Contributions

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History of Ecological Sciences, Part 37: Charles Darwin's Voyage on the *Beagle*

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In 1876, when Charles Robert Darwin (1809–1882) wrote his *Autobiography*, he commented (1959:76): "The voyage of the *Beagle* has been by far the most important event of my life and has determined my whole career…" Before the voyage, Darwin was a well-educated, well-trained naturalist, though he became so rather haphazardly (Darwin 1959:22–71, Egerton 1976, Hodge 1985:210–213, Porter 1985:973–979, Sloan 1985:73–87, Desmond and Moore 1991:5–97, Browne 1995:3–161, 2004, Bohlin 2000, Desmond et al. 2004, Pauly 2004:xvii–xviii, Grant and Estes 2009:25–41, Sponsel 2009:79–85). English schools during his youth took no more notice of science than had the German schools of Humboldt's youth. Like Humboldt, his early knowledge of natural history came from self-education, assisted in Darwin's case, however, by the example and encouragement of his older brother, Erasmus. At age 10, Charles vacationed for three weeks on the coast of Wales, where (Darwin 1959:45)

> *...I was very much interested and surprised at seeing a large black and scarlet Hemipterous insect, many moths (Zygaena) and a Cicindela, which are not found in Shropshire. I almost made up my mind to begin collecting all the insects which I could find dead, for on consulting my sister, I concluded that it was not right to kill insects for the sake of making a collection.*

Six years later, in October 1825, he went to the University of Edinburgh to study medicine. He stayed only two years and learned as much or more outside the classroom as he did in it. He associated with zoologist Robert Grant, who encouraged his studies on marine life and told him about Lamarck's theory of transformism, and probably discussed Erasmus Darwin's also (Desmond and Moore 1991:40). Darwin made some original discoveries about several marine invertebrates from the Firth of Forth, which he reported to the Plinian Society (Allan 1977:35, Darwin 1977, II:285–291, Desmond and Moore 1991:37–39, Browne 1995:82–87, Stott 2003:35–36). Although Darwin later remembered

Professor Robert Jameson's geology lectures as boring (Darwin 1959:52), he probably heard or read Jameson's comprehensive "On the Growth of Coral Islands" (1827 [Sponsel 2009:83]). After two years, Darwin decided against a medical career and left Edinburgh. His four years at Cambridge University (1828–1831) were meant to prepare him to become a Church of England clergyman, but his most important education there came outside clerical preparatory classes (van Wyhe 2009), from friendship with Professor of Botany John Stevens Henslow (1796–1861) (Barlow 1967, Mathew 1972, Walters and Stow 2001:78–104, Walters 2004*a*, *b*, Kohn et al. 2005) and his geological field trip with Prof. Adam Sedgwick (1785–1873) in the summer of 1831 (Barrett 1974, Dolan 2004, Herbert 2005:36–46, Secord 2005). "But no pursuit at Cambridge was followed with nearly so much eagerness or gave me so much pleasure as collecting beetles" (1959:62).

Darwin had been inspired by reading Humboldt's *Personal Narrative* of travels in Spanish America to plan his own expedition to Teneriffe, Canary Islands (Darwin 1959:67–68), but it never materialized. Then, in August 1831, Henslow received an appeal to serve as a naturalist on a naval survey ship, *Beagle*, under Captain Robert FitzRoy (1805–1865); Henslow declined and recommended Darwin instead (Darwin 1985–1988, I:127–129). The purpose of the voyage was to map the coastlines of South America and some oceanic islands. During most of the 1800s the best British education in physical sciences was offered to army engineers and naval officers (Ratcliff 2008:26). FitzRoy was an officer who benefited from this training, and he made important contributions to hydrography and meteorology (Mellersh 1968, Basalla 1972, Nichols 2003, Gribbin and Gribbin 2004, McConnell 2004*a*, *b*). His habits of precision and thoroughness set a good example for Darwin. Contrary to the assumption of two historians (Gruber 1969, Burstyn 1975), Darwin went on the voyage as the official naturalist, though his expenses were paid by his father, Dr. Robert Darwin. There was a substantial library aboard the *Beagle*, including multi-volume reference works on zoology (Stoddart 1962:118–120, Burkhardt and Smith 1985*a*). As a parting gift, Henslow gave Darwin a copy of Humboldt's *Personal Narrative*.

Like all great scientists, Darwin was a hard worker, and during the almost five years voyage (27 December 1831–1832 to October 1836), he diligently observed, collected specimens, took notes, and preserved superb evidence of his work. Virtually all his evidence still exists, mostly published. All his works that he himself published are now accessible at ‹Darwin-online.org.uk›. His surviving correspondence from the period of the voyage consists of 152 letters, about half of which he wrote (Darwin 1985–1988, I:192–504). He drew upon his records, collections, and his memories to write one of the most valuable science travel books ever published, *Journal of Researches into the Geology and Natural History of the Various Countries Visited by H. M. S. Beagle* (1839). Three modern books discuss his voyage (Barlow 1945, Moorehead 1969, Keynes 2003), and numerous briefer accounts add to our understanding and appreciation of what he experienced and achieved (including von Hagen 1945:169–229, Life Editors and Barnett 1960, Hopkins 1969, Armstrong 1991, 1992, 2004, Rice 1999:230–259, McCalman 2009:15–81). Darwin made a good collection of fishes, though he said little about them in his *Journal of Researches* (Pauly 2004:213–240). Although he would have four entomologists describe his new species of insects, he did have interesting discussions of insects in his *Journal of Researches* (Riley 1882:71–73, Remington and Remington 1961).

Duncan Porter points out (1980:515) that Darwin's geological notes from the voyage (1383 pages) are almost four times longer than his biological notes (368 pages), and Darwin's geological observations have now received the attention they deserve (Herbert 2005). Since Darwin had learned little geology

before participating in geological field work in the summer of 1831, a few months before the voyage began, why did he so quickly become a geologist? He became deeply influenced by Charles Lyell's *Principles of Geology* (three volumes, 1830–1833), volume I of which was given to him by FitzRoy, while Henslow sent him volume II (1832) during the voyage (Darwin 1959:77, 101, Barlow 1967:10–11, Gruber 1985:15–18, Herbert 2005:63–70). A major attraction was that Lyell defended the uniformitarian theory that Darwin found more creditable than Georges Cuvier's catastrophist theory. Natural histories of plants and animals contained very limited theories—in contrast to Lyell's theory of geology, which seemed to encompass all geological phenomena (1959:77). Geology and natural history merged in Darwin's studies of fossils and of coral islands. The first of three volumes he published on the geology of the voyage (Freeman 1965:41) was on the structure of coral reefs.

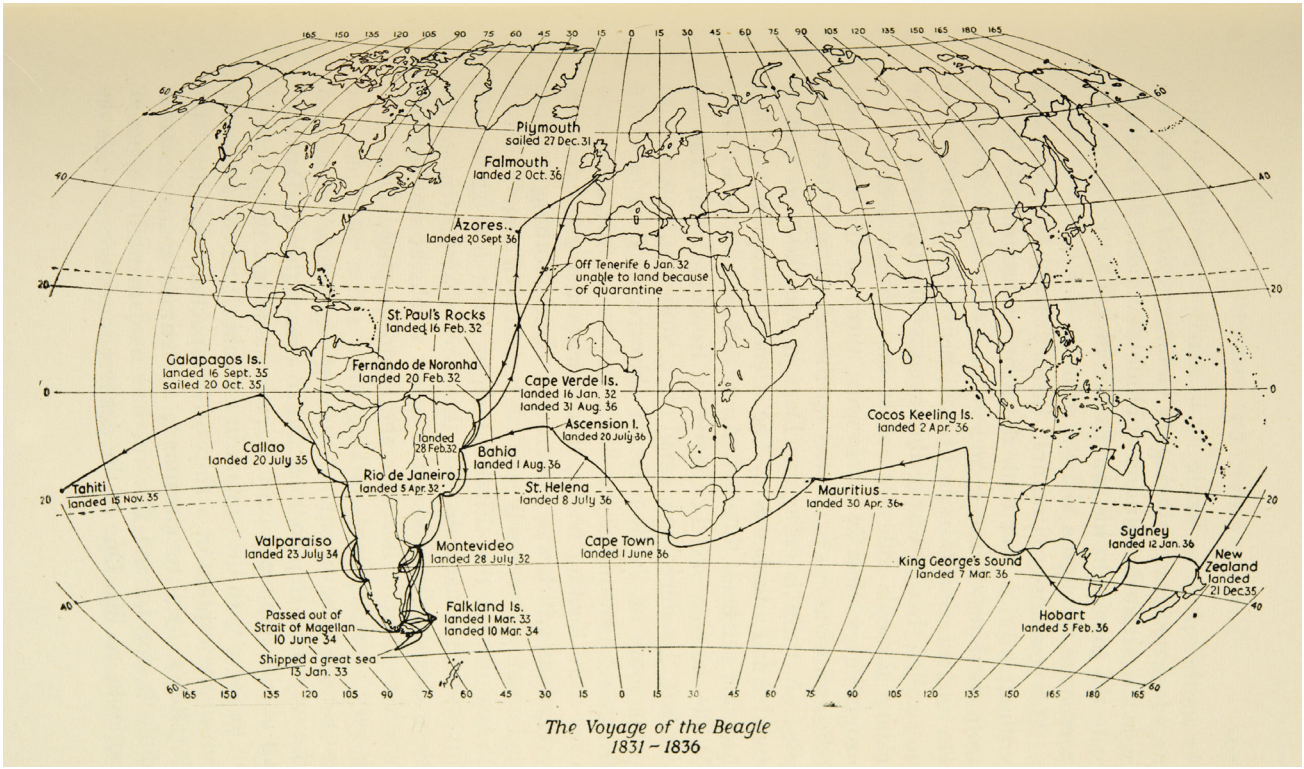


Fig. 1. The route of H. M. S. *Beagle* in its voyage around the world. De Beer 1967:39.

