Darwin and His Finches: The Evolution of a Legend

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First collected by Charles Darwin in the Galapagos Archipelago, the Geospizinae, or "Darwin's finches," have rightly been celebrated as a classic instance of the workings of evolution through natural selection. Among birds, Darwin's finches are rivaled only by the Hawaiian honeycreepers (Drepanididae) as a microcosmic exemplification of the principle of adaptive evolutionary radiation. Although the Drepanididae have undergone more evolution and adaptive radiation than the Geospizinae, the latter are in some ways more valuable to ornithologists. "Their special interest today," writes David Lack, "is in providing the best example, in birds, of an adaptive radiation into different ecological niches that is sufficiently recent, geologically speaking, for intermediate and transitional forms to have survived" (1964:178).

The Galapagos Archipelago, where Darwin spent five weeks collecting these finches during the voyage of H.M.S. *Beagle* (1831-1836), comprises sixteen principal islands located on the equator some six hundred miles west of Ecuador (Fig. 1). The islands, most of which are several million years old, are wholly volcanic in origin and have never been connected to the mainland. Darwin's finches were evidently one of the earliest colonists of the Galapagos, since their degree of evolutionary complexity – thirteen species distributed among four genera – is unmatched by any other avian group in this archipelago. A fourteenth species, belonging to yet another genus, inhabits Cocos Island, four hundred miles to the northeast. Unlike other endemic species of Galapagos birds, the Geospizinae no longer have any close relatives on the American mainland. They are therefore classed in their own separate tribe or subfamily, which is placed with the Emberizidae.[1]

Being one of the earliest colonists of the Galapagos Islands, the ancestral form of Darwin's finches found an environment in which the types of niches occupied by other, diverse birds on the continent

1. Darwin's finches have been the subject of numerous systematic treatments, of which the most important are by Gould (1837a, 1841, 1843), Salvin (1876), Ridway (1890, 1897), Rothschild and Hartert (1899, 1902), Snodgrass and Heller

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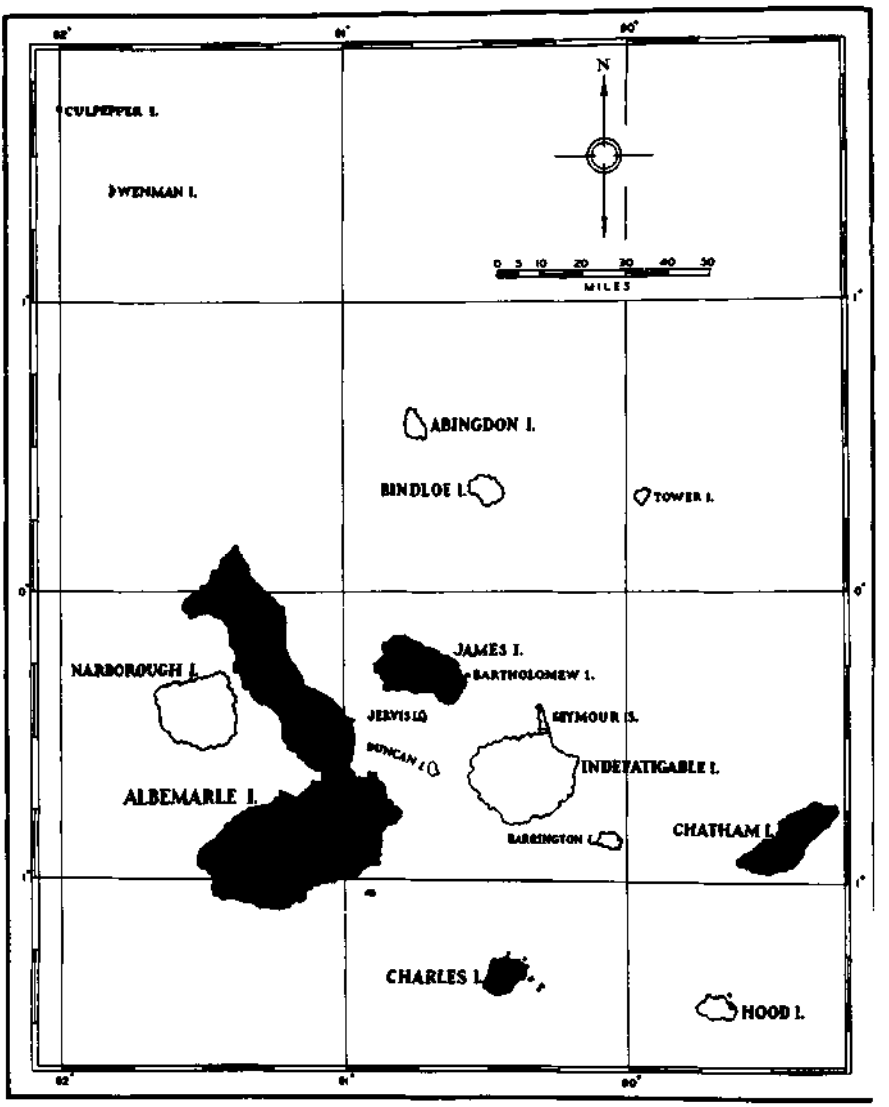

Fig. 1. The Galapagos Archipelago. Darwin visited the four shaded islands. (From Lack 1945: Frontispiece.)

were largely vacant. After becoming isolated from one another on the different islands of the archipelago, various finch populations gradually evolved reproductive isolation and hence status as separate species. Certain of these species then successfully recolonized neighboring islands, and the ensuing competition between closely related forms encouraged divergence and increasing specialization in the many unoccupied niches presented by the Galapagos environment. Through this four-part process of geographic isolation, speciation, recolonization, and ensuing adaptive radiation, the Geospizinae have evolved a remarkable disparity in the form of their beaks, from one as massive as that of a grosbeak to one as small as that of a warbler. There are three species of seed-eating ground finches with large, medium, and small beaks; another ground finch with a sharp, pointed beak; two species of ground finches that feed on cactus; a vegetarian tree finch; three species of insectivorous tree finches; a mangrove finch; a finch that closely resembles a warbler in both habits and morphology; and finally a 'tool-using' "woodpecker" finch, which employs twigs and cactus spines to extract its prey from crevices in tree trunks (see Fig. 2). As Darwin remarked in the second edition of his *Journal of Researches*, "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).

(1904), Swarth (1931), Hellmayr (1938:130-146), Lack (1945, 1947, 1969), Bowman (1961, 1963), Harris (1974), and Steadman (in press). Monographic works, such as those by Swarth (1931) and Lack (1945, 1947), have usually given Darwin's finches family or subfamily status – the latter being the general consensus. Nevertheless, some authors have recommended that they be accorded only tribal status within the Emberizinae subfamily (Paynter and Storer 1970: 160-168). Differentiation between subfamilies and tribes is a subjective matter, and I have preferred to follow the monographic tradition on this point. Species and genus names of certain forms of the Geospizinae have changed over the years, making for some minor inconsistencies in terminology in discussions of the literature. For example, *Cactornis scandens* (Gould 1837a) is no longer given separate generic status, but is classified instead with the other species of *Geospiza*. I have followed the policy of using the original names proposed by Gould (1837a, 1841) when discussing individual *Beagle* specimens or Darwin's views about them. Otherwise, the current nomenclature has been followed, with the exception that I recognize *Geospiza magnirostris magnirostris* and *G. magnirostris strenua* as valid trinomials and also recognize the name *G. nebulosa* as having priority over *G. difficilis*. See note 34 and Sulloway (1982b).

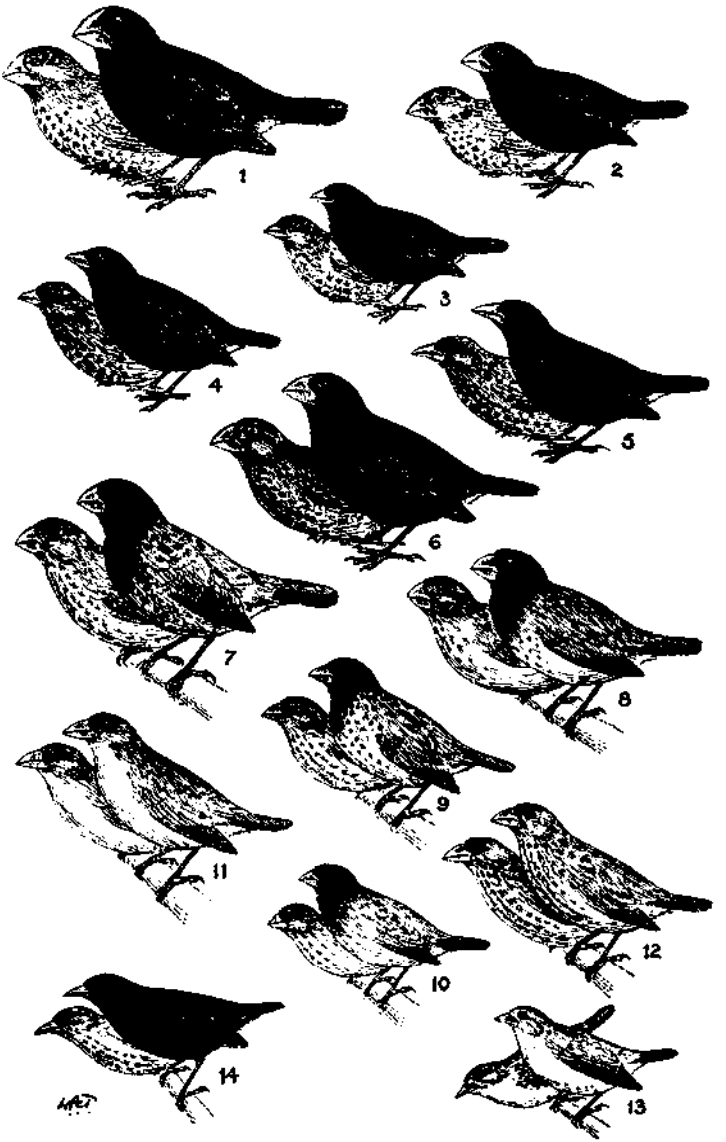

Fig. 2. Darwin's finches, the male (in dark plumage) and female of each species: *1*, *2*, *3*, the large, medium, and small ground finches (*Geospiza magnirostris*, *G. fortis*, and *G. fuliginosa*); *4*, the sharp-beaked ground finch (*G. nebulosa* [formerly *difficilis*]); *5* and *6*, the cactus and large cactus finches (*G. scandens* and *G. conirostris*); *7*, the vegetarian tree finch (*Platyspiza crassirostris*); *8*, *9*, and *10*, the large, medium, and small insectivorous tree finches (*Camarhynchus psittacula*, *C. pauper*, and *C. parvulus*); *11*, the woodpecker finch (*C. pallidus*); *12*, the mangrove finch (*C. heliobates*); *13*, the warbler finch (*Certhidea olivacea*); and *14*, the Cocos Island finch (*Pinaroloxias inornata*). (From Lack 1947:19.)

Given the remarkable nature of these birds, it is of considerable historical interest to reconstruct the role they played in Darwin's intellectual development. This problem really involves three separate questions. First, how did Darwin initially interpret the morphology and behavior of the various species of this unusual avian group while he was in the Galapagos Archipelago? Second, to what extent did he appreciate the striking correlation between geographic isolation and the diversity of endemic finch forms and thus take steps to separate his collections according to the different islands he visited? Third, what aspects of Darwin's understanding of this avian group were retrospective, that is, developed after he had left the Galapagos and had returned to England? Given the fame of this episode in Darwin's life, there has been a surprising degree of misunderstanding and misinformation regarding these three questions. In fact, over the years Darwin's finches have become the focus for a considerable legend in the history of science, one that ranks alongside other famous stories that celebrate the great triumphs of modern science.

DARWIN IN THE GALAPAGOS

Morphology and Classification

It has frequently been asserted that Darwin's finches, along with certain other organisms from the Galapagos Archipelago, were what first alerted Darwin to the possibility that species might be mutable.[2] But as David Lack (1947:9) has pointed out, Darwin did not even discuss the finches in the diary of his voyage on the *Beagle*, except for a single reference in passing; and his treatment of them in the first edition of his *Journal of Researches* (1839:461-462) was brief and matter of fact compared with the famous statement about them that he added to the 1845 edition. Given these facts, Lack concluded that Darwin's evolutionary understanding of the finches was largely retrospective. This interpretation is essentially correct, although Lack, who did not examine Darwin's unpublished scientific notes from the *Beagle* voyage, failed to appreciate the reasons for Darwin's gradual insight.

There are two different versions of Darwin's voyage scientific notes that discuss his Galapagos finches. The first version, which forms part

2. See notes 33, 54, and 64.

of his manuscript notes on zoology, was drafted in late October 1835, shortly after he left the Galapagos Archipelago on his way to Tahiti. The second and somewhat expanded version, which nevertheless follows the first in its general contents, was copied into a separate notebook for ornithological observations some nine months later.[3] Both accounts describe the tendency for the various finch species to feed together on the ground in the arid and sparsely vegetated lowlands of the islands. Darwin emphasized that insects were surprisingly scarce in the Galapagos and remarked that seeds, laid down in the loose volcanic soil after the annual rainy season, supplied the principal source of food for the birds. "Hence these Finches," he commented in his *Ornithological Notes*, "are in number of species & individuals far preponderant over any other family of birds" (1963[1836]:261). Darwin also noted the impossibility of distinguishing species on behavioral grounds, given the similar feeding habits of most of the birds. "There appears to be much difficulty," he acknowledged, "in ascertaining the species."[4]

Oddly, Darwin seems to have been more preoccupied with the unusual coloration of the finches than with the extreme variation in their beaks. "Amongst the species of this family," he wrote in this connection, "there reigns to me an inexplicable confusion" (1963[1836]:261). Some of his specimens were jet black, and others, by intermediate shades, passed into a brown or olive plumage. His collections, he believed, tended to show that the jet black coloration was peculiar to the old cock birds alone, but exceptions to this rule also seemed to exist. Finally, he noted almost as an afterthought that "a gradation in the form of the bill, appears to me to exist" (1963[1836]: 261).[5] In these voyage notes Darwin did not comment further on this problem of the bills, and he also offered no explanation as to why so many similar species of finches were to be found in the Galapagos.

