the biology textbooks and especially in the popular literature about Darwin and the Galapagos, is largely a natural extension of the first two Darwin–Galapagos myths. As a typical manifestation of this third myth, Darwin is frequently credited with insights about his famous Galapagos finches that were actually the product of extensive post-Darwinian ornithological research. For example, in spite of Darwin's own famous *Journal* (1845 : 380) remark about one species of finch appearing to have been "modified for different ends", Darwin was by no means personally convinced that all thirteen species of Galapagos finches (especially the warbler finch) were indeed derived from a single ancestor (see also Darwin, 1841:105). Darwin's lingering

[24]There are apparently only two other nineteenth-century naturalists, besides Darwin, who appreciated the Galapagos evidence in an evolutionary light prior to 1859. Robert Chambers made use of Darwin's Galapagos findings in his *Vestiges of Creation* (1844); but Chambers was converted to the theory of evolution by other considerations, and he also placed a very different evolutionary interpretation on the Galapagos evidence than Darwin did (Hodge, 1972). Alfred Russel Wallace (1855) later called special attention to the Galapagos Islands in his first (and somewhat guarded) evolutionary publication. But Wallace, who was converted to the theory of evolution after reading Chamber's *Vestiges of Creation*, was also largely indebted to Darwin's *Journal* (1845) for his evolutionary interpretation of the Galapagos case. On Darwin's intellectual individualism, see Ghiselin's (1971) valuable treatment; and, for a developmental and psychological approach to this topic, Sulloway (in press).

doubts about the finches' possible common ancestry apparently contributed to his decision, when writing the *Origin of Species*, to omit any specific reference to this now famous biological paradigm of "evolution in action" (Sulloway, 1983:372). During the remainder of the nineteenth century, ornithologists generally believed Darwin's finches were descended from two or three different ancestors—a warbler, a ground finch, and a separate form that gave rise to the six species of *Camarhynchus*. This issue of ancestry was not resolved for more than half a century after the *Origin of Species* was published.

As I have shown elsewhere, David Lack's classic book *Darwin's Finches* (1947) did much to perpetuate this third aspect of the legend, even though Lack himself personally knew better. Indeed, Lack, in reversing his original position on the possible adaptive significance of the beaks among the different species of Darwin's finches (1945, 1947), went through much the same experience of *ex post facto* 'discovery' that Darwin himself did. For it was only after leaving the Galapagos Islands that Lack reached his new theoretical position and then realized the need for the kind of follow-up studies of the finches' feeding behavior that Bowman (1961, 1963), Abbott, Abbot & Grant (1975, 1977), and various other ornithologists have subsequently carried out.[25] Similar 'delayed discoveries' have undoubtedly characterized the work of numerous other Galapagos researchers, who—unlike Darwin—have often had the opportunity to return to the Galapagos Islands in order to collect crucial data, and to make observations, that previously seemed unimportant. Thus the history of research in the Galapagos Islands has been anything but the history of 'mopping up' the scientific tidbits that Darwin left behind. Rather, it is only after repeated expeditions by six generations of post-Darwinian scientists that the Galapagos Archipelago has yielded—with a seeming air of reluctance—many of its richest biological treasures to the world of science. And even today, after so much scientific progress, almost as many questions remain about evolution in the Galapagos as there are answers to the mysteries that Darwin and others have successfully resolved (Patton, 1984).

Of all the numerous scientists who have gone through the experience of making important discoveries in the Galapagos, only to realize sometime later that they have merely scratched the scientific surface and thereby created the need for further research, Charles Darwin perhaps expressed it best. In 1846, shortly after Joseph Hooker had so delighted him with the results of his analysis of Darwin's Galapagos plants, Darwin declared to his friend: "The Galapagos seems a perennial source of new things."[26] The Darwin–Galapagos legend notwithstanding, these famous islands will doubtless remain "a perennial source of new things" in science; and no one would be more disappointed than Charles Darwin if this were not the case.

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[25]On the subject of feeding behavior among Darwin's finches, see also Grant *et al.* (1976); Smith *et al.* (1978); Grant (1981a, 1981b, 1983); and Boag & Grant (1981). For a recent survey of the considerable literature (and debates) concerning the role of interspecific competition in nature, see Schoener (1982).

[26]DAR 114, letter no. 63, dated July 1846.

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