The *Beagle*'s first landing was at St. Jago in the Cape Verde Islands on 18 January 1832 (Armstrong 2004:38–45, Chancellor and van Wyhe 2009:3–6). Darwin wanted to see the kind of tropical vegetation that Humboldt had described at Teneriffe in the Canary Islands and was at first disappointed because the Cape Verde Islands were rather arid. However, he eventually found a deep valley that retained moisture and provided the emotional experience he sought (Darwin 1988:23). The commonest bird was a kingfisher (*Dacelo jagoensis*) that sat on castor-oil plants and darted out to catch grasshoppers and lizards (Darwin 1839:2). He took extensive notes on marine invertebrates (Darwin 2000:9–21), but only the notes on an octopus appeared in his *Journal of Researches* (1839:6–7). He watched it change color, squirt ink, and when he bent down to look more closely, it squirted water at him.

They departed on 8 February, and their second stop, 16–19 February 1832, was at the uninhabited (by

people) St. Paul's Rocks, near the equator (Edwards 1985, Campbell 1997:42–48, Armstrong 2004:46–50, Chancellor and van Wyhe 2009:6). Darwin (1839:8) gave the location as 0°58′ North latitude and 29°5″ West longitude, and 540 miles from South America.

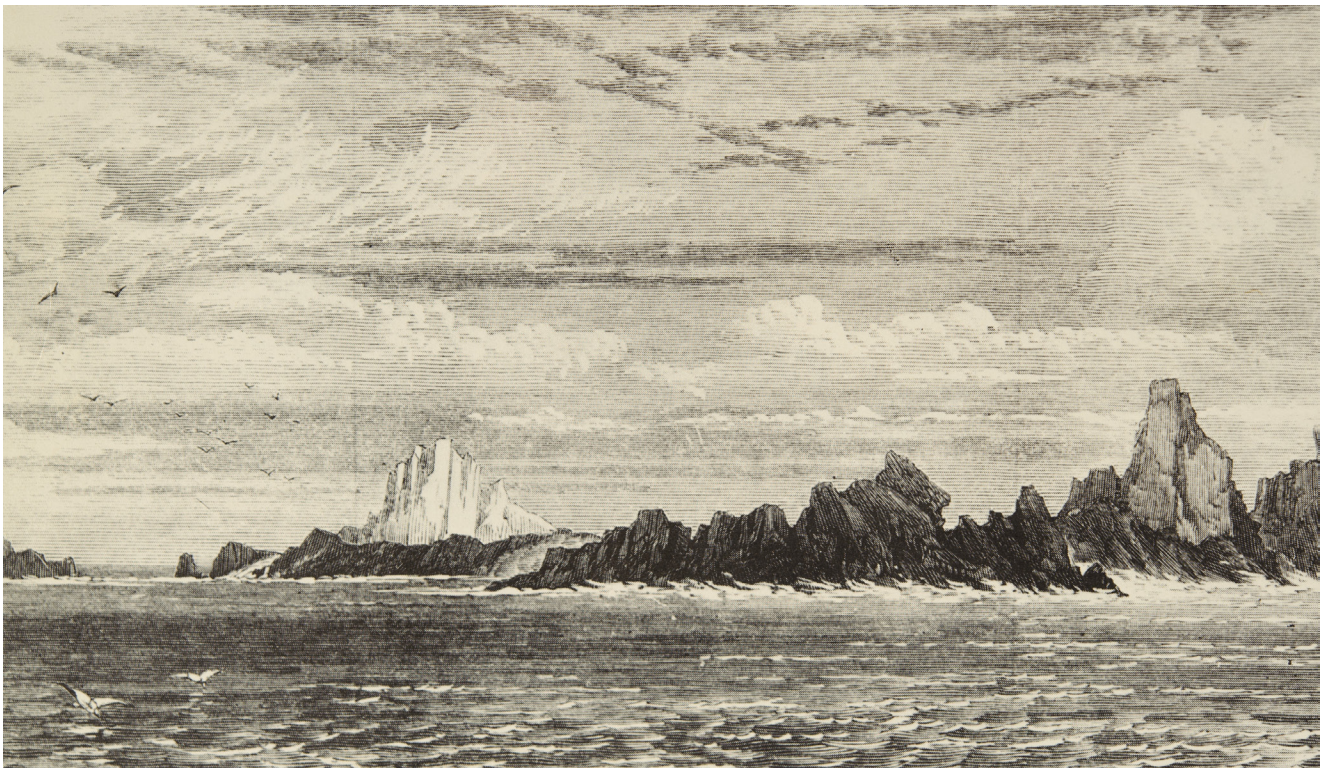


Fig. 2. St. Paul's Rocks, from the east. Illustrated London News.

From a distance, the rocks appeared white, due partly to a glossy white substance in some rocks and partly to accumulated bird guano. In 1813 H.M.S. *Rhin* visited the rocks and Lt. George Chrichton drew a map and profile chart, but in 1832 FitzRoy did both again (Edwards 1985: Figs. 1a and 2). St. Paul's highest point is only about 60 feet (18.3 m) above sea level, and the islets are only 3/4 of a mile (2 km) in diameter.

The conspicuous inhabitants were sea birds—boobies (a gannet) and noddy terns. Darwin did not mention their scientific names. Now there are two species of noddy terns nesting there, the White-capped Noddy (*Anous minutus*) and the Brown Noddy (*A. stolidus*), the former nesting at 3–6 m above sea level, and the latter at lower elevations on bare rocks (Edwards et al. 1981). He reported that the booby nested on bare rocks and the noddy made a simple nest of seaweed. The seaweed nest fits the description of those made by White-capped Noddies. Perhaps that was the only noddy species that had colonized the rocks when he was there. Besides the birds, there were only arthropods and crustaceans, no plants. The paucity of species enabled Darwin to describe the earliest known food web (1839:10).

> *By the side of many of these nests a small flying-fish was placed, which I suppose, had been brought by the male bird for its partner…quickly a large and active crab (*Graspus*), which inhabits*

> *the crevices of the rock, stole the fish from the side of the nest, as soon as we had disturbed the birds. The following list completes, I believe, the terrestrial fauna: a species of Feronia and an acarus, which must have come here as parasites on the birds; a small brown moth, belonging to a genus that feeds on feathers; a staphylinus (*Quedius*) and a wood louse from beneath the dung; and lastly, numerous spiders, which I suppose prey on these small attendants on, and scavengers of the waterfowl.*

After reading this account, Rear-Admiral William Symonds told Darwin that he had seen at St. Paul's crabs drag young birds from nests and eat them. Darwin added this information to this account in the second edition of his *Journal* (1845:10).

Because this is the earliest known food web (Egerton 2007:51), Darwin's brief observations now carry a historical significance that they lacked when published, and so more details about the species he observed are desirable. He collected two unknown tick species, now named *Amblyomma hirtum* (Neumann 1906:201–203) and *A. darwini* (Hirst and Hirst 1910:239–240), which are only known from two locations: St. Paul's Rocks and the Galapagos Islands. He was first to collect them in both places. His specimens are now in the Natural History Museum, London (Robinson 1926:156–158, 221–222). He also collected the argasid tick, *Ornithodoros capensis*, and a bird louse, *Actornithophilus* sp. from the brown booby nests and hippoboscid flies from dead brown boobies. No spiders were in his collections, but *Scytodes* sp. now lives there and may be what he saw (Edwards and Lubbock 1983:54–55). Darwin's brown moth, *Erechthias darwini*, was only named in 1983, because no specimen survived in his collections. It resembles the genus Darwin had in mind but is in a different family that cannot digest the keratin of feathers. It eats instead the dried seaweed of the nests (Robinson 1983).

As previously mentioned, (Egerton 2009), Darwin was the second known user of what we now call a plankton net (with Lesueur earlier using a dip net). He drew a crude sketch of his, four feet deep, and first discussed its use on 10 January 1832 in his *Beagle* diary, which he never published (Darwin 1988:21). On 11 January he wrote in his diary (1988:22): "I am quite tired having worked all day at the produce of my net—The number of animals that the net collects is very great & fully explains the manner so many animals of a large size live so far from land." His *Zoology Notes* (2000:3–7) contain notes and drawings on the animals collected in his net on these two days. In *Journal of Researches* (1839:14–18), he first discussed phytoplankton observations after his account of St. Paul's Rocks, on 18 March; the account consists mostly of superficial anatomical descriptions. Next, he discussed numerous small crustaceans which sealers called whale-food, but he failed to make explicit here a food chain that was implicit--from minute organisms to crustaceans to whales—and only much later in his *Journal of Researches* (1839:189) did he even mention using his net.