The unusual nature of the bills in Darwin's finches has given rise to one of the more dramatic aspects of the legend that surrounds these birds. According to several commentators, the finches prompted

3. Toward the end of the voyage Darwin prepared a series of separate specimen catalogues for the use of the specialists who later took charge of his collections after the *Beagle*'s return to England. Darwin's *Ornithological Notes* (1963[1836]) constitutes one of twelve such catalogues. On the dating of these catalogues, see Sulloway (1982a).

4. DAR 31.2: MS p. 340. All DAR numbers refer to the Darwin MSS, Cambridge University Library.

5. Darwin did not mention the apparent gradation in the bills in his earlier account, written in October 1835.

Darwin and Captain Robert FitzRoy, while they were visiting the Galapagos, to fall into "one of their numerous disputes" (Grinnell 1974:260-261). FitzRoy, noting that the shape of the beaks varied slightly by island, supposedly concluded that each form was a separate species created for the particular island on which it was found. Darwin, on the other hand, is said to have thought the finches were derived from a mainland species and had become modified by their new surroundings. They were therefore, Darwin concluded, only varieties of a single species, a conclusion that FitzRoy considered "blasphemous rubbish."[6] Thus what most impressed Darwin, according to Grinnell (1974) and others, was the remarkable similarity and gradation in the characters of the various Geospizinae.[7]

The claim that Darwin and FitzRoy must have argued over the evolutionary implications of the Galapagos finches – although frequently presented with considerable conviction – is supported by little real evidence. There is, moreover, considerable evidence to the contrary. The supposed basis for this argument is a brief comment about the finches that FitzRoy made in his subsequently published *Narrative*. There he remarked: "All the small birds that live on these lava-covered islands have short beaks, very thick at the base, like that of a bull-finch. This appears to be one of those admirable provisions of Infinite Wisdom by which each created thing is adapted to the place for which it was intended" (1839:503). FitzRoy went on to say that such thick beaks were ideally suited for picking up insects or seeds from the hard lava and were also useful in crushing berries to obtain the moisture contained in them. He did not, however, comment about any variation in the beaks or about the geographical distribution of these species, and his account seems to apply exclusively to the large-billed forms of *Geospiza*.[8] In any event, FitzRoy was only saying what Darwin himself had noticed, namely, that "the greater number of birds haunt, and are adapted for, the dry & wretched looking thickets of the coast land" (1963[1836]:261).

Had FitzRoy considered the issue of geographic variation among Darwin's finches, it is likely that he would have taken a very different

6. See Moorehead (1969:205-206), whose words are quoted here; Barlow (1963:261n1); and Ralling (1978).

7. See, for example, Bowman (1963:107), Ruse (1979:116), and Ospovat (1981:91).

8. Kottler (1978:283) has likewise made this point in criticizing Grinnell's (1974) account.

stand from the one that legend has assigned him. From his *Narrative* it is clear he believed that "every animal varies more or less in outward form and appearance" owing to local differences in climate and geography (1839:253). Thus he insisted that such island variants as the differing foxes on East and West Falkland islands were only varieties, not separate species, caused by slightly different environments. So plastic did FitzRoy consider species in nature, and so critical was he of naturalists who repeatedly made local geographic races into separate forms, that he actually regarded the two Falkland foxes and the various Galapagos tortoises as mere varieties of species found elsewhere in the world (1839:250-254, 505). As for FitzRoy's religious fanaticism, commonly thought to have motivated his scientific debates with Darwin, FitzRoy himself later made it very clear in his *Narrative* that he did not undergo the religious conversion reflected in certain aspects of that work until after the *Beagle* had arrived back in England.[9]

To return to the related claim that Darwin considered the various finches to be mere varieties modified by their new environment, this assertion is contradicted by perhaps the most curious aspect of Darwin's voyage thoughts about these birds. I am referring to the individual entries by which Darwin recorded each numbered specimen in his voyage notes. From these entries it is clear that what initially impeded his understanding of the finches was not their extreme similarity but rather their apparent differences. In fact, Darwin evidently thought he was dealing with a highly diverse family of birds having at least three and perhaps four different subfamilies. He referred, for example, to the large-beaked birds as "Gross-beaks," to the smaller-beaked birds as "Fringilla," or true finches, and to the cactus finch as "Icterus" (a separate family of birds that now includes the orioles, meadowlarks, and blackbirds). Just how greatly Darwin was misled by certain of the Galapagos finches is poignantly illustrated by his misclassification of

9. In the *Narrative* FitzRoy referred to "men who, like myself formerly, are willingly ignorant of the Bible" and admitted that he had previously known "so little of that [biblical] record . . . that I fancied some events there related might be mythological or fabulous . . . . " To these remarks he added: "While led away by sceptical ideas, and knowing extremely little of the Bible, one of my remarks to a friend [surely Darwin], on crossing vast plains composed of rolled stones bedded in diluvial detritus some hundred feet in depth, was 'this could never have been effected by a forty days' flood' . . . . I was quite willing to disbelieve what I thought to be the Mosaic account, upon the evidence of a hasty glance, though knowing next to nothing of the record I doubted . . . " (1839:657-659). See also Keynes (1979:6) on this point.

the warbler finch as a "wren," or warbler.[10] As for the remarkable woodpecker finch, thought by many to have stimulated Darwin's greatest evolutionary curiosity, this species was not even collected by Darwin; and its unusual tool-using behavior was not reported until 1919.[11] Darwin collected, in fact, only nine of the present thirteen species of "Darwin's finches." Of these, he properly identified as finches only six species – less than half the present total – placing them in two separate groups, large- and small-beaked Fringillidae.[12]

Darwin's difficulties in properly classifying his Galapagos finches during the *Beagle* voyage should by no means be taken as a sign that he was ornithologically inexperienced or inadept. Darwin was quite

10. See Darwin's *Ornithological Notes*, where twenty-one specimens are classified "Fringilla," four "Icterus," four "Fringilla/Gross-beaks," one "Wren," and one without a name (1963[1836]:262-264). Similarly, in his voyage zoology notes he wrote that "far the preponderant number of individuals belongs to the Finches & the Gross-beaks" (DAR 31.2: MS pp. 340-341). These four separate designations are confirmed by Darwin's master catalogue of specimens, now at Down House. For the cactus finch, however, he wrote "Icterus (??)" after specimens 3320, 3321, 3322, and 3323, showing his obvious puzzlement over the whole problem of how to classify this divergent species. He also referred to this last species as the "Icterus like Finch" in his voyage zoology notes, but reiterated the "Icterus" classification nine months later in his *Ornithological Notes*. Darwin's use of these various designations was by no means an impressionistic or hasty manner of describing his specimens. Darwin was not in the habit of using ornithological terminology imprecisely in his voyage notes and catalogues. The term "Icterus," for example, is used throughout his *Ornithological Notes* to characterize many bona fide members of the Icteridae.

11. See Gifford 1919:256. The erroneous presumption that Darwin saw all the species of Darwin's finches, including the woodpecker finch, is endorsed by Peterson (1963:12), Huxley and Kettlewell (1965:136n44), Taylor and Weber (1968:877), Moorehead (1969:202), Thornton (1971:163), Thompson (1975:10-11), and Kimball (1975:434-435, 1978:587).

12. Although Gould indeed named thirteen species of Darwin's finches, four of these have since been recognized as variant forms of the other nine species. Thus Gould's *Geospiza strenua* is a subspecies of *G. magnirostris*. *G. dentirostris* and *G. dubia* are both examples of *G. fortis*. In addition, Gould's *Cactornis assimilis* is a subspecies of *G. scandens*. Of the nine true finch species that Darwin actually collected, two were misidentified by him as nonfinches, leaving only seven species that he might have distinguished in the field. I am assuming, however, that Darwin, like Gould, confused at least one large-billed specimen of the sharp-beaked ground finch (*G. nebulosa nebulosa*) with the cactus finch (*G. scandens*), because the requisite number of specimens of the latter species cannot otherwise be accounted for in his voyage catalogue. This leaves only six species apparently distinguisued and recognized by Darwin as finches while on the *Beagle*.

knowledgeable as a taxonomist, and he generally managed to classify his *Beagle* specimens under the appropriate family, genus, and sometimes even species using the published guides available to him on the voyage.[13] With the current triumph of Darwin's evolutionary views, however, it has become difficult for us to appreciate the confusion and puzzlement that such an unusual avian group as the Geospizinae was capable of eliciting among nineteenth-century ornithologists.

What evidently misled Darwin most of all in his voyage understanding of these birds is the odd relationship that prevails between beak and plumage in the group. As David Lack (1947:12) has pointed out, closely related species of continental passerine birds are usually extremely similar in their beaks and other structural features, differing chiefly in their plumage. Most of Darwin's finches, on the other hand, are almost identical in plumage, whereas the beaks differ considerably between even the closest species. So anomalous is this condition that an ornithologist basing his classifications upon the customary relationship between beak and plumage would unhesitatingly place Darwin's finches in at least six or seven genera, and perhaps even several subfamilies (Lack 1947:14). This is precisely what Darwin did and is why, in part, he was so preoccupied with the confusing nature of the plumage in these birds.[14] John Gould, the eminent British ornithologist who later named and classified Darwin's finches, astutely recognized the misleading nature of these traditional characters; and he was subsequently able to persuade Darwin and others of the close affinities of the whole group (Gould 1837a, 1841). Thus it was not until the *Beagle* voyage

13. On the voyage Darwin had with him Lesson's *Manuel d'ornithologie* (1828), the seventeen-volume *Dictionnaire classique d'histoire naturelle* (Bory de Saint-Vincent 1822-1831), Molina's *History of Chili* (1809), and various other books dealing with natural history, voyages, and travels.

14. Darwin was not alone in mistaking certain of the Galapagos finches for the forms they appear to mimick. Adolphe-Simon Néboux, who visited the Galapagos Islands in 1836 as surgeon of the French frigate *Vénus*, later described *Geospiza scandens* (the cactus finch) as a "Tisserin," or weaverbird (Néboux 1840). A case parallel to that of Darwin's and Néboux's confusion about the Galapagos finches may be seen in the initial efforts of ornithologists to classify the various species of Hawaiian honeycreepers, the other celebrated case of adaptive radiation among birds. Ornithologists at one time placed these birds in four families and eighteen genera before the evolutionary unity of the group, which is now recognized as a single family with only ten genera, was finally accepted. See Greenway 1964:374; Tyne and Berger 1976:545; and Gruson 1976:162.

was over that Darwin's finches actually became Darwin's *finches* in the sense that we now comprehend.

Geographic Distribution

Darwin's thoughts on the geographic distribution of his finches, and especially the nature of his labeling practices while he was in the Galapagos, have been the subject of much discussion. The importance of resolving these issues lies in ascertaining to what extent Darwin appreciated the highly endemic nature of each separate island's flora and fauna as he proceeded from island to island within the Galapagos.

In his *Journal of Researches* Darwin later reported that the possibility of the different islands possessing separate forms was first brought to his attention by Nicholas O. Lawson, the vice-governor of the archipelago. Lawson, whom Darwin met on Charles Island, informed him that "the tortoises differed from the different islands, and that he could with certainty tell from which island any one was brought" (Darwin 1845:394). This discussion took place sometime between September 25 and 27, during the second of Darwin's five weeks in the archipelago.[15] "I did not for some time," Darwin commented, "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 material to establish this most remarkable fact in the distribution of organic beings" (1845:394).

Darwin did, fortunately, notice that the mockingbird he had collected on Charles Island differed from the form he had previously collected on Chatham Island. This discovery made him pay particular attention to their collection; and he subsequently made efforts to obtain, and to keep separate, specimens from the next two islands he visited (1841:63). These next two islands were Albemarle, where Darwin spent only part of a day, and James, where he spent a week. To Darwin's eyes, the mockingbird specimens from Chatham and Albemarle appeared to be the same, but those from James and especially Charles

15. According to FitzRoy (1839:490), Lawson came on board the *Beagle* on September 25 and then escorted a party, including Darwin and FitzRoy, to the settlement in the highlands. Darwin spent four days on Charles Island, the last being September 27. See also Darwin's *Diary* (1933:336).

were noticeably different.[16] In his zoology notes Darwin commented about these specimens at the time: "This bird which is so closely allied to the Thenca of Chili (Callandra of B. Ayres) is singular from existing as varieties or distinct species in the different Is^{ds}. – I have four specimens from as many Is^{ds} – There will be found to be 2 or 3 varieties. – Each variety is constant in its own Island. – This is a parallel fact to the one mentioned about the Tortoises."[17] It was this singular fact in the distribution of the mockingbirds that subsequently prompted Darwin to write in his *Ornithological Notes*:

> 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 and 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. (1963[1836]:262)

This famous statement, written approximately nine months after leaving the Galapagos Archipelago, is Darwin's first tentative admission of the possibility that species might be mutable.[18]

To what extent, then, did the finches help to reinforce this insight? According to Lack (1947:23), Darwin also began to separate the

16. DAR 31.2: MS p. 342v. "The Thenca of Albermarle [*sic*] Island is the same as that of Chatham Is^{d} –." Contrary to Darwin's voyage opinion, the mockingbirds from Albemarle (*Nesomimus parvulus*) and Chatham (*N. melanotis*) are now recognized as separate species by some ornithologists, whereas the James and Albemarle forms are both assigned to *N. parvulus*. Gould (1841:62-63), to confuse matters further, later synonymized the Chatham and James forms under the name *melanotis*, which merely goes to show that the Chatham, Albemarle, and James forms are all very similar in appearance and would be classified by many ornithologists as subspecies. The Charles Island form of the mockingbird (*N. trifasciatus*) is more noticeably distinct, but even this form would be ranked as a subspecies by some ornithologists. See Harris 1974:128; and Mayr and Greenway 1960:447-48.

17. DAR 31.2: MS pp. 341-342.

18. On the dating of Darwin's *Ornithological Notes*, see Sulloway (1982a).

members of the finch tribe as a result of the vice-governor's remarks to him on Charles Island. Thereafter, Lack maintains, Darwin kept his ornithological collections from each island separate. Lack's assertion is based upon a detailed examination of Darwin's type specimens, many of which are labeled as coming from the last island Darwin visited, and upon the following statement made by Darwin in his *Journal of Researches*:

> Unfortunately most of the specimens of the finch tribe were mingled together; but I have strong reasons to suspect that some of the species of the sub-group Geospiza are confined to separate islands. If the different islands have their representatives of Geospiza, it may help to explain the singularly large number of the species of this sub-group in this one small archipelago, and as a probable consequence of their numbers, the perfectly graduated series in the size of their beaks. Two species of the sub-group Cactornis, and two of Camarhynchus, were procured in the archipelago; and of the numerous specimens of these two sub-groups shot by four collectors at James Island, all were found to belong to one species of each; whereas the numerous specimens shot either on Chatham or Charles Island (for the two sets were mingled together) all belonged to the two other species: hence we may feel almost sure that these islands possess their representative species of these two sub-groups. (1845:395)

Darwin's own testimony clearly implies that only the specimens from Chatham and Charles were mingled together, since he was later able to compare those specimens as a group with the specimens collected on James Island.

David Lack's insistence that Darwin began to separate and label his specimens by locality after leaving Charles Island is nevertheless called into question by the seemingly inaccurate nature of several of the island localities actually recorded by Darwin. Indeed, Darwin's type specimens have provided a considerable nightmare of taxonomic problems for subsequent ornithologists, based largely upon their controversial localities. Darwin claimed, for example, that specimens of a peculiarly large-beaked form of *Geospiza magnirostris* came from Chatham and Charles islands. But after more than a century of subsequent collecting without finding any such large-billed specimens, ornithologists found themselves faced with a puzzle. Either this form had become extinct on Chatham and Charles islands, where no *magnirostris* specimens (large

or small) had ever been founded by other expeditions; or else Darwin's specimens must have come from islands other than those indicated. Swarth (1931:147-149), noting that the largest bills among *G. magnirostris* are found in the northern part of the archipelago, including James Island, believed that Darwin's specimens came from that island. Although Darwin's specimens are still somewhat larger than the present James Island race of this species, Swarth concluded that some evolution in bill size must have occurred since Darwin's visit. Darwin also reported taking specimens of the smaller-billed *G.* [*magnirostris*] *strenua* on Chatham Island, and these specimens as well have generally been thought to have come from James Island (Fig. 3).[19]

David Lack, who at first agreed with the judgment of Swarth and others,[20] later changed his mind, given Darwin's testimony that only the specimens from the first two islands had been mingled together. Yet Lack himself distrusted other of Darwin's localities, including some involving specimens from the one island – James – where Lack claimed Darwin had kept his specimens separate. According to Lack (1945:14), one of Darwin's specimens of *Cactornis scandens*, labeled as coming from James Island, is actually an example of *Geospiza difficilis* (now *nebulosa*), the sharp-beaked ground finch, and belongs to a form that is not found on James Island today. So either measurable evolution has occurred in the size of the beak, or, more probably, the specimen came from Charles Island, where FitzRoy collected a very similar specimen of this now extinct island race. Altogether, there is serious doubt about the accuracy of eight of the fifteen localities recorded on Darwin's Geospizinae type specimens.[21]

Not only is the accuracy of Darwin's localities in doubt, but so is

19. See, for example, Rothschild and Hartert 1899:155; Swarth 1931:149; and Lack 1945:9. Similarly, Hellmayr has concluded: "There seems hardly any doubt that in the case of *G. strenua* and *G. magnirostris* the localities, as given . . . in the 'Zoology of the Beagle,' are altogether untrustworthy" (1938:130n3).

20. See Lack 1940:49; 1945:9-10.

21. These doubtful localities involve the following birds: two specimens of *Geospiza magnirostris* (British Museum registry nos. 1855.12.19.80 and 1855.12.19.113, labeled as coming from Chatham Island but thought to have come from James); two specimens of *G. parvula* (British Museum nos. 1855.12.19.167 and 1855.12.19.194, labeled as coming from Chatham Island but elsewhere assigned to James [Darwin 1841:102]); one specimen of *Cactornis scandens* (British Museum no. 1855.12.19.20, labeled as coming from James but assigned by Lack to an extinct race of *G. nebulosa* [formerly *difficilis*] on Charles or Chatham Island); and three specimens of *G. strenua* (British Museum nos. 1855.12.19.81, 1855.12.19.83, and 1855.12.19.114, labeled as coming from Chatham but thought to have come from James).

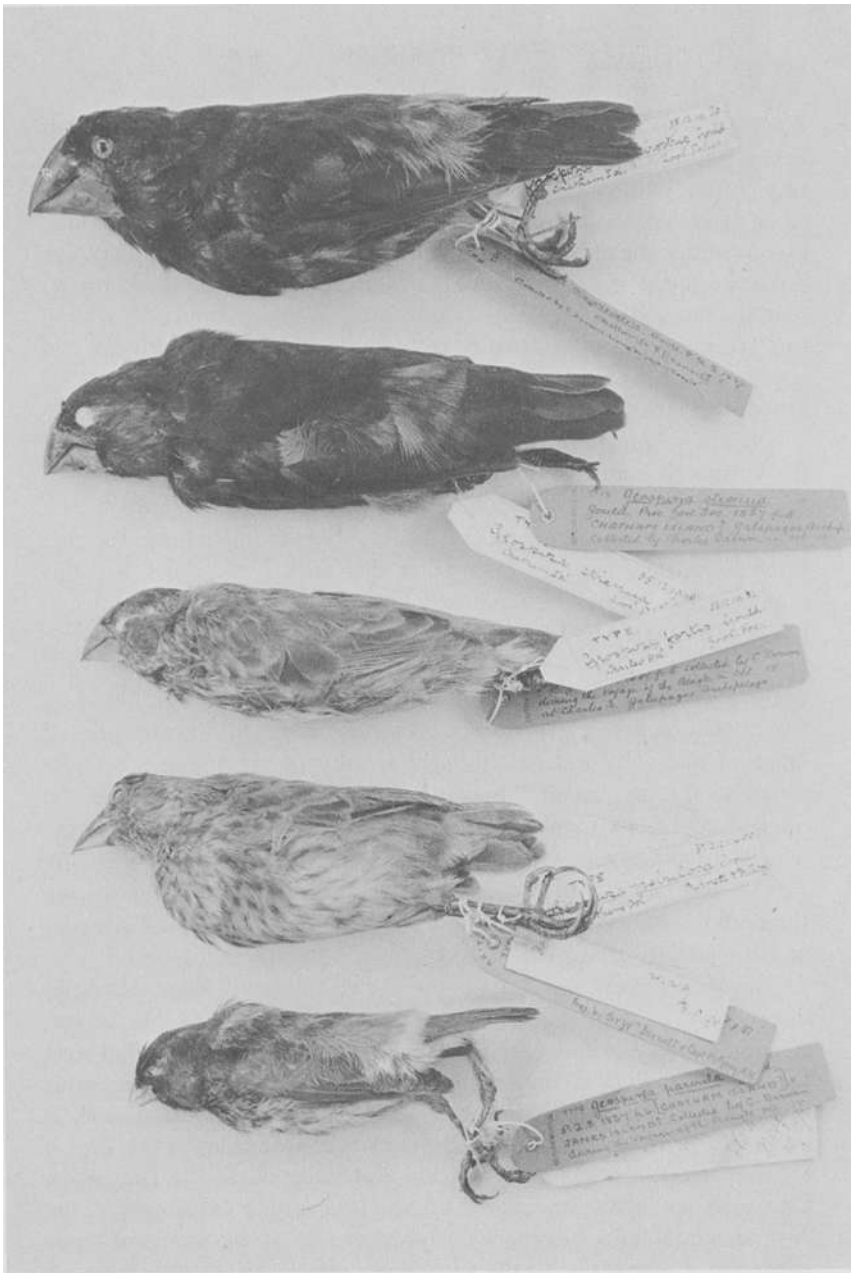

Fig. 3. *Beagle* type specimens of Darwin's finches. From top to bottom: *Geospiza magnirostris magnirostris*; *G. magnirostris strenua*; *G. fortis*; *G. nebulosa nebulosa*; and *Camarhynchus parvulus parvulus*. (Courtesy of the British Museum [Natural History], Sub-department of Ornithology, Tring.)

the means by which Darwin might have recorded this information. From his voyage specimen catalogues and other scientific notes it is very difficult to see how he could have supplied as much information as he later did in this regard. His *Ornithological Notes*, for example, lists localities for only three of his thirty-one Geospizinae, namely, for three specimens of a very distinctive species (*Camarhynchus psittacula*) that he recalled having seen on only one island – James. Moreover, this information was apparently recorded to indicate the rarity of the species rather than its locality per se. For the same reason Darwin also noted such information for two other Galapagos birds.

Darwin is known, of course, to have used FitzRoy's collections after the voyage to supplement his own record of localities. But this source of information still does not account for the localities entered on Darwin's own type specimens. Presumably, Darwin might have recorded localities on his specimen tags rather than in his catalogues. For this reason ornithologists have repeatedly bemoaned the fact that no original labels in Darwin's or John Gould's hand have ever been found among Darwin's type specimens at the British Museum. In the nineteenth century it was the custom of the museum curators to throw away the original collector's labels and to replace them with neatly printed museum labels. Information thought worthy of preserving was transferred to the new labels. But much valuable information, such as the original collector's numbers, was inevitably lost. George Robert Gray, who assisted Darwin with the *Birds* volume of the *Zoology of the Voyage of H.M.S. Beagle* and who later received Darwin's types from the Zoological Society when it closed its museum, was a typical offender in this regard (Sharpe 1906:84-85).

The question of whether or not Darwin recorded island localities directly on the specimen tags is largely resolved, however, by the fortunate discovery of one (and probably the only surviving) original label for his ornithological specimens. Having vainly sought, like previous investigators, for original labels among Darwin's type specimens, it occurred to me to examine all those Darwin specimens at the British Museum (National History) that are not endemic to the Galapagos. One such specimen was at last found (*Dolichonyx oryzivorus* – the American bobolink), bearing what appears to be Darwin's original crude paper tag. Comparison of the specimen number (3374) with Darwin's manuscript catalogue shows that the number is indeed Darwin's and that it is inscribed in his own hand (Fig. 4).[22] On the reverse side of the

22. In addition, the paper is similar to that used by Darwin on the *Beagle*

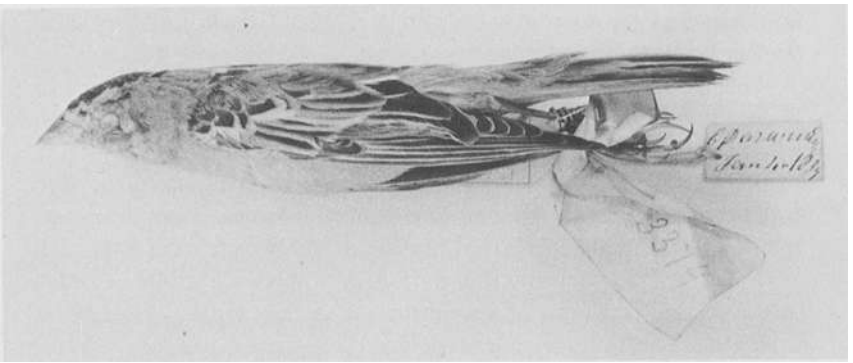

Fig. 4. Darwin's specimen of *Dolichonyx oryzivorus*, with the only surviving label in Darwin's hand. (Courtesy of the British Museum [Natural History], Sub-department of Ornithology, Tring.)

tag the genus name, 'Dolychonyx," is written in pencil, in an unidentified hand; and below it, in ink, the species name, "oryzivorus," appears, apparently in John Gould's hand. A second and smaller label, added when the specimen was presented to the Zoological Society in 1837, records Darwin's name, the date of accession, and, on the back, Darwin's original specimen number. The specimen was acquired by the British Museum in 1881, after Gould's death, along with many other birds from his huge personal collection. A third label (not shown) was attached to the specimen at this time.

Being a migrant species with an unusually wide range (from Canada to Chile), the bobolink is an occasional visitor to the Galapagos in the autumn of each year. Coincidentally, in its autumn plumage the bobolink is not unlike a Darwin's finch, although Darwin initially thought the bird was a pipit of very unusual structure.[23] When Gould first examined the bird in 1837, he thought it was a new species of finch. But he later discovered that it was an already described North American species and apparently decided to keep the specimen for his

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voyage. The registry number of this specimen at the British Museum is 1881.5.1. 2394.

23. In this *Ornithological Notes* he wrote: "Anthus. was shot by Fuller on James Isd: it was the only one specimen seen during our whole residence. It is described as rising from the ground suddenly & again settling on the ground. – Showed in its flight long wings, like a Lark; uttered a peculiar cry. – Its structure appear[s] very interesting" (1963[1836]:265).

own collection.[24] This circumstance, together with the lack of scientific importance of the specimen, enabled its original Darwin and Zoological Society labels to survive.

What is particularly important about this specimen with regard to Darwin's labeling practices is that no island locality is recorded on either of the two earliest tags. Darwin did consider this information worth recording in his *Ornithological Notes*, however, since the bird had been encountered on one island only – James. Thus it appears that whatever island localities Darwin thought worth recording, such as those for three finch and four mockingbird specimens, were recorded in the master catalogue of specimens and in the *Ornithological Notes* rather than on the crude paper tags.[25]

In short, Darwin does not appear to have altered his collecting or labeling practices while he was in the Galapagos Archipelago. After he left Charles Island, his collecting procedures continued to reflect the

24. Whether Gould acquired the specimen in 1837, or whether he perhaps acquired it as late as 1855, when the Zoological Society closed its museum and sold all its ornithological specimens, is not known. Gould also possessed other Darwin type specimens. In 1857 he sold 251 ornithological specimens to the British Museum, including 2 specimens of *Geospiza* that once belonged to Darwin (reg. nos. 1857.11.28.247 and 1857.11.28.248). See "Zoological Accessions Aves 1854-1873," p. 64, and "Zoological Accessions Aves 1880-1884," p. 106; British Museum (Natural History), Sub-department of Ornithology, Tring.