Darwin had been pleased to find a small sample of tropical rain forest on St. Jago in the Cape Verde Islands, but when he reached the Brazilian rain forest outside Bahia (Salvador), his emotional experience matched the expectations that he had gotten from reading Humboldt. On 29 March, he wrote in his Diary (1988:42)

> *The day has passed delightfully: delight is however a weak term for such transports of pleasure: I have been wandering by myself in a Brazilian forest: amongst the multitude it is hard to say what set of objects is most striking: the general luxuriance of the vegetation bears*

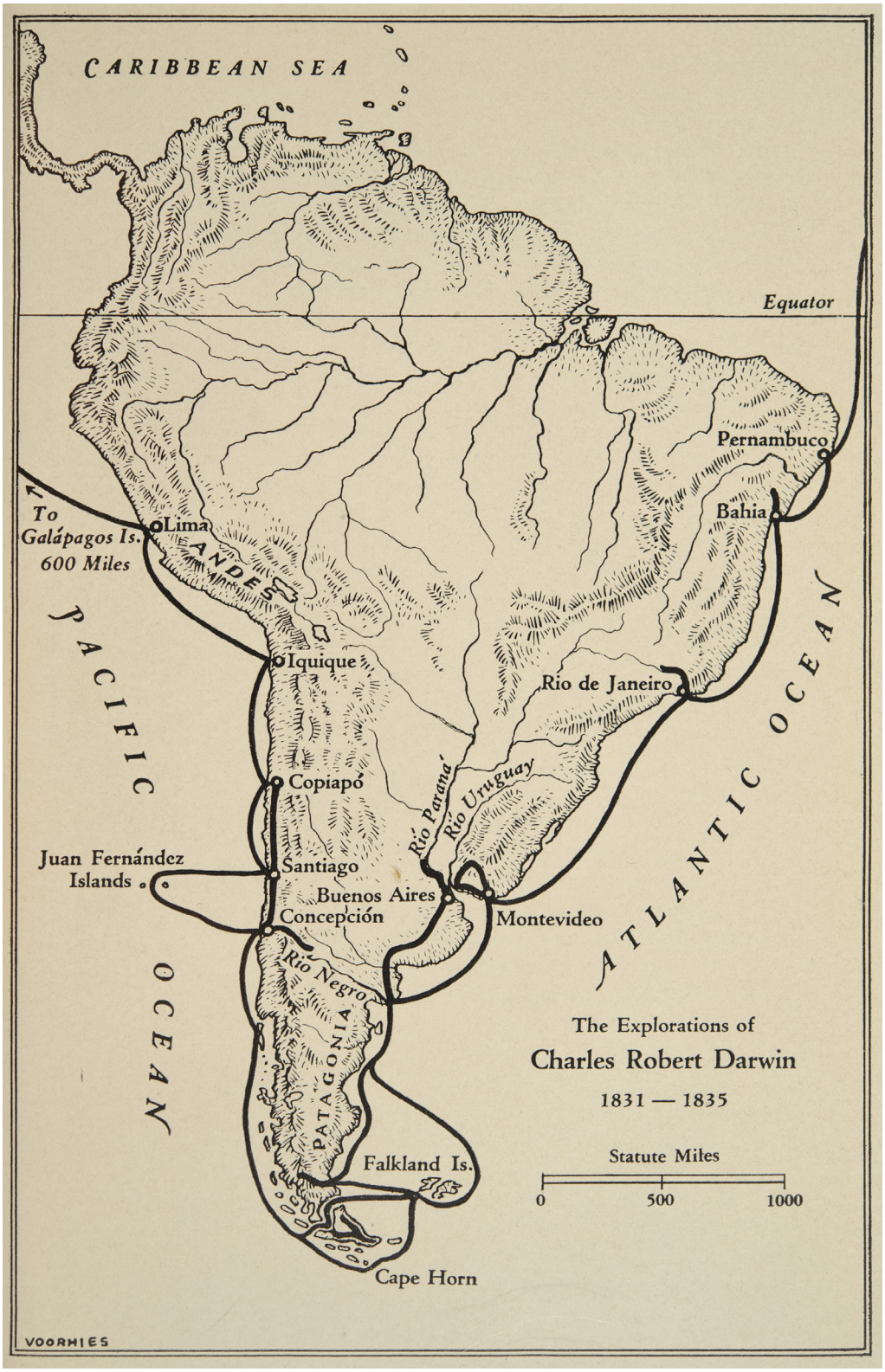


Fig. 3. Darwin's South American travels. Von Hagen 1945:228.

> *the victory, the elegance of the grasses, the novelty of the parasitical plants, the beauty of the flowers.—the glossy green of the foliage, all tend to this end.—A most paradoxical mixture of sound & silence pervades the shady parts of the wood.—the noise from the insects is so loud that in the evening it can be heard even in a vessel anchored several hundred yards from the shore.*

The next day, he gushed: "I can only add raptures to the former raptures." However, rapture does not necessarily lead to discernment. A commentator on his bird watching in South America points out (Haupt 2006:54–56) that he was on the continent having the greatest diversity of bird species and in the forest that contains most of that diversity, yet he was unable to see much more than the vegetation and insects. This was early into the voyage, and he lacked the binoculars which every birder now takes to any rain forest.

There are so many ecologically relevant observations in *Journal of Researches* that only a selection can be discussed here. Darwin was very interested in the contrast between the temperate environment from which he came and the contrasting tropical, desert, mountain, and stormy (at Tierra del Fuego) environments he encountered on the voyage. He also noted the impacts of Old World species on South America and the islands visited. For example, he noted that cabbage and lettuce in English gardens were food for multitudes of slugs and caterpillars, but that those pests had not been imported with these crops, which grew undisturbed near Rio de Janeiro (1839:37). Whatever advantages came from introduced cabbage and lettuce, however, were offset by the massive takeover of whole areas by foreign weeds (1839:138)

> *Near the Guardia we find the southern limit of two European plants, now become excessively common. The fennel in great profusion covers the ditch banks in the neighbourhood of Buenos Ayres, Monte Video, and other towns. But the cardoon (*Cynara cardunculus*) has a far wider range: it occurs in these latitudes on both sides of the Cordillera, across the continent. I saw it in unfrequented spots in Chile, Entre Bios, and Banda Oriental. In the latter country alone, very many (probably several hundred) square miles are covered by one mass of these prickly plants, and are impenetrable by man or beast.*

This was "the earliest documented transformation of a landscape by alien plants" (Mack 1989:160).

Darwin was already a knowledgeable entomologist when he sailed on the *Beagle* (Riley 1882:70, Remington and Remington 1961:1–2). From Rio de Janiero he wrote to Henslow on 18 May 1832 (Darwin 1977, I:4)

> *...if what was told me in London is true, viz. that there are no small insects in the collections from the Tropics, I tell entomologists to look out and have their pens ready for describing. I have taken as minute (if not more so) as in England, Hydropori, Hygroti, Hydrobii, Pselaphi, Staphglini, Cuscaliones, Bimbidia, &c. &c. It is exceedingly interesting to observe the difference of genera and species from those which I know…as a specimen how little the insects are known, Noterus, according to* Dic[tionnaire] Class[ique d'histoire naturelle, 17 volumes] *consists solely of three European species. I, in one haul of my net, took five distinct species…*

Many of Darwin's biological observations recorded at Rio were not entirely new to science, though new to him and seen in newly discovered species, and so not previously published (Chancellor and

van Wyhe 2009:7–49). He had been preceded in biological exploration of South America by Azara (see below), Humboldt (Egerton 2009), and Alcide Charles Victor Dessalines d'Orbigny (1802–1857); d'Orbigny collected zoological specimens for the Muséum d'Histoire Naturelle in Paris in 1826–1834 and published *Voyage dans l'Amerique meridionale* (10 volumes, 1834–1847; for English translated extracts, see von Hagen 1948:182–200), a notable achievement, which did not attract as wide an audience as did Darwin's *Journal of Researches* (Goodman 1972:301–303, Tobien 1974, Boulinier 1995, Brygoo 1995, Legre-Zaidline 2002, Moreau and Dory 2005:11–17, 81–89), though his contributions are now well appreciated (Taquet 2002). Near Rio de Janeiro Darwin observed army ants which caused other insects to either flee or be eaten, he watched a wasp paralyze a spider to provide food for its young when they hatched from eggs, and he watched spiders kill and feed on insects (1839:39–42). The insects he collected and his notes about them are now published and his specimens surveyed (Smith 1987). Some of his specimens were described in print by specialists, and Smith (1987:115–123) includes citations to that literature in his bibliography. *The Zoology of the Voyage of H.M.S. Beagle* (Darwin 1839–1843) was limited to vertebrates.

Darwin's remarks about the people he encountered were what one expects in a travel book, but he also followed Humboldt's example of providing figures or estimates of human populations (Egerton 1970). Both travelers frequently commented on environmental conditions in places visited that either favored or inhibited population increase. Henslow had given Darwin the first two volumes of the English translation of Humboldt's *Personal Narrative* to take on the voyage, and the *Beagle* diary that he never published has frequent references to Humboldt (Darwin 1988); some of these references later appeared in his *Journal of Researches* (1839). He reported that Buenos Ayres had 60,000 people, Monte Video 15,000 (1839:140), Coquimbo 6000–8000 (1839:421), Charles Island in the Galapagos 200–300 (1839:456), Sydney 23,000 (1839:516), Port Louis 20,000 (1839:570), Cape Town itself 15,000, and the whole colony 200,000 (1839:575), and St. Helena Island 5000 people and 746 plant species, of which only 52 were native (1839:580). In Brazil Darwin remarked that the country would support a vast population when the land became more extensively cultivated (1839:27). When Darwin expressed shock at the massacre of Indians near Bahia Blanca, the response was, "Why, what can be done, they breed so!" (1839:120).

Darwin focused on mammals and birds not in the rain forest where they were abundant though elusive, but where they were more visible on "the grassy plains around Maldonado," east of Montevideo at the mouth of Rio de la Plata. His Diary (Darwin 1988:152–162, Chancellor and van Wyhe 2009:50–58) shows he was there from 28 April to 23 July 1833. The *Beagle* had visited Montevideo from 26 July to 19 August 1832, and in his *Journal of Researches* (1839:45) Darwin mentions his arrival there on 26 July, then warns: "To prevent useless repetitions, I will extract those parts of my journal which refer to the same districts, without always attending to the order in which we visited them." Then follow his observations on mammals and birds mostly, if not entirely, from 1833. During that stay in Maldonado he hired the *Beagle*'s cabin boy, Syms Covington, to be his servant to collect biological specimens and also to be his secretary. The number of specimens then increased.

Darwin began this part of his *Journal of Researches* (1839:51–60) by describing a partridge (*Tinamus rufescens*) that was "very silly" in allowing men to ride up and lazo them. The only large mammal on this plain was a deer, *Cervus campestris*, which was abundant as far south as Rio Negro (latitude 41°). It could be approached close enough to kill by crawling, but it fled from men on horseback; it was not

frightened by gunfire. Rodentia was very numerous in species. *Hydrochaerus capybara* was common. One weighed 98 pounds, was 3 feet two inches long, with a girth of 3 feet 8 inches. They lived on islands at the mouth of Rio de la Plata, and more abundantly along borders of lakes and rivers, and they ate aquatic plants. They were tame because jaguars had been eliminated and gauchos did not hunt them. On Rio Parana they were the ordinary prey of jaguars. Tucutuco (*Ctenomys Braziliensis*) was a small rodent with habits of a mole, living in sandy soil with a gentle slope. They were gregarious, nocturnal, and ate plant roots. The name comes from its sound; it was easily tamed.