25. This conclusion is confirmed by an analysis of the locality information published by Waterhouse (1845) in his paper on Darwin's Galapagos insects. Of twenty-nine species, fourteen have island localities and fifteen do not. Each of these fourteen localities is recorded as well in Darwin's specimen catalogue; and the island and habitat information given by Waterhouse corresponds exactly to Darwin's own wording in that catalogue. Thus only where this information was recorded in Darwin's notes was it preserved for later use. Darwin apparently recorded such information incidentally as part of the habitat description. For example, specimens 3363 and 3364 are followed by the comment: "Small insects, sweeping; high up, central parts of Charles Island" ("Printed Numbers 3345[-3907]," Down House). In his section on advice to collectors, which appeared only in the first edition of his *Journal of Researchers* (1839:598-599), Darwin recommended that a number be placed on each specimen immediately after it was procured and that this number be entered in the specimen catalogue "during the very same minute" so that the locality would never be subject to doubt. If localities had been recorded on the numbered tags, this precaution would have been unnecessary. Finally, that none of Darwin's ornithological specimens had localities on the labels is reinforced by Gould's failure to provide any island designations for the Galapagos species he named in January and February of 1837. See "Zoological Society of London. Minutes of Scientific Meetings Oct. 1835 to Aug. 1840," pp. 120-121, 123-124, 129-130, 134; and Gould 1837a, b, c, d.

typological and creationist assumptions he had brought with him to that archipelago. What localities he did record were noted as largely incidental information to remind himself later of scarce species or noteworthy habitats. He continued, moreover, to collect only a few specimens of each species; and he entirely failed to collect finches on the third island he visited – Albemarle – even though almost every finch within miles was gathered in front of him at a spring near Bank's Cove.[26] Darwin thereby passed up the chance of collecting an additional species, and two endemic subspecies, of Galapagos finches. Similarly, although Darwin (1844:98) asked his fellow shipmates to bring him geological specimens from all the larger islands he was personally unable to visit, he made no such request for zoological specimens. Even after leaving James Island and setting sail for Tahiti, Darwin apparently continued to treat the vice-governor's comment about the tortoises, and his own discovery with regard to the mockingbirds, as isolated anomalies. For if he had fully appreciated the revolutionary implications of these facts, he would never have allowed his *Beagle* shipmates to devour and discard all thirty adult tortoises brought on board ship as a source of fresh meat for the cruise across the Pacific (FitzRoy 1839:498).[27]

26. In his *Diary*, Darwin wrote in this connection: "To our disappointment the little pits in the Sandstone contained scarcely a Gallon [of water] & that not good. It was however sufficient to draw together all the little birds in the country; Doves & Finches swarmed round its margin" (1933:338; entry for October 1, 1835). Similarly, FitzRoy commented: "Around this scanty spring draining continually through the rock, all the little birds of the island appeared to be collected, a pretty clear indication of there being then no other fresh-water within their reach . . . " (1839:495).

27. These tortoises, from Chatham Island, were brought on board the *Beagle* just five days before Darwin returned from James Island. FitzRoy had earlier embarked eighteen Chatham Island tortoises, and these were devoured as well. FitzRoy did, however, bring two Hood Island tortoises back to England ("Zoological Accessions 1837," p. 1; British Museum [Natural History], Mammals Library, London). Two other very small tortoises also survived the *Beagle* voyage – apparently brought home as pets (DAR 29.3:40, MS p. 7v). When Darwin finally realized the significance of having an expert taxonomist decide whether the reported differences between the tortoises were of specific distinction, these four tortoises were the only ones available. Although they were from three different islands (Hood, Charles, and James), they were all too young to be of value (Darwin 1839:465). Darwin also missed an opportunity to bring back an adult carapace of the unusual saddleback form of tortoise on Charles Island. According to FitzRoy (1839:492), numerous shells were lying around at the Charles Island settlement, where they were being used as flower pots. Within about ten years of Darwin's visit, the Charles Island tortoise was extinct. Zoologists had to wait nearly a century to find remains of this form in a lava cave (Broom 1929).

These conclusions regarding Darwin's collecting procedures during his Galapagos visit bring us back once again to the problem of his finches and their dubious localities. In particular, if Darwin recorded only three island localities for these birds in his scientific notes, how and when did he derive the many additional localities that are now to be found on his type specimens? To answer this question I must take up the topic of what happened to Darwin and his finches after they returned from the *Beagle* voyage.

DARWIN'S RETURN TO ENGLAND

The *Beagle* anchored in Falmouth, England, on October 2, 1836, after a voyage of nearly five years. During the next several months Darwin arranged for the disposal of his collections and began to prepare his *Journal* for publication. In mid-December he took up residence in Cambridge in order to look over all of his geological specimens. It was not until January 4, 1837, that he finally delivered his collection of birds and mammals to the Zoological Society in London.[28]

For the next two months Darwin continued to reside in Cambridge, with the exception of a brief visit to London on February 18 to hear Charles Lyell's anniversary address to the Geological Society.[29] At this meeting Darwin learned about the latest taxonomic findings regarding his valuable collection of South American fossil Mammalia. Richard Owen, who had taken charge of these bones, had recently reported his preliminary results to Lyell and had given him permission to make them public at the anniversary meeting. In his address, Lyell (1837:511)

28. Several of his specimens, including his bobolink, still bear this date of accession on the labels. It seems likely that Darwin presented the specimens in person since he came to London from Cambridge that same day to deliver a paper before the Geological Society (Darwin 1837a). He also wrote a letter dated January 4 that was read that afternoon at a meeting of the Zoological Society Council. According to the minutes of that meeting, Darwin's letter "announced a present to the Society of his entire Collection of Mammalia and Birds made during His Majesty's Surveying Vessel Beagle. It was ordered that the best thanks of the Society be returned to Mr. Darwin for his liberal and valuable contribution to its preserved Collections: and that his wishes with respect to the disposal of the duplicate specimens in this Collection, and to the mounting and describing of the same be strictly complied with" (unpublished "Zoological Society Minutes of Council," *5*:79-80).

29. According to Wilson (1972:442n21) and Herbert (1974:248n99), Darwin did not attend this meeting; but his presence is recorded in the manuscript minutes of the society's meetings. See "Ordinary Minute Book," *8*:219.

emphasized that Darwin's fossils had confirmed a law previously deduced with regard to Australia, namely, the close relationship that prevails between the past and present Mammalia of large continents. With this confirmation of "the law of succession," Darwin had received a source of evidence that would shortly prove instrumental in his conversion of the theory of transmutation. But it was the case of the Galapagos birds that was to be the most decisive in this respect.

On March 6, having finished looking over his geological specimens in Cambridge, Darwin moved to London in order to be near the various specialists who were working on his zoological collections. His first meeting with John Gould, who had been busy naming Darwin's ornithological specimens over the previous two months,[30] took place between March 7 and 12. It was at this time that Darwin first learned the results of Gould's analysis of his Galapagos collections.[31] The Galapagos finches were not, as Darwin had previously thought, members of widely different genera or even families, but rather one peculiar group of thirteen species that Gould placed in one genus and three closely allied subgenera (1837a). Gould had astutely realized the basic peculiarity of these birds, namely, that "the bill appears to form only a secondary character." Furthermore, he had even got the warbler finch right.[32]

30. After receiving Darwin's specimens, Gould exhibited, discussed, and named portions of Darwin's collection at the next five consecutive meetings of the Zoological Society (January 10 and 24, February 14 and 28, and March 14). See Gould 1837a, b, c, d, and e.

31. For the dating of this meeting, and evidence that Darwin and Gould had not discussed the Galapagos specimens before this time, see Sulloway (1982a).

32. See "Zoological Society of London. Minutes of Scientific Meetings Oct. 1835 to Aug. 1840," p. 120; manuscript record of the meeting of January 10, 1837. At this meeting, Gould recognized only eleven or twelve species of finches in three genera (*Geospiza*, *Camarhynchus*, and *Cactornis*), apparently not at first realizing that the warbler finch (*Certhidea olivacea*) was one of the Geospizinae. As Gould continued to work his way through the rest of Darwin's collection, group by group, he soon realized his mistake, which he had probably corrected by the time Darwin moved to London in March. The discrepancy between the number of finches reported as being named by Gould on January 10 (twelve species in the Zoological Society's "Minutes" and eleven species in three contemporary newspaper accounts) is probably the result of Gould's subdivision of one species into two shortly after the January 10 meeting. For further information, see Sulloway (1982a). On May 10 Gould again brought Darwin's finches before the Zoological Society, naming fourteen species in four genera, including *Certhidea* (see the manuscript "Minutes," pp. 164-165). Gould's fourteenth species, *Geospiza incerta*, lived up to its name, for he subsequently synonymized it under one of the others. A curious remnant of this change of mind remains in the published *Proceedings of the Zoological Society*, for although it is said that

More important still for Darwin's evolutionary thinking, Gould (1837d) had declared that three of the four island forms of Galapagos mockingbird brought to England by Darwin were distinct species, a possibility that Darwin had already asserted "would undermine the stability of Species." For the Galapagos as a whole, Gould pronounced twenty-five of the twenty-six land birds as new and distinct forms, found nowhere else in the world. Even four of the eleven waders and waterbirds – a gull, a rail, a heron, and a turnstone – were considered new by Gould (Darwin 1839:461). Darwin was frankly stunned, not only by the realization that three separate species of mockingbirds indeed inhabited the different islands of the Galapagos, but also by the fact that most of these Galapagos species, even though new, were closely related to those found on the American continent.[33] It was these two conclusions, together with the findings about his fossils, that finally convinced him that species must be mutable and that subsequently prompted the famous entry in his private journal: "In July [1837] opened first note book on 'Transmutation of Species' – Had been greatly struck from

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fourteen species were named, only thirteen names and descriptions follow (Gould 1837a). Also of interest is the fact that the published *Proceedings* lists under the January 10, 1837, meeting the names and descriptions that were given only later by Gould at the May 10 meeting. Thus the published record, by transferring the events of May 10 back to January 10 and by deleting the earlier presentation, obscures the difficulties that Darwin's finches caused even such a celebrated ornithologist as John Gould.

33. It is often claimed that Darwin was impressed by the American character of his Galapagos finches (see, for example, Silverstein 1974:505; and Ruse 1979: 164). But Darwin's finches played no role in this aspect of his evolutionary insight. Rather it was the mockingbirds, the flycatchers, the dove, and numerous other typically American species that established this generalization about the Galapagos avifauna. The finches, in contrast, were placed with the Fringillidae in the nineteenth century, and this family of birds was then believed to be worldwide. It is only in this century that the Fringillidae and Emberizidae, under which Darwin's finches are now classified, have been distinguished as families of Old and New World finchlike species, respectively. Although Darwin's finches have no close ancestor on the American continent today, some ornithologists believe they arose from a form related to the emberizine genus *Volatinia* (and several similar genera). These species are all seed-eating ground birds that range from the southern United States to northern Chile and Argentina (Paynter and Storer 1970:vii). Relying on osteological and other evidence, Steadman (in press) has argued that the Geospizinae evolved from *Volatinia jacarina*, the blue-black grassquit. He also contends that the Cocos Island finch and the Galapagos finches were established by two independent invasions of this species from Central and South America, respectively.

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).

Reconstructing the Finch Localities

In the wake of Gould's taxonomic findings, many of them quite unexpected, Darwin soon realized that the enigma of the finches could largely be explained if they, like the mockingbirds, were confined to separate islands. He therefore began to solicit information from those shipmates on the *Beagle* who had made their own private ornithological collections and who, unlike himself, had fortunately kept accurate records of the islands from which they had procured their specimens. Captain FitzRoy's extensive collection, which had gone to the British Museum on February 21, 1837, offered relatively easy access, and Darwin later acknowledged his use of it in the *Zoology* (1841:99).[34] What Darwin did not say in the *Zoology*, however, was that he also employed two other shipmates' collections, including that of his own servant, in attempting to reconstruct these island localities. The first of these sources of information came from Harry Fuller, who had spent a week collecting with Darwin on James Island. Altogether Fuller collected eight specimens of *Geospiza*, one from Chatham Island and seven from James. The collection of Darwin's servant, Syms Covington, was somewhat smaller and included only four finches, one from Chatham Island and three from Charles Island.[35]

34. For the date of FitzRoy's presentation of specimens, which included 187 skins, see the manuscript catalogue "Zoological Accessions Aves, 1837-1851-3," pp. 7-15; British Museum (Natural History), Sub-department of Ornithology, Tring. FitzRoy presented one further specimen on March 15, 1837, an egg of *Rhea darwinii*. FitzRoy's Galapagos portion of the collection included 50 skins, 21 of them finches, all with an island locality. Some of these Galapagos specimens were retained by FitzRoy, however; and only 24 Galapagos skins, 13 of them finches, actually went to the British Museum. Because FitzRoy's specimens were all labeled by island, his collection establishes that *Geospiza nebulosa* (Gould 1837a), an extinct race of the sharp-beaked ground finch (*G. difficilis*), was once present on Charles Island. According to the international rules of nomenclature, the name *G. nebulosa* therefore has priority over *G. difficilis*, which was first applied by Sharpe (1888) to another subspecies of this species. Thus the name of this taxon will henceforth be *G. nebulosa*. For further details about FitzRoy's collection, see Sulloway (1982b).

35. I have recently succeeded in locating and identifying these twelve specimens, which are now at the University Museum of Zoology, Cambridge (Fuller's

Records of Darwin's use of locality information from the collections of FitzRoy, Fuller, and Covington are among Darwin's manuscripts at Cambridge University Library (Figs. 5 and 6.).[36] There are four such

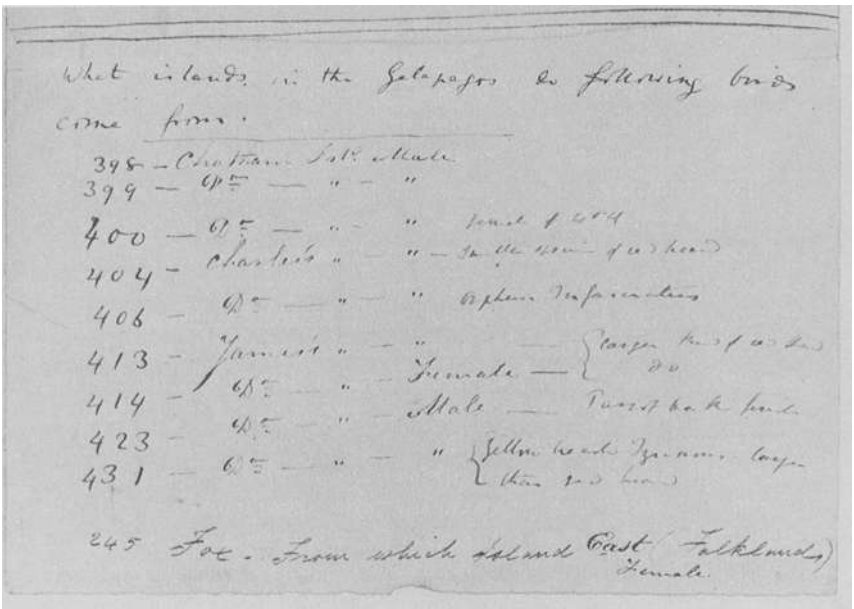

Fig. 5. Darwin's request for information regarding the island localities of FitzRoy's Galapagos birds, with replies in the hand of an unidentified amanuensis. A second unidentified amanuensis, who is known to have worked for Darwin after the *Beagle* voyage, addressed the last question on the list, which 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.)

collection), and the British Museum (Natural History), Sub-department of Ornithology, Tring (Covington's collection). Although only two of the birds have island localities on their labels, I have been able to resupply this information for the other ten specimens based upon two independent manuscript sources. Of particular importance is the fact that Fuller and Covington collected specimens of the large-billed form of *Geospiza magnirostris* on Chatham and Charles islands, respectively. For further details about these collections and their history, see Sulloway (1982b). Ironically, that other shipmates on the *Beagle*, but not Darwin, recorded island localities for their birds marks Darwin as the only real scientist aboard that ship. For Darwin collected with a theory, however mistaken, in mind. The other shipmates were mere collectors, and their labeling practices reflect that fact.