An earlier Spanish military engineer and amateur naturalist, Félix de Azara (1742–1821), had discovered that cowbirds were parasitic in their reproductive behavior (Friedmann 1964:295, Guerra 1970, Egerton 2009:263), as cuckoos were in Europe. Darwin later misremembered that he had discovered Azara's work only after he had published his *Journal of Researches* (Darwin 1870), probably misled because Azara is not listed in the index. In fact, he three times (1839:60–62) cited Azara's *Voyages dans l'Amerique meridionale* (1809, III:169–170) on brood parasitism. Darwin was quite interested in this behavior in two unrelated species on different continents. They otherwise had very different behavior, cuckoos being solitary and secretive and cowbirds being gregarious and associating with livestock. Azara had observed this behavior in Shiny Cowbirds *Molothrus bonarienses*, and probably Darwin observed the same species in the Maldonado area near Monte Video, though there were two other cowbird species in the area, one of which practices brood parasitism while the other does not (Ortega 1998:11, 67–68, 214).

Darwin devoted an extensive amount of time and notes (Darwin 1963:233–245) to carrion-feeding hawks and vultures, which frequented the extra-tropical parts of South America. He found them interesting, though at times also disgusting. They were easily observed. Many of his notes on them were incorporated into his *Journal of Researches* (1839:63–69). He discussed four species of caracara (*Polyborus*), plus the turkey buzzard, gallinazo, and condor. Besides carrion, carranchas (*P. Braziliensis*) ate eggs and picked scabs from the backs of horses and mules. Azara reported that they also ate worms, shells, slugs, grasshoppers, and frogs. They also pursued gallinazos and forced them to vomit up carrion recently eaten. *P. Braziliensis* was larger than *P. chimango* and lived farther north than the latter. A third species ("allied to d'Orbigny's *P. montana*, but distinct") was seen in only one Patagonian valley, and a fourth species, *P. Novae Zelandiae*, lived on the Falklands and other islands but not on the mainland. The Turkey Vulture (*Vultur aura*) lived in moderately damp country from Cape Horn to North America and was solitary or lived in pairs. Gallinazos (*Cathartes atratus*) lived near fresh water, were abundant in Brazil and La Plata, and never occurred south of latitude 41°. Since condors were uncommon in Patagonia, he discussed them later. Darwin found pampas woodpeckers *Colaptes compestris* living on the pampas devoid of trees (1859:184). When Argentine immigrant naturalist William Henry Hudson (1841–1922), who had grown up near Buenos Aires (Shrubsall 2004), challenged this observation in 1870, claiming these woodpeckers only fly over the pampas from trees on one side to trees on the other, Darwin cited Azara (1802, II:311) in support of his observation (Darwin 1870).

Darwin developed a persistent interest in the distribution of species and in similar species that are geographically adjacent. Two examples were rheas and foxes. He had a number of chances to observe *Rhea americana* on the Patagonian plains in September 1833 (Chancellor and van Wyhe 2009:66–67), and he provides a detailed account of its natural history in *Journal of Researches* (1839:105–109, 1963:268–276). Like ostriches in Africa and emus in Australia, females lay in a communal nest and

males incubate eggs and tend the young. Although generally vegetarians, when bodies of water are drying up, they go there and catch small fish. At Rio Negro in northern Patagonia, he heard of a smaller species, and one day when a rhea was being cooked for dinner he realized that this bird was of the smaller species, and he gathered its head, neck, legs, wings, skin, and feathers and sent them to London, where, after his return, John Gould (1804–1881) named it *Rhea darwinii* (Gould 1837*b*), though d'Orbigny had already named it *Rhea pennata* in 1834 (Simkins 1972, Lambourne 1987:45, Tree 1991:55–56, England 2004, Sauer 2004). Haupt (2006:96–97) observed that Darwin began his observations of Rheas at Bahia Blanca in September, when there were eggs in nests, and so he had missed the breeding season, when he might have noticed that Rheas have a claw on their wings and the males have a penis. A third species, *R. macrorhyncha*, lives in the high Andes (Cutright 1940:171).

The *Beagle* visited East Falkland Island 26 February–April 1833 and in March–April 1834. Darwin found the desolate island of more geological than biological interest (Darwin 1988:144–149, 228–231, Armstrong 1992, 2004:79–106, Chancellor and van Wyhe 2009:91–94). A modern explorer found more interesting wildlife there than Darwin did (Campbell 1997:108–142). Darwin easily observed the foxes, which had no fear of humans (1839:249–250). He agreed with the gauchos that black rabbits in the Falklands were introduced and were the same species as the gray rabbit of the mainland, as they produced piebald offspring when bred together. However, he was equally confident that the Falkland fox (now *Dusicyon australis*), which he collected, was a distinct species because the gauchos and Indians said there was no such fox on the mainland. Later, he saw the mainland fox, *Vulpes Magellanicus*, and agreed it was a different species. More recently, zoologists have speculated the Falkland fox may have been a hybrid between a fox and an Indian or Spanish dog (Bourne 1992:30). He knew of no other island so far from a mainland that had so large a native quadruped (land mammal). The Falkland fox stole food when it could, and Darwin predicted correctly that it would soon be exterminated (Armstrong 2004:79–106). On Chiloe, offshore from Chile, he encountered and collected another, related fox (now Darwin's fox *Pseudalopex fulcipes*), also fearless of humans (Darwin 1839:341). It was not found again until 1922 (Bates 1964:81–82), and now is endangered (Schafer 2010).

Although the Falklands seemed desolate, the surrounding ocean did not. Darwin discovered that the kelp growing offshore sheltered a complex group of animals, and he included this important account of them in his *Zoology Notes* (2000:214–215).

> *The Zoology of the sea is I believe generally the same here as in Tierra del Fuego. Its main striking feature is the immense quantity & numbers of kinds of organic beings which are intimately connected with the Kelp. This plant (the* Fucus giganticus *of Solander) is universally attached to rocks. From those which are awash at low water & those being in fathoms water, it even* frequently *is attached to round stones lying in mud. From the degree in which these Southern lands are intersected by water, & the depth in which Kelp grows, the quantity may well be imagined, but not to a greater degree than it exists. I can only compare these great forests to terrestrial ones in the most teeming part of the Tropics; yet if the latter in any country were to be destroyed I do not believe that nearly the same number of animals would perish in them as would happen in the case of Kelp. All the fishing quadrupeds & birds (& man) haunt the beds, attracted by the infinite number of small fish which live amongst the leaves: (the* kinds *are not so very numerous, my specimens I believe show nearly all).*

Fig. 4. *Rhea darwinii* (now *Pterocnemia pennata*). Darwin 1838–1843:part III.

Fig. 5. Falkland fox (*Canis antarcticus*, now *Dusicyon australis*). Darwin 1838–1843: Part II.

Amongst the invertebrates I will mention them in order of their importance. Crustaceae of ev[e]ry order swarm, my collection gives no idea of them, especially the minute sorts. Encrusting Corallines & Clytia's [bryozoans] *are excessively numerous.* Every *leaf (excepting those on the surface) is* white *with such Corallines or Corallinas* [coralline algae] *& Spirobeae* [fan worms] *& compound Ascidiae* [sea squirts]. *Examining these with a strong microscope, infinite numbers of minute Crustaceae will be seen. The number of compound & simple Ascidiae is a very observable fact, as in a lesser degree are the Holuthuriae* [sea cucumbers] *Asterias* [starfish]. *On shaking the great entangled roots it is curious to see the heap of fish, shells, crabs, sea-eggs, cuttle fish, star fish, Planariae* [flatworms], *Nereidae* [polychaete worms], *which fall out. This latter tribe I have much neglected. Among the Gasteropoda* [snails], *Pleurobranchus* [comb jelly] *is common: but Trochus* [top snails] *& patelliform shells* [limpets] *abound on all the levels. One single plant form is an immense & most interesting menagerie. If this fucus was to cease living, with it would go many: the seals, the cormorants & certainly the small fish & then sooner or later the Fuegian man must follow. The greater number of the invertebrates would likewise perish, but how many it is hard to conjecture.*

Since Darwin thought there was little difference between the offshore life of the Falklands and Tierra del Fuego, in his *Journal of Researches* he placed much of this account in a chapter on the latter (1839:304–305). Patrick Armstrong explains the significance he finds in the *Zoological Notes* account (1992:102–103)