36. See DAR 29.3:26, 28-30.

sheets, in Darwin's hand. Although none of the sheets dated, indirect evidence indicates that Darwin lost little time after he became an

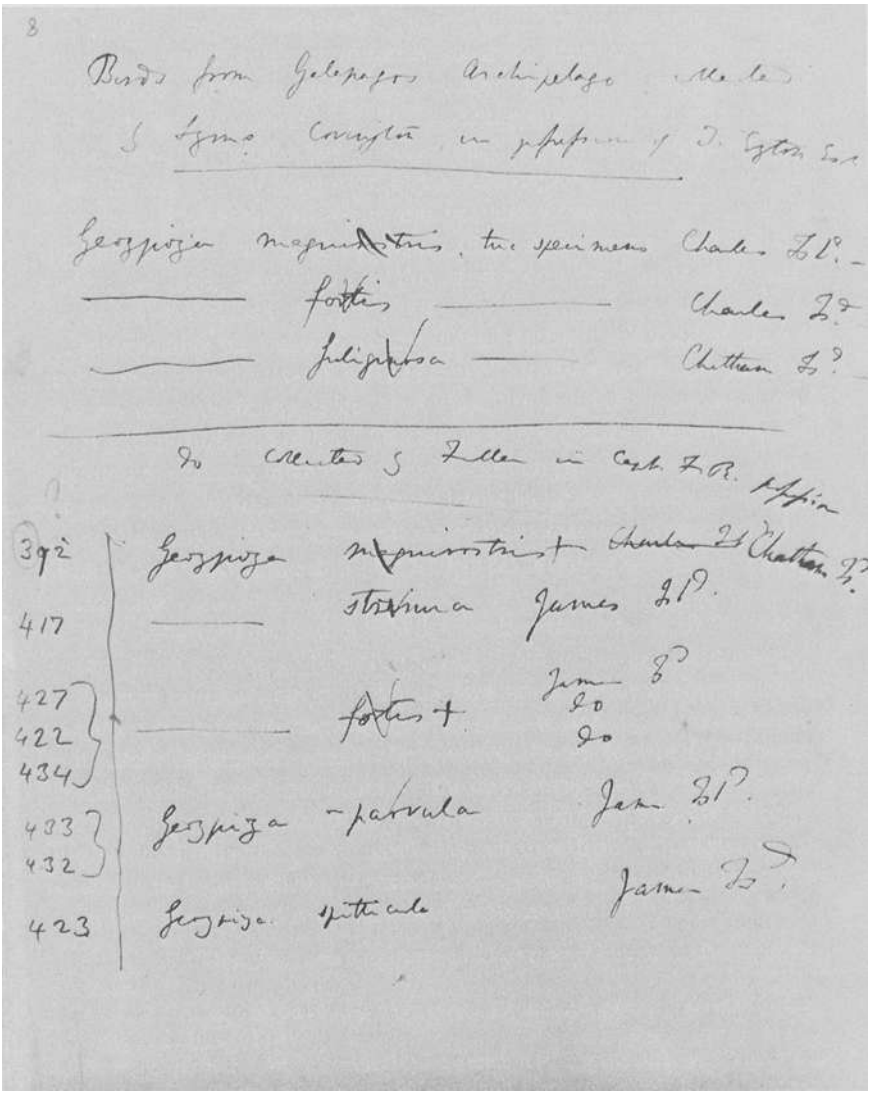

Fig. 6. Darwin's notes on the island localities of Covington's and Fuller's Galapagos finches. (Courtesy of the Syndics of Cambridge University Library.)

evolutionist in trying to reconstruct the Galapagos finch localities. One of the four sheets, which bears an 1836 watermark (manufacturer unknown), comprises a series of questions about Galapagos specimen localities that Darwin evidently sent to FitzRoy, and that was answered by an unidentified amanuensis or clerk (Fig. 5). On this same sheet an amanuensis working for Darwin also asked from what island of the Falklands a specimen of fox had come. Darwin mentioned the results of this latter inquiry in his *Journal of Researches* (1839:250-251), which was already in press by mid-August 1837. Similarly, Darwin's statement in his *Journal* (1839:475) that he "very much" suspected that certain species of Galapagos finches were confined to separate islands corroborates the conclusion that he had already examined the various *Beagle* collections by the time his *Journal* went to press. Since Darwin had reached the Galapagos chapter of his *Journal* by late May or early June and since he had finished with the whole of the *Journal* by the end of June, his efforts to collate the various *Beagle* Geospizinae by locality probably date from June at the latest.[37]

It was undoubtedly at this time, that is, sometime in the spring or early summer of 1837, that Darwin also tried to reconstruct the island localities of his *own* Galapagos specimens. For a few birds Darwin was able to infer from his notes or from memory that he had collected these specimens on only one island. This was the case, for example, for an owl, a swallow, a flycatcher, and for three finch specimens with a

37. That Darwin's manuscript notes on this question were initially compiled in connection with the writing of his *Journal* is reinforced by another consideration. On the list of Covington's and Fuller's birds, which occupies one of the four sheets, Darwin mistakenly referred *Camarhynchus psittacula* to the genus *Geospiza* (see Fig. 6). He also misspelled *psittacula* as *spittacula*. This same species name is misspelled and assigned to the genus *Geospiza* in a list of Galapagos species that Darwin compiled in the spring of 1837 during a meeting with John Gould (Sulloway 1982a). Darwin was not, therefore, entirely familiar in the spring of 1837 with the generic or specific names that Gould had just given these species. The use of erroneous generic and specific names on the locality list for Covington's and Fuller's birds suggests that these notes too were compiled about this time. The name *psittacula* was altered to *psittaculus* in the *Zoology* (1841: 103), so these notes on Covington's and Fuller's specimens clearly predate that change. I would assign Darwin's two other sheets of notes on his Galapagos finch localities to late 1840, when he was working on the final installment of the ornithological portion of the *Zoology*. One sheet, which records all thirteen of FitzRoy's finch localities, may be dated by the use of the specific name *Camar*[*h*]*y*[*nchus*] *psittaculus*. The other, although it bears the name *psittacula*, is probably of the same date, since it contains a collated list of localities for all the *Beagle* collections as published in the *Zoology* (1841:100-106).

peculiar beak shaped like that of a parrot (*Camarhynchus psittacula*). In addition, from his *Beagle* shipmates Darwin apparently acquired several finch specimens that were lacking in his own collection, and at least one of these had a locality attached (Sulloway 1982b).

Unfortunately, certain of Darwin's attempts to reconstruct the island localities of his own specimens involved guesswork, and errors inevitably crept in. In his master catalogue of specimens, for example, he drew a line under the first eight Geospizinae and wrote "?Chatham Is^{d}??"[38] The reason Darwin surrounded this locality designation with three question marks is evident from the order of the catalogue entries as a whole. As may be seen from the number sequence assigned to his birds, Darwin ticketed, numbered, and catalogued the entire collection only after leaving the Galapagos Archipelago in late October 1835. Within the list of birds, the entries proceed topsy-turvy, with specimens from the different islands entered in no apparent order.[39] It is hardly surprising, then, that at least two of the eight specimens that Darwin later assigned to Chatham Island appear to have been mislabeled (Sulloway 1982b).

In the process of attempting to correlate the results from four different collections, Darwin inadvertently made other mistakes. In the *Zoology* (1841:101) he later gave the locality of *Geospiza fortis* as Charles and Chatham islands; but this was clearly an error, since the

38. See "Printed Numbers 3345[-3907]," Down House, under specimen nos. 3312-3319. The catalogue is written in ink. The line under the first eight specimens and the comment "?Chatham Is^{d}??" were added later in pencil, almost certainly after Darwin's return to England.

39. Of those specimens for which island localities are listed (eighteen) or were later published by Darwin (two), or for which localities can be reconstructed on the basis of other evidence (nine), the sequence runs: James (3299); James (3303); James (3304); Charles (3306); Chatham (3307); Chatham (3308); Charles or James (3309); James (3310); the eight specimens of finch that Darwin later assigned to Chatham with three question marks (3312-3319); James (3330-3332); James (3340); Charles or James (3342-3344); Chatham (3345); Albemarle (3349); James (3350); James (3356); James (3362); and James (3374). I have deduced seven of these twenty-nine localities from information unknown to Darwin. *Certhidea olivacea* exhibits distinctive characteristics by island, and Darwin's specimens (3310 and 3340) definitely belong to the James Island form of this species. *Pyrocephalus dubius* (3345) is confined to Chatham Island, and hence Darwin's specimens of *P. nanus* (3309, 3342-3344), a form that replaces *dubius* elsewhere in the archipelago, must have come from either Charles or James Island. The localities of two other specimens (3299 and 3362) can be deduced from Darwin's statement that they came from a salt lagoon, which he visited on James Island. Darwin also visited a salt lagoon on Albemarle Island, but he does not appear to have collected at this site.

Beagle specimens all came from Charles and James.[40] Further inaccuracies are associated with Darwin's claim about geographic representation among the various species of the Geospizinae. Eager to squeeze whatever evolutionary evidence he could from these finches, Darwin systematically collated the island localities of the four *Beagle* collections to see if any of the species represented one another on the different islands. In two genera, *Cactornis* and *Camarhynchus*, he claimed this to be the case. Of the numerous specimens shot by four collectors at James Island, he reported, all belonged to *Cactornis scandens* and *Camarhynchus psittacula*, whereas the specimens collected either on Chatham or Charles were those of *Cactornis assimilis* and *Camarhynchus crassirostris*. "Hence we may feel almost sure," he concluded, "that these islands possess their representative species of these two subgroups" (1845:395).

Darwin's analysis of these two genera was plagued by several errors. In actual fact, FitzRoy had collected a specimen of *Cactornis assimilis* on James, not Charles or Chatham Island, thus invalidating half of Darwin's claim. Furthermore, Darwin had not collected long enough on any of these islands to realize that the various finch species are by no means confined to single islands. *Camarhynchus crassirostris*, for example, is found not only on Charles Island, where Darwin believed his own specimens had probably been taken, but also on Chatham and James. Similarly, *Cactornis scandens* and *Camarhyncus psittacula* are not confined to James Island, as Darwin had thought, but are found on the other islands he visited. Thus Darwin's claim about geographic representation in this group of four species is not only wrong in every detail, but it is not even substantiated by the *Beagle*'s own collections. It is no wonder, then, that Darwin was so excited and relieved in 1845 by Joseph Hooker's rigorous demonstration of representation in his several hundred species of Galapagos plants. To Hooker he wrote 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

40. In his manuscript notes on the collections of FitzRoy, Fuller, and Covington, Darwin listed this locality correctly as "Charles [and] James Is^{d}." See DAR 29.3:28. Nevertheless, because John Gould probably mistook at least one Chatham Island specimen of *Geospiza fortis* for that of *G.* [*magnirostris*] *strenua*, the actual locality for the *Beagle* collections of *G. fortis* should have been Chatham, Charles, and James islands. Similarly, *G.* [*magnirostris*] *strenua*, reported as coming from Chatham and James islands in the *Zoology* (1841:101), was in fact collected only on James Island. See Sulloway (1982b) for further discussion of Gould's classification mistakes.

my assertion on the differences in the animals of the different islands, about which I have always been fearful" (1877, *2*:22). Darwin lost no time in adding Hooker's welcome results to his *Journal of Researches*, which he was then engaged in revising for the second edition.[41]

Fortunately, the errors and uncertainties associated with Darwin's ornithological specimens did not affect the published results of the *Zoology of the Voyage of H.M.S. Beagle* that much. Of the seventeen type localities that Darwin published for his finches, fifteen were either provided or corroborated by the other shipmates' collections. Darwin himself, employing an educated guess, was able to supply localities for two additional species that only he had collected. In the end only two species of finches remained without any locality whatsoever.

Unfortunately, what later ornithologists generally failed to appreciate was that these published localities were not necessarily those of Darwin's own specimens. In fact, the largely borrowed nature of Darwin's published localities for his Galapagos finches has had one curious repercussion that has confused even further the localities of the *Beagle* type specimens. A number of originally unlabeled Darwin specimens appear to have acquired island localities later in a completely circular fashion, based upon the published information provided in the *Zoology of the Voyage of H.M.S. Beagle*. Curators at the British Museum apparently noticed that certain Galapagos species were indicated in the *Zoology* as coming from one island only. They therefore assumed that unlabeled Darwin specimens of these species must have come from those published localities. The specimens in question now carry these island localities on their labels; and in the British Museum's published list of type specimens there are notes to see the relevant pages of the *Zoology of the Voyage of H.M.S. Beagle*.[42] In certain

41. It is ironic, and Darwin (1839:629) was the first to admit it, that his Galapagos plants proved so valuable precisely because he was least accomplished in that field of natural history. For this reason he collected "blindly" from each island he visited, mistaking representative species for duplicate specimens. That he fortunately recorded the island localities of his plant specimens reflects the way in which they were collected. Plants must be placed in a plant press soon after collection, and the plants from a given island would all tend to be pressed together rather than intermixed with plants from a separate island. Similarly, Darwin recorded separate island localities for his saltwater fish because they had to be numbered and preserved in spirits of wine soon after being caught.

42. The following specimens at the British Museum (Natural History), Subdepartment of Ornithology, Tring, appear to have acquired localities – either on the labels or in the published type specimen catalogue – by reference to the

instances (for example, in the case of Darwin's specimens of *Otus galapagoensis*, *Hirundo concolor*, and *Dolichonyx oryzivorus*), these derivative localities are indeed correct, since Darwin was the only person on the *Beagle* to collect these species, whose localities he was later able to recall. But this same process of circular relabeling is apparently what accounts for at least four of Darwin's finches being given localities that do not necessarily belong to them.[43]

More ironically still, three of Captain FitzRoy's accurately labeled specimens have also suffered from this relabeling process, based once again upon Darwin's published testimony. In one instance FitzRoy's specimen of *Camarhynchus psittacula*, which was procured on James Island, was relabeled as coming from Charles Island. This error was precipitated by the loss of Darwin's three type specimens of *C. crassirostris*. *C. crassirostris* and *C. psittacula* are somewhat similar species. FitzRoy's slightly aberrant specimen of *psittacula*, which was later thought to be the missing type of *crassirostris*, was accordingly reassigned to that species. But the island locality now had to be altered as well to agree with Darwin's dubious but "official" information for the type of *C. crassirostris*![44] The classification error was eventually caught by Swarth (1931:208), but the specimen in question still bears two island localities. Similarly, two other FitzRoy specimens, one

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Zoology: Camarhynchus psittacula (reg. no. 1855.12.19.22); two specimens of *Cactornis scandens* (nos. 1855.12.19.20 and 1855.12.19.125); two specimens of *Geospiza parvula* (nos. 1855.12.19.167 and 1855.12.19.194); *Otus galapagoensis* = *Asio flammeus* (no. 1855.12.19.153); *Larus fuliginosa* (no. 1855.12.19.218); *Hirundo concolor* = *Progne modesta* (no. 1860.1.16.54); and *Dolichonyx oryzivorus* (no. 1881.5.1.2394). See Warren 1966:104, 108; Warren and Harrison 1971:127, 420, 448, 494; and Mayr and Greenway 1960:87.

43. Darwin's specimens of *Geospiza parvula* (nos. 1855.12.19.167 and 1855.12.19.194) do not necessarily come from James Island, as the labels and Warren and Harrison (1971:420) have claimed. According to Lack (1945:14-15), one of the two Darwin specimens of *Cactornis scandens* (no. 1855.12.19.20), which are both labeled as coming from James Island, is actually a specimen of *G. difficilis* (now *nebulosa*) and belongs to the extinct Charles Island form of this species. Darwin was unable to supply the island locality for *C. assimilis*, which he probably did not distinguish from *C. scandens*, so it is unlikely that he was certain about the localities of any of his *scandens* specimens. One again, see Warren and Harrison (1971:494) for the circular derivation of these *C. scandens* localities.

44. Both the reassignment of this specimen to *Camarhynchus crassirostris* and the change in its island locality were apparently done prior to Sharpe's (1888:16) catalogue of specimens at the British Museum.

being the type of *Geospiza nebulosa*, were also relabeled incorrectly, owing once again to Darwin's published localities.[45]

In short, the published designations of the *Zoology* were seen by later ornithologists and museum curators as more definitive than the accurately labeled FitzRoy specimens that had largely supplied this information. Swarth (1931:11) actually dismissed FitzRoy's localities wholesale, assuming his specimens could have come from practically anywhere in the archipelago.[46] David Lack (1945, 1947), although not going quite so far, assumed that all of FitzRoy's specimens were really Darwin's and that those specimens labeled as coming from either Chatham or Charles Island could have come from either locality. With all of these confusions about the localities of Darwin's and FitzRoy's

45. The source of the first of these two errors began with Salvin's (1876:482) reassignment of the species *Geospiza nebulosa* to *G. fortis*. Since Darwin's specimens of *G. fortis* were supposed to have come from Chatham and Charles islands, and since the only extant specimen of *G. fortis* in the British Museum bears a Charles Island locality, subsequent ornithologists apparently assumed the FitzRoy specimen had come from the other published locality (e.g., Sharpe 1888:11). Later, the erroneous Chatham Island locality was crossed out and the Charles locality reinstated, possibly by Kinnear (see note 46), but the presence of two island localities on this specimen has proved confusing for subsequent ornithologists (e.g., Lack 1945:14-15).

The second incorrectly labeled FitzRoy specimen is the type of the Galapagos rail (*Zapornia spilonota* Gould = *Laterallus spilonotus*, British Museum reg. no. 1837.2.21.404). Rothschild and Hartert (1899:184-185), noting that Darwin (1839:459) had described seeing water rails on James Island, erroneously concluded that the bird was collected by him on that island. FitzRoy, however, collected his specimen on Charles Island. In the *Zoology* (1841:132), Darwin gave only "Galapagos Archipelago" as the locality for this species. Swarth (1931: 53) and Warren (1966:279), following Rothschild and Hartert, have perpetuated the erroneous James Island locality for FitzRoy's specimen.

46. Swarth's erroneous conclusion was reinforced by the fact that some of FitzRoy's specimens have their localities recorded not on the specimen tags but only in the museum's "Zoological Accessions Aves 1837-1851-3" register. Norman B. Kinnear, who worked in the Bird Room of the British Museum (Natural History), nevertheless understood that the localities of FitzRoy's specimens had been recorded in this old register. Using this information, he inserted a number of footnotes into Swarth's (1931) monograph indicating the localities of various unlabeled FitzRoy specimens. Swarth, however, chose to disregard this information, arguing that "there have been so many chances for dissociation of specimens and data that my every instinct impels me to rely upon the evidence supplied by the specific or subspecific characters of the specimens rather than on what has been written about them" (1931:146n). Unfortunately, Swarth's ornithological intuitions were not as accurate as FitzRoy's recorded localities.

specimens, it is little wonder that the *Beagle* types have proved so problematical to ornithologists over the last hundred years.

Darwin's Finches and Darwinian Theory, 1837-1859

The largely retrospective nature of Darwin's understanding of his Galapagos finches is apparent not only from his postvoyage attempts to reconstruct their island localities but also from his theoretical conceptions about these birds. Contrary to the legend, Darwin's finches do not appear to have inspired his earliest theoretical views on evolution, even after he finally became an evolutionist in 1837; rather it was his evolutionary views that allowed him, retrospectively, to understand the complex case of the finches.

Not only was this retrospective understanding surprisingly slow in coming; but it was far more limited than is generally assumed. The finches are not mentioned, for example, in any of the four notebooks on "Transmutation of Species" that Darwin commenced in July 1837 and kept until later 1839. Nor are they mentioned in the later portions of the *Red Notebook*, written between March and July 1837, which predate this series and which contain his earliest speculations on the transmutation of species.[47] Although Darwin frequently discussed in these notebooks the two subjects with which the finches are usually associated – speciation through geographic isolation and adaptive radiation into unfilled niches – he always cited examples other than the finches.[48]

47. The *Red Notebook* has been transcribed with extensive editorial annotations by Herbert (1980), who supplies documentation for an approximate dating of this notebook. Elsewhere I provide a more precise dating of the evolutionary passages in the *Red Notebook* (Sulloway 1982a).

48. In the first of the four notebooks on transmutation of species (July 1837 to February 1838), Darwin's favorite examples of speciation through geographic isolation were the Galapagos tortoises and mockingbirds (p. 7); the English and Irish hares (pp. 7, 221, 262); and various other cases of representative forms in archipelagoes or on islands and nearby continents (pp. 11, 31, 50, 69 [excised], 82, 138, 156, 166 [excised], 187 [excised], 221, 241, 249 [excised]). Darwin broached the topics of divergence and adaptive radiation in this first notebook in a number of different contexts: the prevalence of Edentata in South America (pp. 13, 54, 106); the prevalence of marsupial types in Australia (pp. 14-15, 141); the tendency for every organic group to adapt some of its forms to air, land, and water (pp. 23-24, 45-46, 263); and instances of species that have adopted new stations, often evolving new structures and new behaviors, normally occupied by other, very different species (pp. 55-56 [excised], 137, 141, 144, 193). See de Beer 1960-1961; and de Beer, Rowlands, and Skramovsky 1967.

In the first edition of his *Journal of Researches* (1839), Darwin said very little about the finches except to comment that certain subgenera of *Geospiza* probably had their representative forms on different islands and that this circumstance would help to explain the "wide range of character" found in the group. In the spring and early summer of 1837, when Darwin was preparing his *Journal* for publication, he believed that species diverged primarily through geographic isolation and ensuing adaptation to varying local circumstances. Since he considered the different islands of the Galapagos to have identical climates and geographic conditions, he apparently believed isolation alone was the cause of the small differences that separate most representative species in archipelagoes. But he did not address himself, either publicly or privately, to the enigma of how such differences might arise under identical environmental conditions or how they could become as pronounced as they are in some species of Darwin's finches. It should be pointed out that Darwin's brief discussion of the finches in his *Journal* predates by more than a year his discovery of the principle of natural selection. He therefore did not have an adequate appreciation of how evolution, and particularly adaptation, are effected through competition between life forms. Nor did he appreciate that islands within an archipelago might differ biotically without differing climatically or geographically.[49]

Even after he had hit upon the principle of natural selection and was writing about the finches in the *Zoology of the Voyage of H.M.S. Beagle* (1841:99-106), Darwin simply reiterated what he had already said in his *Journal* about the possibility that geographic representation contributed to the group's "fine gradation" of character. It was not until he drafted his Essay of 1844, in which he set down a 230-page outline of his theory of evolution by natural selection, that he finally set forth a theoretical model with sufficient sophistication to begin to

49. Later, in the *Origin of Species*, Darwin reflected upon these conceptual difficulties: "But this dissimilarity between the endemic inhabitants of the [Galapagos] islands may be used as an argument against my views; for it may be asked, how has it happened in the several islands situated within sight of each other, having the same geological nature, the same height, climate, &c., that many of the immigrants should have been differently modified, though only in a small degree. This 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).

deal with the enigma of the Galapagos finches. Imagining a volcanic island newly elevated from the ocean floor and far from any point of land, Darwin noted that the first colonists would rarely be completely adapted to the many vacant "stations" they encountered there. Not only would the physical conditions of the new and rugged volcanic environment differ from those in the colonists' homeland, but the absence of the colonists' usual competitors would further ensure altered conditions of existence. Each successive colonist would in turn contribute to "new and varying conditions" for the island biota as a whole (1909[1844]:185). Hence natural selection would act continuously on the various colonists, Darwin concluded, to produce ever more adapted forms. If the island were turned into an archipelago by the continued action of subterranean forces, new opportunities for colonization and evolution would eventually give rise to representative species or races, "as is so wonderfully the case with the different islands of the Galapagos Archipelago" (1909[1844]:187).

One of Darwin's novel insights in his Essay of 1844 was that no two islands in an archipelago that is continually stocked by random colonists would ever possess exactly the same inhabitants. It is this circumstance, he now appreciated, that causes differential evolution among the representative species of neighboring islands. Commenting in the related context of temporary archipelagoes created by the repeated elevation and subsidence of a continent, Darwin concluded that through evolution "the inhabitants of the most *dissimilar* stations . . . would be more closely allied than the inhabitants of two very *similar* stations on two of the main divisions of the world" (1909[1844]:190). Although Darwin did not apply this Essay idea to the case of the Galapagos finches, he clearly had some such general concept in mind when, the following year, he added the famous remark to his *Journal of Researches* that "one might really fancy that from an original paucity of birds in this archipelago, one species [of finch] had been taken and modified for different ends" (1845:380).

In spite of these declarations in the Essay and in the 1845 edition of the *Journal*, Darwin had not yet fully grasped the notion of adaptive radiation. At this time he still did not understand why divergence *necessarily* takes place after a species multiplies itself through geographic isolation and then comes into secondary contact with its geographic representatives. It is not immediately clear, for example, why any divergence at all should occur among the species of a scantily populated archipelago. With few competitors or predators to challenge the colonists of an isolated island group, what real evolutionary pressure

would there be for representative species, once formed, to evolve significant differences beyond simple reproductive isolation?

Looking back in his *Autobiography*, Darwin recalled that his failure to resolve this problem of divergence was the one major omission from his Essay of 1844. The solution, which finally came to him in the 1850s, was that "the more diversified the descendants from any one species become in structure, constitution, and habits, by so much will they be better enabled to seize on many and widely diversified places in the polity of nature, and so be enabled to increase in numbers" (1859: 112).[50] In other words, natural selection favors the most divergent offspring of every species because divergence, by minimizing competition, increases the individual's chances for survival. With his principle of divergence, Darwin at last had an explanation for why adaptive radiation tends to occur in those cases, such as the Galapagos finches, where geographic isolation enables early colonists to exploit the many unoccupied stations of a new environment.

Surprising as it may seem, Darwin did not publish anything more about his famous finches after the brief and cryptic hint about them he had inserted into the second edition of his *Journal*. And publicly, at least, he never actually put his finches forward as evidence for the theory of evolution.[51] In the *Origin of Species* (1859) the Geospizinae go unmentioned, although the Galapagos Islands are employed on six different occasions to illustrate the general relation between the inhabitants of oceanic islands and those of the nearest continent, the phenomenon of representative species, and the absence of certain classes of organisms, such as mammals, from remote islands. The closest that Darwin came in these later years to discussing the origins of his Galapagos finches from an evolutionary point of view was in *Natural Selection*, the longer version of the *Origin* that was interrupted in 1858 by Alfred Russel Wallace's anticipation of the theory of natural selection. In that larger work Darwin contrasted the situation of Madeira, which annually receives stray birds from the neighboring continent and which possesses only one endemic species among its twenty land birds,

50. On the dating of Darwin's insight into the principle of divergence, see Browne (1980), who argues that it occurred in 1857. Darwin himself dated this discovery to about 1852. Actually, the idea came to him in a series of stages between the late 1840s and 1857, being applied first to species and higher taxa with allopatric distributions, and being extended later to include sympatric divergence among varieties of the same species. See Ospovat 1981:170-190.