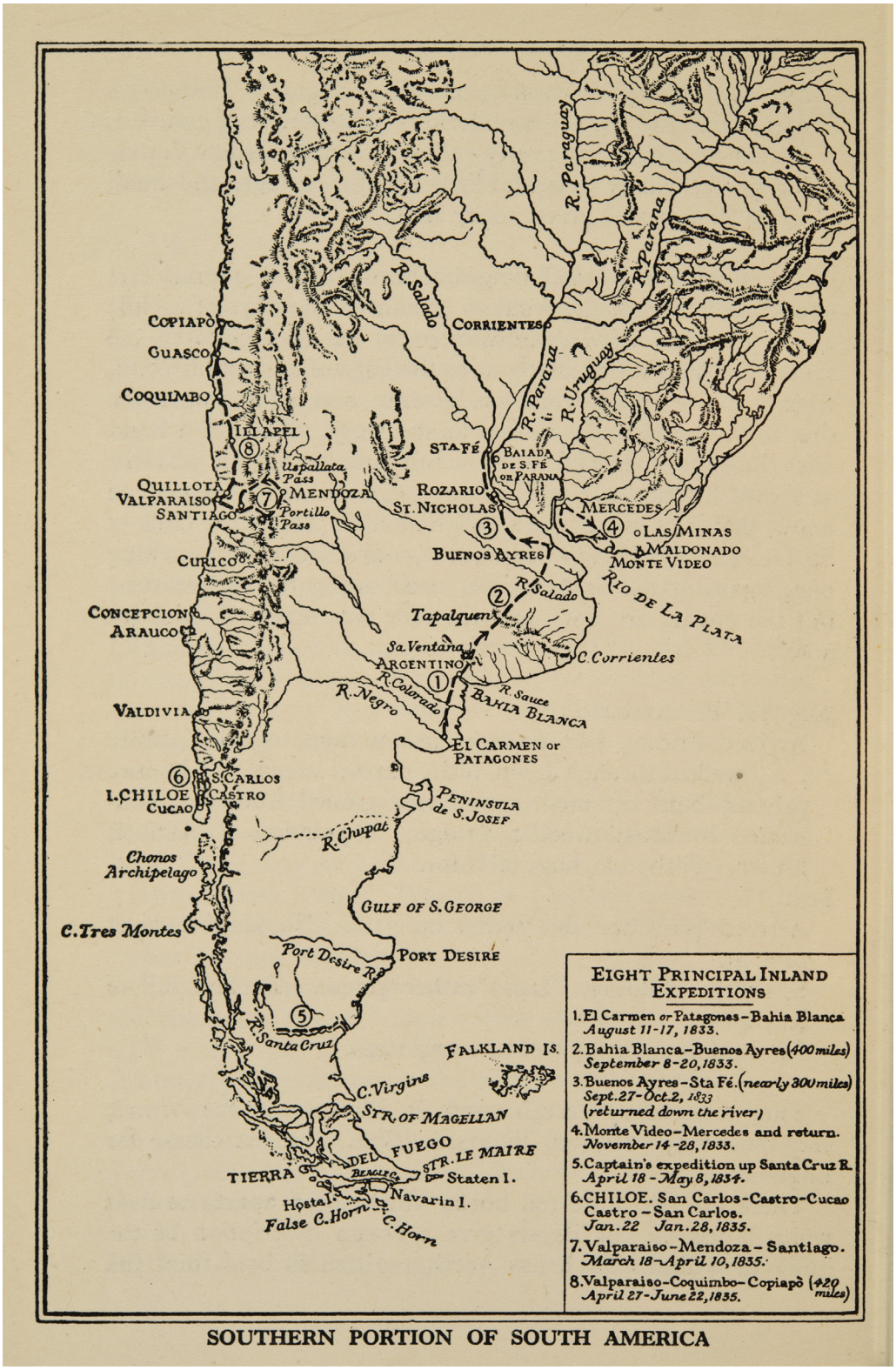
> *There are a number of sophisticated ecological concepts expressed and implied in the passage. Darwin is comparing the* productivity *of the Kelp beds on the margins of the Southern Ocean to that of the tropical rain forest, distinguishing carefully between* population size *(number of individuals) and* species diversity *(number of species). He comes close to using the concepts of* food-chain, food web, ecological niche *and* dominant species*, although of course these actual terms were not coined until nearly a century later. He appreciates that there are links between microscopic and macroscopic forms, and also, very clearly, that humans are linked to their environment. The passage represents a truly integrated and holistic viewpoint…*

A modern book on the kelp forest quotes Darwin on it with approval (McPeak et al. 1988:130). Darwin's descendant, Richard Darwin Keynes, a zoologist who edited three books on the *Beagle* voyage and wrote one on it, claims (2003:218–219) Darwin as a founding father of ecology and as supporting evidence quotes the above paragraph from the *Zoology Notes.*

The majestic Andean Condor attracted Darwin's interest, as it had Humboldt's (Egerton 2009:264–265). Humboldt saw it in the northern limits of its range; Darwin, who traveled around South America's coast from Brazil to Peru, could define its range rather precisely (1839:219–223, 1963:240–245). It inhabited the entire Andes and eastward along the coast as far north as the Rio Negro, latitude 41°, but only lived around steep cliffs. Like Humboldt, Darwin reported gaucho complaints about condors killing young goats and lambs. John James Audubon had reported (1826*a*, *b*) experiments in which he demonstrated that Turkey Vultures and crows had a poor sense of smell: he placed meat covered with paper near caged birds and they ignored it until the cover was removed. Darwin tried the same experiment with condors and got the same result (1838–1843, III:3–6). His and Audubon's experiments seemed decisive, but we now know that turkey vultures can smell but reject rotten meat; condors cannot smell (Cutright 1940:182–186, Steinheimer 2004:308, Haupt 2006:141–144).

The Patagonian plains south of 41° impressed Darwin with its barrenness (1839:194–197). Some nomadic Indians lived there, but the Spanish attempt to colonize the area had failed. He collected a cactus which Henslow (1837) described and named *Opuntia Darwinii*. Darwin also collected a few beetles and found parts of other insects in the stomachs of birds he collected. One of the birds was *Ibis malanops*, whose call resembled the neighing of guanacos, the only mammal seen. Guanacos were known to be in the camel family, and their ability to live in deserts, in herds of six to thirty, was no surprise. He reported that some naturalists considered them to be wild representatives of domesticated llamas (2000:181–183). He never mentioned having seen llamas, and he expressed no opinion on this possibility. Some decades ago they were considered to be the same species (Bates 1964:93), but today they are considered distinct species, *Lama glama* and *L. guanicoe* (Bonacic and Franklin 2001).

In early January 1835, when the *Beagle* visited the Chonos Archipelago, small islands south of Chiloe Island, along the Chilean coast, Darwin showed his potential for becoming a competent botanist—when the vegetation seemed more conspicuous and interesting than either the animals or the geology. His



SOUTHERN PORTION OF SOUTH AMERICA

Fig. 6. Darwin's travels in southern South America. Barlow 1945:256.

attention was first attracted to a wild potato that reminded him of Humboldt's discussion (*Essay on the Kingdom of New Spain*, Book 4, Chapter 9) of the domestic white potato. Humboldt thought that its native soil was in Chile and that Indians had brought it to Peru, Quito, and New Granada, from 40° south to 5° north latitude. The wild potato of Chonos was similar to, but not identical with the domestic potato. Aside from that, Darwin found it remarkable that "the same plant should be found on the sterile mountains of central Chile, where a drop of rain does not fall for more than six months, and within the damp forests of the southern islands"(1839:348). Henslow examined Darwin's dried specimens without reaching a conclusion on its systematic status.

While at Chonos, Darwin also observed that (1839:348–349)

> *In the central parts of the Chonos Archipelago in lat. 45°30', the forest has assumed very much the same character which is found along the whole west coast for 600 miles to Cape Horn. The arborescent grass of Chiloe has here ceased to exist; while the beech of Tierra del Fuego both grows to a good size, and forms a considerable part of the wood; not, however, in the same exclusive manner as it does further to the southward. Cryptogamic plants have a most congenial climate. In the neighbourhood of the Strait of Magellan, I have before remarked that the country appears too cold and wet to allow of their arriving at perfection; but in these islands, within the forests, the number of species, and great abundance of mosses, lichens, and small ferns, is quite extraordinary.*

He then discussed insightfully and in some detail the species and climate that led to the formation of the extensive peat bogs he observed (1839:349–351). And, of course, he obtained plant specimens and took notes on species he discussed at Chonos (Allan 1977:87–88, Porter 1987:178–180).

In February 1835, along the Chile coast, Darwin studied his Patagonian notes from the previous year and decided that his geological evidence did not accord with Lyell's logical arguments about the causes of extinction for Darwin's Patagonian mammalian fossils. Those fossils were of extinct species related to species living in Patagonia. The problem was that there was evidence for neither a diluvial (geologic) nor a climate change—extinctions had occurred under conditions still present in Patagonia (Hodge 1983:19–22). This was a puzzle that he was unable to solve during the voyage, but which would come back to mind in 1837 when he was searching for a theory of evolution.

In retrospect, Darwin's visit to the Galápagos Islands, 15 September–20 October 1835, was the climax of his investigations, but he did not realize it while there (Moorehead 1969:187–208, Browne 1995:296–305, Keynes 2003:307–330, Chancellor and van Wyhe 2009:408–412, 416–425, Grant and Estes 2009:75–250). While he explored these islands, his attention focused on how different species survived in a desert environment. Like Falkland foxes, birds and reptiles of the Galápagos lacked fear of humans. Darwin collected specimens of all plants and animals on the four islands he visited—Albermarle, Charles, Chatham, James—but since the islands were in sight of each other, he did not always record from which island specimens came.