51. The first published evolutionary account of the Galapagos finches is apparently that of Salvin (1876).

with the far more isolated state of the Galapagos, where twenty-five of the twenty-six land birds have reached endemic status. In Darwin's view, as few as eleven species originally colonized the Galapagos, and there they must have encountered a wide range of open places in the economy of nature:

> hence I suppose that nearly all the birds had to be modified, I may say improved by selection in order to fill as perfectly as possible their new places; some as Geospiza, probably the earliest colonists, having undergone far more change than other species; Geospiza now presenting a marvellous range of difference in their beaks, from that of a gross-beak to a wren; one sub-species of Geospiza mocking a starling, another a parrot in the form of their beaks. (1975[1856-1858]:257)

When he abstracted material from his "Big Book" for the *Origin of Species*, Darwin dropped the example of the finches from the corresponding discussion (1859:104-105, 390-391).

How is it that Darwin elected to omit from his *Origin of Species* what today is probably the most cited "textbook" example of the validity of his evolutionary views? The answer to this question is that Darwin clearly did not consider the case of the Galapagos finches to be in any way crucial to his argument. In this connection we must distinguish what we now know about Darwin's finches from what Darwin knew about them in 1859.

To establish a presumption that his Galapagos finches had indeed evolved such divergent forms through adaptive radiation, it was first necessary to show that the different shapes of their beaks were in some way effective in reducing competition. But Darwin lacked precisely this information. According to his own testimony, the several species of *Geospiza* were "indistinguishable from each other in their habits," feeding together on the ground in large irregular flocks (1841:99). These observations were not only incomplete but also incorrect. *Geospiza magnirostris*, the large ground finch, is actually a solitary species that rarely feeds on the ground with the other seed eaters. Moreover, all four species of ground finches have somewhat different diets; and one species, *G. nebulosa*, is restricted to the humid zone on the islands visited by Darwin. Similarly, Darwin erroneously believed that the habits of three other tree-dwelling species were identical to those of the genus *Geospiza*. But two of these species (*Camarhynchus parvulus* and *C. psittacula*) are insectivorous, and the third (*Platyspiza crassirostris*)

has a purely vegetarian diet. To Darwin's eyes, only the cactus finch (*G. scandens*) seemed to be distinguishable by its habit of feeding upon the prickly-pear cactus. Thus Darwin failed to correlate feeding habits in the Galapagos finches with their diverse beaks, and partly for this reason most subsequent ornithologists thought that there was no relationship.

As for *Certhidea olivacea*, the warbler finch, there were frequent debates throughout the remainder of the nineteenth century about whether this species was really a finch at all; and Darwin himself entertained some doubts about the matter (1841:105). Most ornithologists actually rejected Gould's perceptive classification until after the turn of the century, when anatomical studies and observations of breeding behavior finally convinced them that *C. olivacea* was indeed one of the Geospizinae.[52] Similarly, some nineteenth-century ornithologists also doubted that the genus *Camarhynchus*, which includes five of the thirteen species of Galapagos finches, had the same evolutionary origins as the six species of *Geospiza*.[53] Thus as a case of divergence, or adaptive radiation, Darwin's finches were a speculative and problematical example at best, lacking proof on just those points that were crucial to the whole argument.

Above all, what now sets the Geospizinae apart as a convincing paradigm of evolution in action is the evidence associated with their geographic distribution and intraspecific variation. In 1859 Darwin had scant knowledge of the role geographic isolation had played in the evolution of the Geospizinae. Moreover, what evidence he did possess was unfortunately wrong. This fact became readily apparent after Dr.

52. Salvin (1876:476), Sclater (1886:27-28), and Ridway (1897:497) placed *Certhidea olivacea* with the Coerebidae. Rothschild and Hartert (1899:148) were less certain, placing this species either with the Mniotiltidae or the Coerebidae. Snodgrass and Heller (1904:234) preferred to classify it with the Mniotiltidae. On anatomical grounds, however, Snodgrass (1903), Sushkin (1925, 1929), and Lowe (1936) all recognized the close affinity between the warbler finch and the rest of Darwin's finches. This opinion, which was accepted and corroborated by Swarth (1931:138) and Lack (1947:13), is no longer questioned.

53. Species of the genus *Camarhynchus* differ from those of *Geospiza* not only in their beaks and diets but also in plumage. The males of *Camarhynchus*, in particular, are never fully black, developing that coloration only around the head and upper body. This difference in plumage is partly what prompted Salvin (1876:470) to doubt that *Camarhynchus* and *Geospiza* had the same evolutionary origins. Similarly, three decades earlier, Lafresnaye (1843) doubted the relatedness of these two genera, referring a species of *Camarhynchus* to the South American finch genus *Guiraca*. Lafresnaye's classification was followed by Prévost and des Murs (1855:209-212).

Habel visited the Galapagos in 1868 and brought back an extensive collection of Geospizinae described by Philip Sclater and Osbert Salvin (1870). In his 1876 monograph on the avifauna of the Galapagos, Salvin rather charitably commented that "Mr. Darwin's views as to the exceedingly restricted range of many of the species must be considerably modified" (1876:461). In fact none of the species of Geospizinae collected by Darwin have turned out, as he suggested, to be restricted to single islands. Only when ornithologists returned to the Galapagos Archipelago in a series of expeditions from the late 1880s to the 1930s, collecting numerous finch specimens from each of the islands and analyzing the statistical variations in characters of the different species and subspecies, did it finally become possible to appreciate the evolutionary richness presented by this one group of birds. It was precisely this evolutionary richness that Darwin, with his limited number of specimens from only three islands, did not have at his disposal when he wrote the *Origin of Species*. Only the legend of Darwin's finches makes us think differently.

THE LEGEND OF DARWIN'S FINCHES

The legend of Darwin's finches encompasses two principal themes. The first involves the claim that the different forms of the finches, along with the tortoises and the mockingbirds, first convinced Darwin that species must be mutable while he was still in the Galapagos Archipelago. The legend's second theme holds that Darwin's observations on the finches inspired all his later theories by providing him with a decisive example of evolution in action. In particular, the finches are said to have eludicated the crucial roles of geographic isolation and adaptive radiation as mechanisms of evolutionary change.[54] "Probably

54. Many authorities have stressed the role of Darwin's finches in converting Darwin to the theory of evolution while he was still in the Galapagos. See, for example, Huxley 1954:6, 1960:9; Eibl-Eibesfeldt 1961:18; Peterson 1963:11-12; Darling and Darling 1963:34; Moorehead 1969:202; Grzimek 1973:359; Olney 1976:135; Dobzhansky et al. 1977:12; and Jensen et al. 1979:486. The following commentators, who do not date Darwin's conversion or who place it later than the actual Galapagos visit, still emphasize the critical role of the finches in that conversion: Swarth 1931:10; Wynne-Edwards 1947:687; Mayr 1947:217; Eiseley 1961:172-173; de Beer 1963:132; Moody 1970:303; Leigh 1971:136; Thornton 1971:12, 161-162; Grinnell 1974:259, 263; Gruber 1974:130; Dorst 1974, 2:252; Silverstein 1974:505; Thompson 1975:10; Kimball 1978:587; Freeman 1978:147; Ralling 1978; and Ruse 1979:164. Most of these authors, regardless of their dating of Darwin's conversion, argue that the finches provided Darwin with a decisive model for his general theory of evolution.

no evidence was more important to his [evolutionary] thinking," writes one such spokesman for the legend, "than the example of his finches" (Kimball 1978:587). In the most extreme form of the myth, Darwin is said to have collected species and observed behavioral traits, such as the remarkable tool-using habit of the woodpecker finch, that were not even known in his own lifetime.[55]

As it turns out, Darwin made absolutely no effort while in the Galapagos to separate his finches by island; and what locality information he later published, he reconstructed after his return to England, using other shipmates' carefully labeled collections. As for Darwin's supposed insight into evolution by adaptive radiation while he was still in the Galapagos, the more the various species of finch exhibited this remarkable phenomenon, the more Darwin mistook them at the time for the forms they were mimicking. Even after his return to England, when John Gould had clarified the affinities of this unusual avian group, Darwin was slow to understand how the Galapagos finches had evolved. In particular, he possessed only a limited and largely erroneous conception of both the feeding habits and the geographical distribution of these birds – information that was vital to a proper explanation of their evolution. Lastly, far from being crucial to his evolutionary argument, as the legend would have us believe, the finches were not even mentioned by Darwin in the *Origin of Species*.[56]

In spite of the legend's manifest contradictions with historical fact, it successfully holds sway today in the major textbooks of biology and ornithology, and is frequently encountered as well in the historical literature on Darwin. It has become, in fact, one of the most widely circulated legends in the history of the life sciences, ranking with the

55. See, for example, Peterson 1963:12; Taylor and Weber 1968:877; Moorehead 1969:202; Kimball 1975:434-435, 1978:587; and Thompson 1975:10-11. Even Darwin scholars have occasionally implied that Darwin knew of certain evolutionary evidence, such as the correlation between beaks and the diverse feeding habits of the Galapagos finches, that dates from this century. See de Beer 1963:83; Huxley and Kettlewell 1965:44; and Gruber 1974:160. Similarly, Ruse (1979:164-165) implies that Darwin had a qualitative understanding of the relationship between isolation and endemism among Darwin's finches, but this was first documented by Lack (1947).

56. Because it is so widely held that Darwin's finches led Darwin to develop the theories published in the *Origin of Species*, it has naturally been assumed by some authors that the finches were given a prominent place in that work. See, for example, Lack 1945:4; and Gillsäter 1968:85.

famous stories of Newton and the apple and of Galileo's experiments at the Leaning Tower of Pisa, as a classic textbook account of the origins of modern science.

To appreciate the growth of this pervasive legend, one must understand the tradition of ornithological research that the Galapagos Islands inspired in the post-*Origin* period. In his 1876 monograph on the Galapagos avifauna, Osbert Salvin was already calling that archipelago "classic ground" in the history of biology. It was here, he asserted, that Charles Darwin had made a series of insights and deductions, "the importance of which in their bearing upon the study of natural science has never been equalled" (1876:461). This proud and reverent attitude was echoed by most subsequent ornithologists working on the avifauna of the Galapagos, and Salvin's words were frequently quoted by fellow monographers to bolster their feeling of being on "classic" ground.[57]

Meanwhile, scientific expeditions continued to visit the Galapagos at increasingly regular intervals. Habel's visit in 1868 was followed by eight more expeditions during the remainder of the century, an average of one every four years. More important, with the triumph of Darwin's evolutionary views there had ensued a veritable revolution in collecting techniques. Whereas Darwin, in accordance with prevailing typological collecting procedures, had brought home only 31 finches and 64 birds altogether from this archipelago, Habel collected 460 specimens in 1868, Georg Baur about 1,100 specimens in 1891, Charles Harris 3,075 specimens in 1897, and the California Academy of Sciences an astonishing 8,691 specimens in 1905-1906. Even before this last expedition, Walter Rothschild and Ernst Hartert could proclaim that more ornithological specimens had been collected from the Galapagos than had "ever been brought together from any area of similarly small dimensions" (1899:136). Darwin's finches, in turn, had become perhaps the best known avian group in the world.

With this spectacular growth in the number of collected specimens, there eventually came a similarly impressive advance in the biological understanding of Darwin's finches. It is now recognized that Darwin's original thirteen species constitute only nine present-day species. (John Gould, having insufficient material, split his "species" too finely.) Another four species collected after Darwin's visit have been recognized,

57. See, for example, Ridgway 1890:102n, 1897:459; and Rothschild and Hartert 1899:136.

bringing the present total, coincidentally, back to thirteen.[58] But it was only after half a century of debate about the status of numerous island subspecies, many of which were elevated to the rank of full species by their describers, that the present number of species was finally agreed upon.[59] Among these thirteen species, Lack (1969:254) has recognized thirty-five subspecies; and it is these subspecies, rather than the various species, as Darwin had claimed, that represent one another within the Galapagos group.[60]

This detailed understanding of geographic variation among the various subspecies of Darwin's finches has in turn resolved a long-standing debate over the evolutionary origins of the whole group. As late as the 1930s it was still believed by many ornithologists that Darwin's finches had arisen by some means other than geographic isolation. Percy Lowe (1936) insisted, for example, that the finches constituted "hybrid swarms" of just a few originally unhybridized species. Even Bernhard Rensch (1933), a champion of the theory of geographic speciation, was much puzzled as to how the Geospizinae might have evolved by this means. At this time only Erwin Stresemann (1936) defended the theory of geographic speciation in connection with Darwin's finches.

58. *Camarhyncus pallidus*, the woodpecker finch, was first collected by Habel in 1868. *Geospiza difficilis* (now *G. nebulosa difficilis*), the sharp-beaked ground finch, was also first described from Habel's collection, although FitzRoy's specimen of *G. nebulosa* and one of Darwin's specimens are apparently earlier examples of this species (see Lack 1947:23; and Sulloway 1982b). *G. conirostris*, the large cactus finch, and *C. pauper*, the medium tree finch, were first collected in 1888 by the *Albatross* expedition. The last of the Galapagos finches – *C. heliobates*, the mangrove finch – was collected in 1899 by Heller and Snodgrass. The sole Cocos Island member of the Geospizinae (*Pinaroloxias inornata*) was collected by Richard Hinds in 1840 and was described by Gould (1843).

59. Sixty-seven different specific and subspecific names were at one time applied to the Geospizinae. Among the various authorities, Rothschild and Hartert (1899) recognized twenty-one species of Darwin's finches, Snodgrass and Heller (1904) twenty species, Swarth (1931) twenty-eight species, and Lowe (1936) thirty-seven species. It is to Lack (1945, 1947) that we owe the present reduction to thirteen species.

60. Representation is very infrequent at the species level among the Galapagos finches, since most of the "representatives" long ago spread to other islands. At least eight islands have 9-11 species each of Darwin's finches, and the average number of species for the sixteen main islands is 7.5 (Lack 1969:254). Only 2 of the 13 species (*Geospiza scandens* and *G. conirostris*) may be said to represent one another on different islands of the Galapagos. This instance was unknown to Darwin, because *G. conirostris* inhabits islands he did not visit, and was not collected until 1888.