Concerning the differences in the mocking thrushes on different Galápagos Islands he afterwards commented (1963:262)

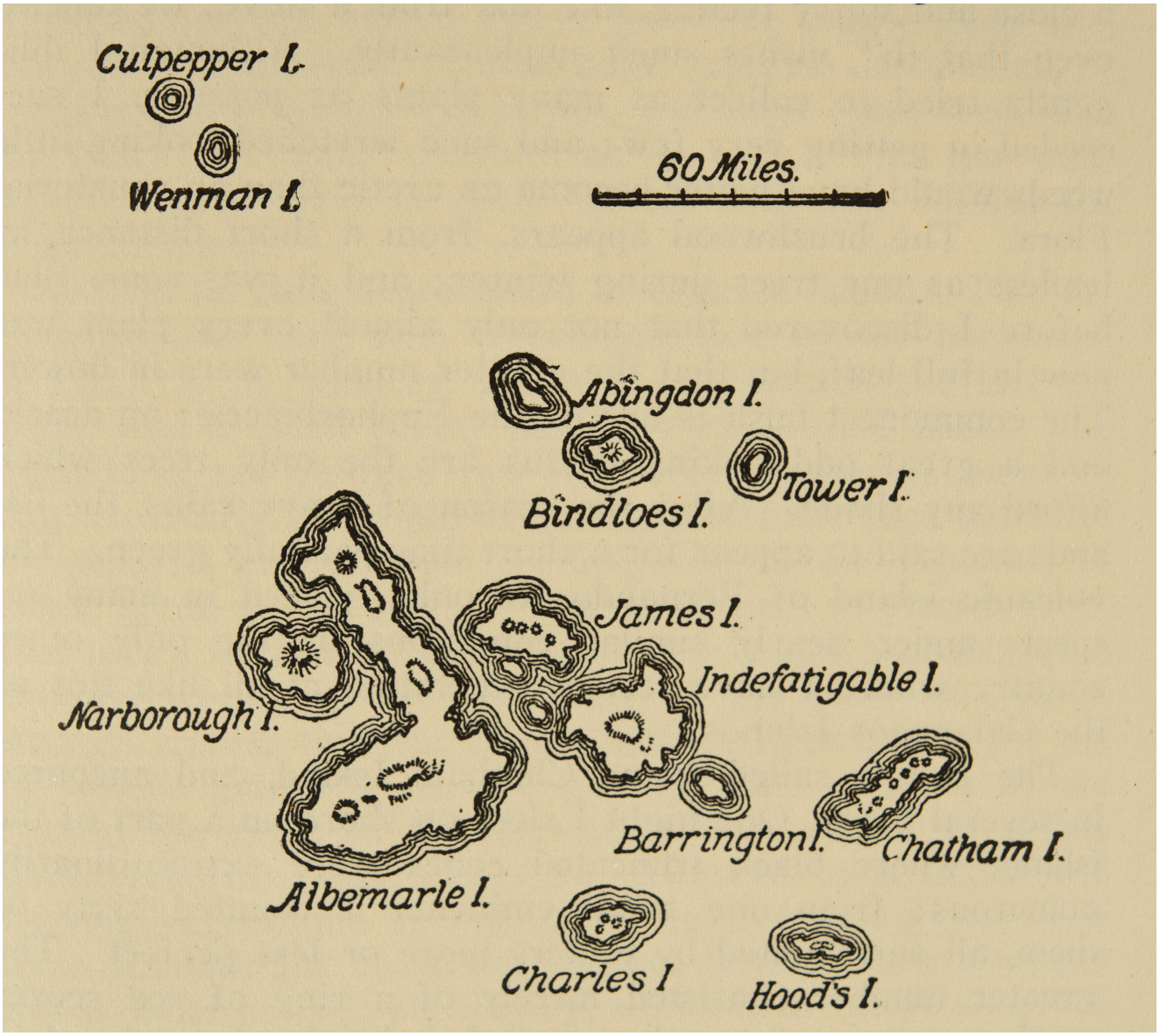


Fig. 7. Galápagos Islands. Darwin 1844. Each island has an official name in Spanish that differs from the names used by the English.

3306, 3307. Thenca: male Charles Isd., male Chatham Isd. These birds are closely allied in appearance to the Thenca of Chile (2169) or Callandra of la Plata (1216). In their habits I cannot point out a single difference;—They are lively inquisitive, active run fast, *frequent houses to pick the meat of the Tortoise, which is hung up,—sing tolerably well; are said to build a simple open nest.—are* very *tame, a character in common with the other birds: I* imagined *however its note or cry was rather different from the Thenca of Chile?—Are very abundant, over the whole Island; are chiefly tempted up into the high & damp parts, by the houses & cleared ground.*

> *I have specimens from four of the larger Islands; the two above enumerated, and (3349: female. Albermarle Isd.) & (3350: male: James Isd.).—The specimens from Chatham & Albermarle Isd appear to be the same; but the other two are different. In each Isld. Each kind is* exclusively *found: habits of all are indistinguishable. When I recollect, the fact that the form of the body, shape of scales & general size, the Spaniards can at once pronounce, from which Island any Tortoise may have been brought. When I see these Islands in sight of each other, & possessed of but a scanty stock of animals, tenanted by these birds, but slightly differing in structure & filling the same place in Nature, I must suspect they are only varieties. The only fact of a similar kind of which I am aware, is the constant asserted difference—between the wolf-like Fox of East & West Falkland Islds.—If there is the slightest foundation for these remarks the zoology of Archipelagoes—will be well worth examining; for such facts [would* inserted*] undermine the stability of Species.*

In *Journal of Researches* (1839:461) he cited John Gould's assessment of new species of Galápagos land birds, but he cautiously omitted the comments in his *Ornithological Notes* about the instability of species, quoted above on mockingbirds. The three species are now named *Mimus macdonaldi, M. mcleanotis, M. parvulus*. Their current distinctions are not those of Gould (Grant and Estes 2009:118–122).

During the return voyage of the *Beagle*, 12 April–19 July 1836, Darwin restudied his bird specimens and compiled his "Ornithological notes" (Sulloway 1982*b*:337, 348–351). He was then ready to speculate in greater detail than previously on the status of some he had collected in the Galápagos Islands. The birds now called Darwin's Finches are plain birds that Darwin mentioned in his Diary (1988:359) only once while collecting them—he observed them being attracted to a sandstone pit holding about a gallon of water. However, in his "Ornithological Notes," he wrote (1963:261)

> *...these Finches are in number of species & individuals far preponderant over any other family of birds. Amongst the species of this family there reigns (to me) an inexplicable confusion. Of each kind, some are jet black, & from this, by intermediate shades, to brown; the proportional number, in all the black kinds is* exceedingly *small; yet my series of specimens would go to show, that, that color is proper to the old cock birds alone. On the other hand—Mr. Bynoe & Fuller assert, they have each a small jet black bird of the female sex. Moreover a gradation in form of the bill, appears to me to exist. There is no possibility of distinguishing the species by their habits, as they are all similar, & they feed together (also with doves) in large irregular flocks... with respect to the probable age of the smaller birds, that in no case were any of the feathers imperfect, or bill soft, so as indicate immaturity, & on the other hand—in no case—were the eggs in the ovarium of the hen birds much developed. I should suppose the season of incubation would be two or* three months *later.*

Fitzroy made his own collection of these finches and believed they represented different, unchanging, species. Darwin thought they only represented subspecies (Grinnell 1974:261). The notes quoted above were likely written after they had argued over the status of the finches. After the voyage, Darwin turned over his bird specimens to ornithologist John Gould, who told Darwin in March 1837 that the finches he had collected on different islands were distinct species (Gould 1837*a*, Lambourne 1987:46, Tree 1991:52–60. Browne 1995:359–360, Keynes 2003:381–382, England 2004).

Fig. 8. Small cactus finch (*Geospiza scandens*). The males are black and females brown. They depend heavily on *Opuntia* flowers, fruit, and associated insects for food and water. Darwin 1838–1843: Part III.

Only then did Darwin conclude that evolutionary divergence was the only plausible explanation for so many species so close together, but separated by water (Sulloway 1982*a*, *b*, *c*). David Lack (1947) called them "Darwin's Finches" and documented their evolutionary significance.

Darwin devoted almost four pages of his *Journal of Researches* (1839:462–466) to the natural history of the Galapagos tortoise, *Testudo Indicus* (now *Geochelone elephantopus*), more than he did to any other Galápagos species (Sulloway 2009). He thought they inhabited all the islands. "They frequent in preference the high damp parts, but likewise inhabit the lower and arid districts." They grew so large it took six or eight men to lift a large one, the males being larger and having a longer tail than the females. Those living on islands without water or in arid parts of other islands, ate chiefly succulent cactus. Those with access to fresh water ate various leaves and berries and made well-worn paths between the water and their feeding places. They could travel four miles in a day. Females lay in October and did so in sand where available, but in any hollow when no sand. The young were vulnerable to buzzards, but adults lived until they either died of accidents or were killed by humans for food. Nicholas Lawson, the Englishman who governed the colony for Ecuador, told Darwin that he could tell from which island a tortoise came by the shape of its shell.

Fig. 9. (Left) Galápagos tortoise (*Geochelone elephantopus*). (Right) *Opuntia galapageia* Henslow. Darwin's account is in Porter 1987:183. Photos courtesy Professor Emeritus Donald Piele, Department of Mathematics, University of Wisconsin-Parkside.

The two species of iguana seemed to Darwin to be ugly and stupid, but still interesting. One, *Amblyrhyncus cristatus*, was unusual because it lived on the rocky beaches of all the islands and subsisted on seaweed which it grazed underwater offshore. It was the only known lizard that lived on aquatic vegetation. It was not breeding when Darwin was there, and he was unable to learn where it laid its eggs (Darwin 1839:466–469). The terrestrial species, *Amblyrhyncus* (now *Conolophus*) *subcristatus*, was also a vegetarian and often ate cactus. It dug burrows in which to raise its young and to use for refuge.

Fig. 10. Land iguana (*Amblyrhyncus* [now *Conolophus*] *subcristatus*). Darwin 1838–1843:part V.

Although Darwin had become an evolutionist in March 1837, his *Journal of Researches* (1839) retained some pre-evolutionary phrasing: "It would appear as if this species [*subcristatus*] had been created in the centre of the Archipelago, and thence had been dispersed to a certain distance" (1839:469).