It was the subsequent researches of David Lack (1940, 1945, 1947) that put an end to these debates and finally turned Darwin's finches into a rigorous and paradigmatic demonstration of speciation through geographic isolation. Among other findings, Lack showed that the percentage of endemic subspecies on each island of the Galapagos is directly proportional to the degree of geographic isolation from the center of the archipelago (Fig. 7). This is why Cocos Island, which is isolated both from the Galapagos and from the mainland, has the highest level of endemism (100 percent) as well as only one species of finch. Isolation promotes endemism; but extreme isolation, by

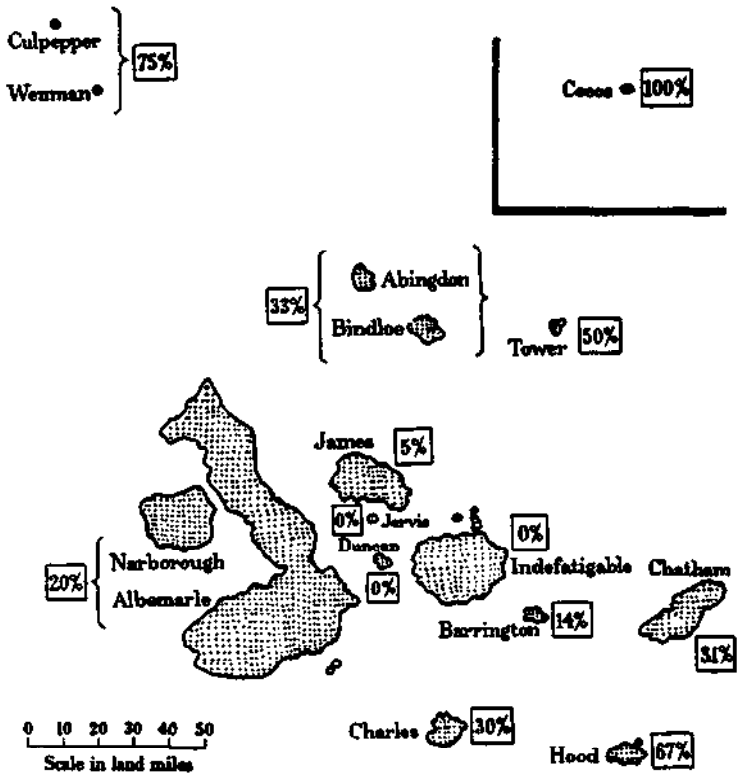

Fig. 7. Isolation and endemism among Darwin's finches. The percentages refer to the proportion of endemic species and subspecies on each island. (From Lack 1947:121.) I have slightly altered the percentages for Charles and Chatham islands to reflect the distributions of *Geospiza magnirostris magnirostris* and *G. nebulosa nebulosa*, as set forth by me elsewhere (1982b).

preventing recolonization, excludes the possibility of speciation and adaptive radiation. The Galapagos Archipelago, unlike Cocos Island, has provided just the right conditions for this radiation process.

Although most species of Darwin's finches have spread throughout the archipelago, thus obscuring the role that isolation has played in their evolutionary origins, there is one species that has apparently just commenced this speciation process. The large tree finch, *Camarhynchus psittacula*, exhibits four well-defined forms in the Galapagos Archipelago (Fig. 8). Because two of these forms have coexisted in the past on

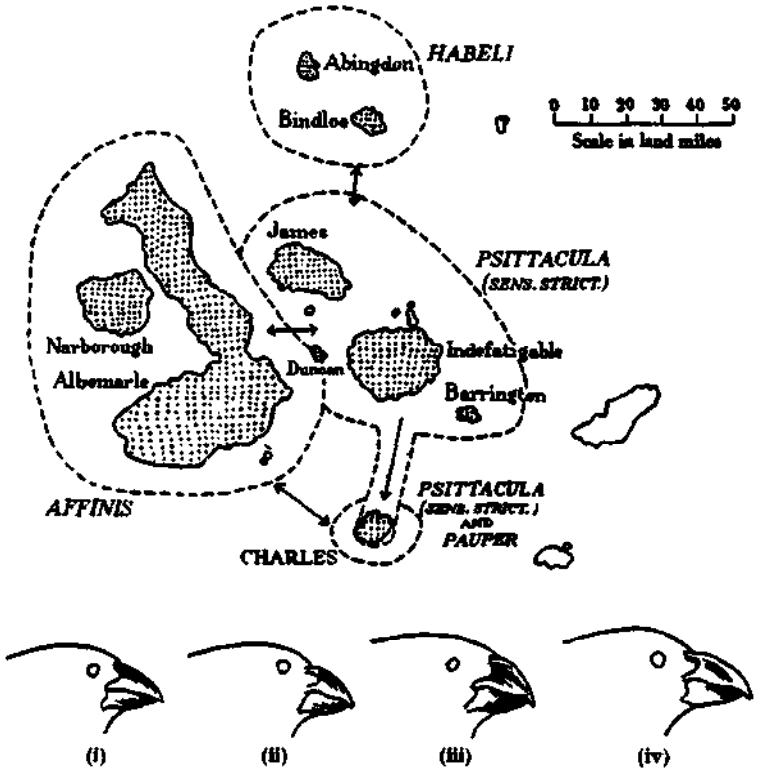

Fig. 8. The forms of *Camarhynchus psittacula* and *C. pauper*: (*i*) *pauper*, the earliest form, on Charles Island; (*ii*) *affinis*, the form that has colonized the western islands; (*iii*) *psittacula* (*sensu stricto*), which occupies the center of the archipelago and has recolonized Charles Island to the south; and (*iv*) *habeli*, closely related to *psittacula* (*sensu stricto*) and occupying the northern islands of Abingdon and Bindloe. (From Lack 1947:127.)

Charles Island, and do not appear to have interbred, they are now classified as separate species (*C. psittacula* and *C. pauper*). With its small finchlike bill, *C. pauper* appears to be the earliest and most primitive form, which must have evolved on Charles Island. From there it evidently spread to the northwest and evolved into the closely related form *affinis*. Another form, *psittacula* (*sensu stricto*), has replaced it in the center of the archipelago. Still another form, *habeli*, is found on Abingdon and Bindloe islands to the north. Had not *C. psittacula* (*sensu stricto*) recolonized Charles Island to the south and remained separate, the four forms would be classified by most ornithologists as races of one species. *C. psittacula* and *C. pauper* therefore represent the earliest stages in the origins of a new species of Darwin's finch. *C. pauper* is, in fact, the only species of the Galapagos finches to be confined to one island (Lack 1947:126-128).

Perhaps the most remarkable discovery about Darwin's finches was first intimated by David Lack. Reversing his own previous opinion (1945) and rejecting the similar views of most earlier ornithologists, Lack argued that the differences in the beaks of the various finches were highly adaptive with regard to feeding. Previously, ornithologists, following Robert Snodgrass (1902:380-381), had maintained that beak size was not necessarily adaptive and that the tendency for certain of the larger species to feed on larger seeds was merely an incidental result of differences in the size of the beaks. The discovery that the different finch species often recognize one another by the size and shape of their bills reinforced this erroneous view that feeding habits were not a primary consideration in bill form.

Impressed by Gregory Gause's (1934:19-20) contention that no two species with similar ecologies can coexist in the same territory, Lack finally acceded to the conclusion that differences in the beaks must help to reduce competition for food resources. Reinterpreting the same data presented in his earlier publications, Lack was able to substantiate this hypothesis by pointing to the phenomenon of character displacement in Darwin's finches (1947:81-90). On islands where the large, medium, and small ground finches (*Geospiza magnirostris, G. fortis*, and *G. fuliginosa*) are found, bill measurements show distinct and confined ranges for the three species. But where one or more of these species is rare or absent, bill size becomes more variable and is always extended in the direction of the missing species. The same phenomenon is found in other species of Darwin's finches and is most dramatically illustrated on the smaller, outlying islands, where only three or four species occupy the niches shared by eight or ten species in the center

of the archipelago. Thus the shape as well as the average size of the bill in most species of Darwin's finches is related to the nature of their competitors on each island, with natural selection tending to minimize competition by inducing character displacement and hence adaptive radiation.[61]

These findings on geographic isolation, speciation, and character displacement among the Geospizinae were first brought together in David Lack's celebrated book *Darwin's Finches* (1947). Altogether this work supplies abundant evidence for considering these birds, more than most other avian groups, as a classic paradigm of evolution and adaptive radiation in action. But Lack's *Darwin's Finches* was not just a milestone in the progress of Darwinism. It was also a crucial step in the evolution of the legend about Darwin and his finches. In fact, with the publication of Lack's book in 1947 the legend became fully established.

Three aspects of Lack's book, in particular, helped to crystallize the legend by blurring the crucial distinction between what was "Darwin's" in connection with his famous finches and what was not. First, as a sweeping testimonial to the validity of Darwinism, Lack's researches were closely associated with the triumph of the evolutionary synthesis in the late 1930s and early 1940s. In line with other biological research in this period, Lack showed that the evolutionary dynamics of the Galapagos finches agreed with a strictly Darwinian model of evolution incorporating genetic variation, geographic isolation, and natural selection as the principal mechanisms of evolutionary change. In this sense, then, *Darwin's Finches* was a return to Darwin's own version of evolutionary theory after nearly a century of disputes among rival doctrines. Reflecting this triumph of Darwinian theory was the whole design of Lack's book, which included relevant quotations from Darwin's *Journal of Researches* and his *Origin of Species* at the heads of each chapter. It is hardly surprising, then, that many readers of *Darwin's Finches* tended to synonymize Darwin's understanding of his finches with the neo-Darwinian understanding of them.

The second aspect of Lack's book that spurred the growth of the legend was Lack's use of the term "Darwin's finches." Although Lack was not the first person to use this term, it was he who succeeded in popularizing it.[62] In one sense the term is felicitous, because not all the

61. More recently, Robert Bowman (1961) has shown by detailed analysis of stomach contents that the various species of Darwin's finches indeed subsist upon different diets related to the size and shape of their beaks.

62. Apparently the first person to use the term "Darwin's finches" was Lowe (1936:310).

Geospizinae are confined to the Galapagos Islands, and thus the name "Galapagos finches" is inappropriate for the whole group. This was, in fact, the chief reason for Lack's use of the expression "Darwin's finches." But as the term became more popularly known through Lack's book, people tended to assume that these birds had been so named because, as one biologist put it, "they helped to persuade Darwin of the truth of evolution" and were crucial as well to his later theories.[63] Through this act of eponomy, Darwin was increasingly given credit after 1947 for finches he never saw and for observations and insights about them he never made. The coincidence that Darwin's Galapagos finches were described by John Gould as thirteen species, the same number that Lack himself recognized in the archipelago, greatly contributed to this additional source of the legend.

Finally, Lack encouraged the growth of the legend in a third way when he mistakenly insisted that Darwin had indeed separated his ornithological collections by island after leaving the second of the four islands he visited. This conclusion provided convincing evidence that Darwin, at the time, had suspected the evolutionary implications of his collections as a whole and that he had taken steps to correct his earlier oversights in this regard.[64] It mattered little that David Lack had also debunked another aspect of the legend when, confronted by the historical evidence, he duly acknowledged the apparently slow growth of Darwin's thinking about the finches. Readers and reviewers of Lack's book, steeped in a Darwinian conception of the finches, naturally assumed that Darwin too had fully understood their evolutionary import and that he had merely chosen to bide his time before making

63. See, for example, Leigh (1971:136), quoted in the text; Thornton (1971: 162); and Moody, who writes: "No group of Galápagos animals is of more interest to students of evolution than are the birds, partly because of the role played by these birds in influencing the thinking of Darwin. He was particularly impressed by the varied adaptations exhibited by the unique finches of the archipelago. In commemoration of this fact, Dr. David Lack, has had the happy inspiration to term them 'Darwin's finches'" (1953:268).

64. Lack's erroneous conclusion that Darwin began to separate his ornithological collections by island while he was still in the Galapagos has been endorsed by Himmelfarb (1959:115), Eiseley (1961:171), Barlow (1967:12), Moorehead (1969:202), and Gruber (1974:130). Lack (1963) later reaffirmed this view in a brief article on Nicholas Lawson, the vice-governor on Charles Island who first told Darwin about the differences in the tortoises. Kottler (1978:282-283) has argued that Darwin labeled his ornithological collections by island from the very beginning, but this view clearly cannot be maintained in the light of the facts presented here.

his revolutionary views public. "One cannot help thinking," V. C. Wynne-Edwards commented in a typical review of Lack's classic treatise, "what a delight his book would have brought to Charles Darwin, who was so deeply stimulated by his own observations of the Galapagos finches during the voyage of the 'Beagle' " (1947:687). "This miniature example of evolution," Lois and Lewis Darling have similarly written of the Galapagos finches, "was as impressive when young Charles Darwin visited the Galápagos in 1835 as it is today" (1963:34). Even Lack himself seems to have become increasingly caught up by the legend he helped to create when he insisted that Darwin's finches had "provided one of the chief stimuli for their discoverer's theory of evolution" and had thereby "change[d] the course of human history."[65]

In the years since the publication of *Darwin's Finches*, the tremendous popular success of Lack's book has helped to make these birds famous far out of proportion to their actual role in furthering evolutionary theory. Certain other avian groups, such as the Hawaiian honeycreepers, as well as the insects of the Hawaiian Islands, offer even more dramatic examples of explosive evolutionary radiation. But these other cases, although well known to evolutionary biologists, have not permeated the popular biological literature as have Darwin's finches. These birds have become, in fact, the standard textbook example of the historical origins and factual basis of Darwin's theory of evolution. It is the textbooks, moreover, that have given fullest expression to the legend of Darwin's finches. By telescoping history around one dramatic moment of insight in the Galapagos Archipelago, the textbooks have developed the legend into a compelling and appropriately empirical account of the origins of modern evolutionary biology.[66] Through the legend, Darwin is continually celebrated as a scientific hero who single-handedly solved the biological riddle of the Sphinx when he recognized the different Galapagos finches for an extraordinary microcosmic example of evolution in action. In many ways it is perhaps asking too much to deny Darwin a share in the scientific triumph that his legendary finches have come to represent for Darwinism. Legends are, after all, to celebrate heroes; and there is something definitely heroic – more so than even the legend has captured – about Darwin's scientific triumph based on only a fraction of the evidence we know today about the Galapagos Archipelago and its famous finches.

65. See Lack 1964:178, 1953:67.

66. The role of textbooks in rewriting history to accord with a linear and strictly empiricist conception of science has been discussed by Kuhn (1970:137-143, 167) and Brush (1974). See also Sulloway 1979:420-422, 503-503.

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