Although Darwin had some botanical knowledge before the voyage (Ayres 2008:55–62), he did not become a botanist until after publishing *The Origin of Species* in 1859 (Heslop-Harrison 1958, Barlow 1967:25–117, Allan 1977:55–104). Yet, out of loyalty to Henslow, he had diligently collected plant specimens and labeled locations throughout his travels and shipped them back to Cambridge. His Galápagos specimens attracted particular attention (Turrill 1953:121–133, Porter 1981, 1984*a*, *b*, 1985, 1987). He had collected 210 specimens of 173 taxa, which is about 24% of the present flora. Henslow (1837) only published descriptions of two species of *Opuntia*. Joseph Hooker found that about half of Darwin's species were endemic. By the time Hooker wrote two articles on the Galápagos vegetation (written 1845, 1846, published 1851), he and Darwin had become close friends and had exchanged a lengthy correspondence that included stimulating exchanges on Galápagos plants and plant geography in general (Darwin 1985–88). Darwin's plant specimens are now described and his notes on them published (Porter 1987). David Kohn believes that Darwin's over 200 Galápagos plants (quoted in Sacks 2008:64)

> *constitute the single most influential natural history collection of live organisms in the entire history of science…They also would turn out to be Darwin's best documented example of the evolution of species on the islands.*

David Lack's book, *Darwin's Finches* (1947), initiated the modern interest in Darwin's own observations and collections in the Galápagos Islands and also in those islands themselves as having an evolutionary exhibit. At least three symposia volumes (Bowman 1966, Berry 1984, Perry 1984) have reported on the biology, geology, and oceanography of these islands, and there are also numerous separate works on them in general (such as Life Editors and Barnett 1960, Thornton 1971, Hickin 1979, Steadman and Zousmer 1988, Kricher 2002, Swash and Still 2006, Stewart 2007, Grant and Estes 2009), on birds in particular (Lack 1947, Grant 1986, Weiner 1994, Castro and Phillips 1996, Heinzel and Hall 2000), and on the history of biological studies on these islands (Larson 2001). Darwin's actual paths through the four islands he visited are documented to the extent that his notes allow (Estes et al. 2000). Darwin's South American travels inspired two modern Englishmen to retrace his steps, one (Campbell 1997) sailing to ports Darwin visited, and one (Green 1999) riding horseback to many places and sailing to others; both also visited the Falkland and Galápagos Islands.

Darwin's first theory was on coral reef formation. In his *Autobiography* he remembered developing it about six months before seeing coral reefs (1959:98), though Sponsel (2009:103) doubts the accuracy of that memory. What Darwin had concluded by 18 August 1834 was that the uplift of the Andes was probably accompanied by the subsidence of the floor of the Pacific (Sponsel 2009:99–100). He had seen the Abrolhos coral islets in the Atlantic in 1832, where he had collected coral and other marine invertebrates (Darwin 1988:48–49, 2000:31–36), but had not thought then about the origin of coral reefs. Those thoughts arose after reading Lyell's explanation (1830–1833, II:283–301) of them arising on the rims of submerged volcanoes, which Darwin found unconvincing (Herbert 2005:242–243). Darwin's first view of coral reefs occurred at Tahiti, where the *Beagle* stayed 15–26 November 1835. He climbed the Tahiti mountain and viewed the reef around Eimeo (Moorea), 15 miles away (Darwin 1839:484–485, 1998:369). He then imagined that peak subsiding, leaving a circular coral reef that continued growing upward as the peak sank (Stoddart 1962:6–7, quoting Darwin 1835 manuscript, 4–5). He suspected that coral species growing inside a lagoon differed from those growing outside. He hired Tahitians to paddle him in a canoe to inner corals, where he collected, but they would not cross the corals to the outside because doing so was dangerous (Stoddart 1962:10, quoting Darwin MS, 11–12). However, natives assured him that the species he collected on the inside did not live on the outside (Stoddart 1962:11, quoting Darwin MS, 14). Darwin apparently wrote his first essay on coral islands on 3–21 December 35 (Sponsel 2009:109, Stoddart 1962:2).

The *Beagle* reached Sydney, Australia on 12 January 1836 and left King George's Sound on March 14. Nicholas and Nicholas (2002) provide an excellent, well-illustrated account of Darwin's Australian explorations, with a series of maps to indicate his itinerary. Although he traveled much more and stayed there twice as long as he did in the Galápagos Islands, his Australian chapter in the first edition of *Journal of Researches* is two pages briefer than his Galápagos chapter. His *Ornithology Notes* (1963) end with Galápagos birds, and his *Zoology Notes* (2000:302–303) have little more than a page on Australia, devoted to several lizards and a snake.

He seems to have collected few, if any Australian plants, but he did offer comments on Australian trees (1839:517–518).

> *The extreme uniformity of the vegetation is the most remarkable feature in the landscape of the greater part of New South Wales. Every where we have an open woodland; the ground being partially covered with a very thin pasture. The trees nearly all belong to one family; and mostly have the surface of their leaves placed in a vertical, instead of as in Europe, a nearly horizontal position: the foliage is scanty, and of a peculiar, pale green tint, without any gloss. Hence the woods appear light and shadowless: this, although a loss of comfort to the traveler under the scorching rays of summer, is of importance to the farmer, as it allows grass to grow where it otherwise could not. The leaves are not shed periodically: this character appears common to the entire southern hemisphere…The greater number of trees, with the exception of some blue gums, do not attain a large size; but they grow tall and tolerably straight, and stand well apart.*

Patrick Armstrong thought these observations "captured the essential nature of eucaluypt woodland extremely well" (2004:167), and Jane Marshall (1970:35–57) thought Darwin's observations in Australia were generally astute.

He and a guide tried to find kangaroos and emus, which formerly had been common, but greyhounds were "utterly destructive" of them, and he feared they might be exterminated (1839:525). They only found a kangaroo "rat" (*Potorus tridactylus*). In a river he saw "the famous Platypus or *Ornithorhyncus paradoxus*" playing in the water, and he saw large flocks of white cockatoos and some "most beautiful parrots," crows, and "a species something like a magpie," but he neither collected nor identified these birds. Nicholas and Nicholas (1989:144–145) list 14 Australian species described in *The Zoology of the Voyage of H. M. S. Beagle* (Darwin 1838–1843). Darwin also collected Australian insects (Smith 1987:97–101). Tasmania was damper than New South Wales, and its vegetation was greener and more cheerful (1839:535).

Chapter 22 in *Journal of Researches* is on the Keeling Islands, two coral atolls (Darwin only visited the south atoll) in the Indian Ocean south of Sumatra (Armstrong 1991, 2004:196–213). The 1839 edition of Darwin's *Journal* includes a foldout map of these islands; the only other map is a foldout of southern South America. Although both of these excellent maps are relevant to the book, they were products of the Navy's mapping project, and these two were included in Darwin's *Journal* mainly because the expedition maps were distributed among three volumes published together in 1839. Such a large map was unnecessary for his chapter, though that chapter contains a good ecological survey. Darwin thought corals formed on rims or sides of volcanoes that slowly sank, and the corals grew up as the volcanoes sank. A substantial account of living corals in Darwin's *Zoology Notes* (2000:305–311) included this account of *Madrepora* (now *Acropora*)

> *This stony branching elegant Coral is very abundant in the shallow still waters of the Lagoon: it lives from the shoalest parts, which are always covered by water, to a depth certainly of 18 ft. & perhaps more. Its color is nearly white or pale brown. The orifice of the cells is either nearly simple, or protected by a strong hood: the polypus is similar in both.—The upper extremity or mouth of the Polypus is closely attached to the edge of orifice: it cannot be protruded, nor*

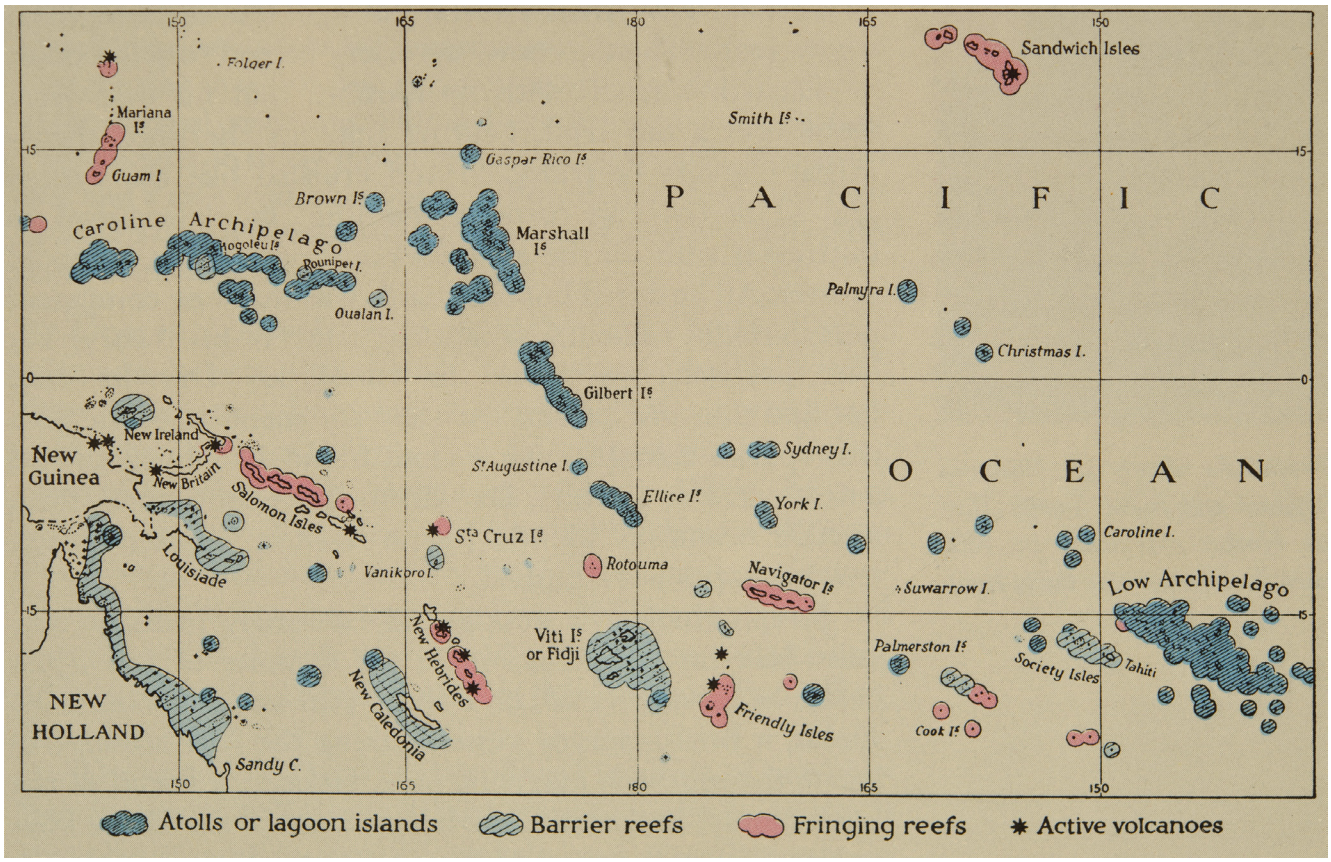


Fig. 11. Portion of foldout map: corals of the Pacific Ocean. Darwin 1842, 1889.

> *drawn back out of sight; it consists of narrow, fleshy lip, which is divided into 12 tentacula or subdivisions of the lip. These tentacula are very short & minute, are flattened vertically, are brown colored, tipped with white. The animal possesses very little irritability, on being pricked the mouth is folded or contracted into an elongated figure & partially drawn back. The body of the Polypus fills up the cell, is so excessively delicate, transparent & adhaesive that I in vain tried to examine its structure. I could see a sort of abdominal sack, & attached to the side of this there were intestinal folds of a whitish color. These when separated from the body possessed a sort of peristaltic motion.*

Six pages of notes (discussed in Keynes 2003:358–360), were reduced to two paragraphs in *Journal of Researches* (1839:552–553). Besides several species of coral, the Keeling animals Darwin and Covington collected were 9 species of fish, 1 mammal, 1 bird, sea anemones, robber crab, and 13 insects (Armstrong 1991:30, 74).

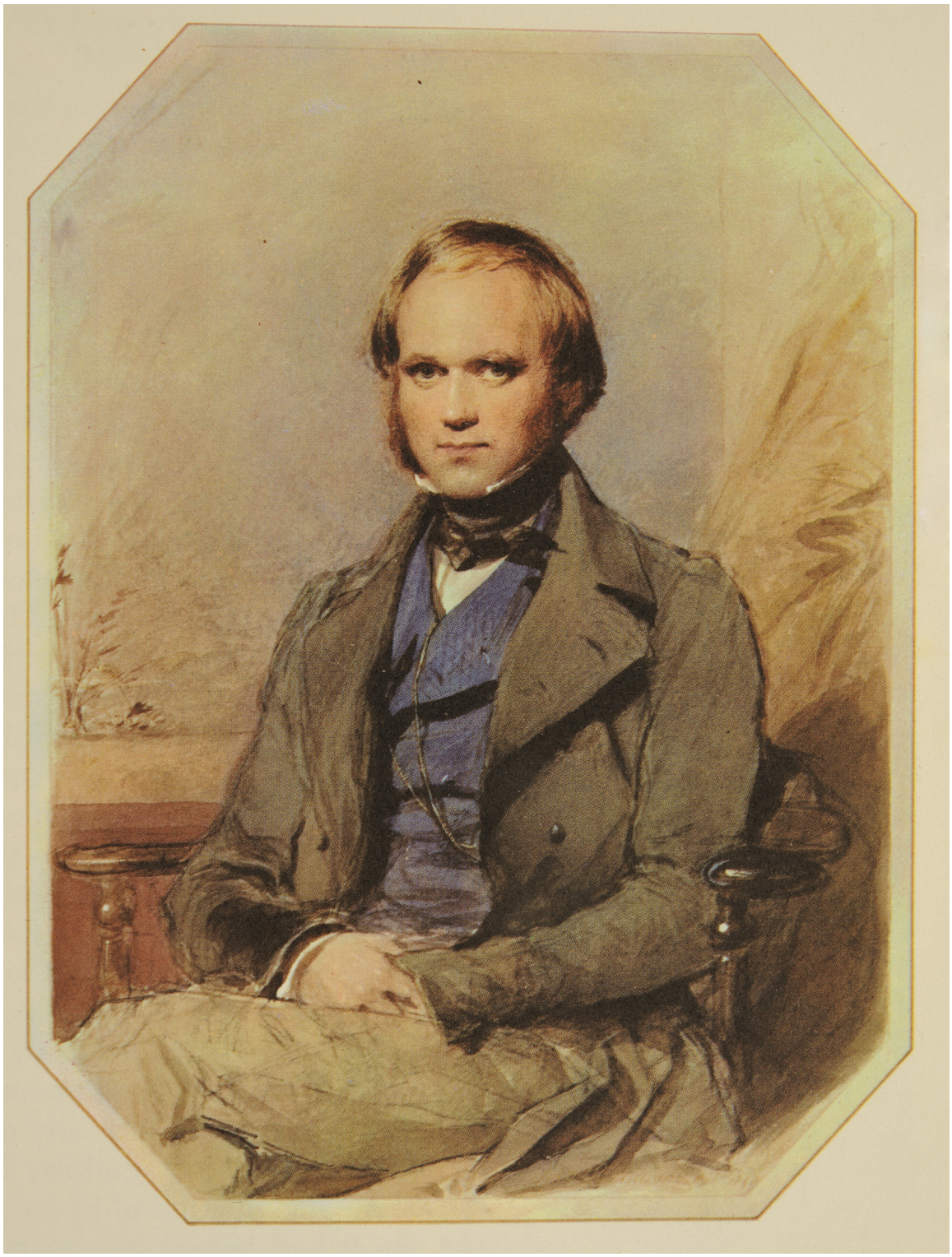


Fig. 12. Charles Darwin, 1840, by George Richmond. Portrait at Darwin Museum, Down House, Downe, UK.

On the south island coconut palms flourished; there was another tree not in flower and so unknown, and a report of a third tree that Darwin did not see. He collected 20 other vascular species, which he called "insignificant weeds" (1839:541), a moss, a lichen, and a fungus (Allan 1977:101–103, Porter 1987:185). A recurrent theme whenever he discussed the indigenous plants and animals of islands distant from continents was the paucity of species, due to the difficulty of their ever arriving there (Armstrong 1991:76–78). Of course, there were also on many islands introduced domestic plants, and on the Keeling Islands these included banana and sugar cane. Mr. A. S. Keating had lived on the island for a year and reported on seeds and plants that washed ashore from Sumatra, Java, and elsewhere. Henslow told Darwin that nearly all his plants from South Keeling Island were "common littoral species in the East Indian Archipelago" (Henslow 1838, Darwin 1839:542, Allan 1977:113–115).

Chapter 22 on coral islands was Darwin's stepping stone from a science travel book to a scientific monograph. Darwin's *Coral Reefs* (1842) was based on a testable theory and also on Humboldtian correlational science. Humboldt's science travel book was a good example for Darwin's, but Darwin took Lyell's *Principles of Geology* as the paradigm for his *Coral Reefs* (Herbert 2005:232–240 + Plate 1). Darwin's observations in the Pacific and Indian Oceans had been brief, yet far better than Lyell's lack of observations (Stoddart 1994*a*:29).

> *He had seen atolls from the deck of the* Beagle *in the Tuamotus as the ship sailed through; he saw the fringing reefs of Tahiti and the reef-encircled island of Moorea from a distance; he passed by the almost atoll of Aitutaki in the southern Cooks; and finally in 1836 he landed for eleven days on Cocos-Keeling Atoll…*

After Darwin's return from his voyage, he and Lyell were eager to meet each other. Lyell invited Darwin to dinner on 29 October 1836, and it was love at first sight. Darwin explained his theory of coral reef formation on the rims or sides of volcanoes that slowly sank, and Lyell went into a "state of wild excitement and sustained enthusiasm, which lasted for days" (Judd 1909:358).

Darwin's *Coral Reefs* was "a model of conciseness and clarity" (Stoddart 1994*a*:28), and he was soon known not only as a world traveler, but also as an authority on coral islands (Darwin 1838, 1842, Yonge 1958). However, he had not actually tested his theory at the Cocos-Keeling Atoll. Instead, much of his persuasiveness depended upon his outstanding map of Pacific reefs, atolls, and islands, based upon several years of research on nautical charts and reports after he returned from the voyage (Stoddart 1994*b*:21). The American Exploring Expedition of 1838–1842 (discussed in Sponsel 2009:249–301) carried a naturalist, Joseph P. Couthouy, and a geologist–naturalist, James Dwight Dana, who had better chances to study coral reefs than Darwin had; Dana found that their detailed data generally supported Darwin's theory of coral reef formation (Appleman 1985:91–95, Stoddart 1994:26–30, Sponsel 2009:268–269). When Darwin published a second edition of *Coral Reefs* (1874), he took into account Dana's work, but made no major changes in his arguments.

Yet, objections to his theory began with Charles Maclaren (1843)—which Darwin answered provisionally—and persisted for decades (Schlee 1973:158–162, Dobbs 2005, Sponsel 2009:297–317). Apparent validation for Darwin came (Scoffin and Dixon 1983:13)

> *when two holes were drilled which reached the volcanic rock basement beneath Enewetak*

*Atoll at depths of 1267 m and 1450 m (*Ladd et al., 1953*). The limestones recovered were all of shallow water origin demonstrating both subsidence of the atoll and the upward growth of shallow water corals since Eocene time…*

However, the situation was more complex than Darwin had realized. Reginald Daly pointed out (1910, 1915) that periodic ice ages had caused sea-level fluctuations that Darwin's theory did not consider. A recent review (Dickinson 2009:8) concludes

Raised atoll rims do not reflect the upward growth of ancient fringing reefs surrounding volcanic islands that have subsided beneath atoll lagoons, but were produced as solution ramparts rimming carbonate platforms exposed to the atmosphere during synglacial drawdowns in sea level. A mid-Holocene hydro-isostatic highstand in tropical Pacific sea level drowned atoll rims and build reef flats above modern sea level….stable atoll islets formed with underpinnings of resistant mid-Holocene paleoreef flats to protect the flanks of the islets from wave attack.

Nevertheless, Darwin's *Coral Reefs* was the foundation on which modern understanding was built.

The voyage of the *Beagle* gave Darwin the opportunity to evolve from a promising neophyte naturalist into a prominent British scientist (Sulloway 1985) who would establish an evolutionary ecology (to be discussed in Part 40). He returned with 1529 species in bottled wine spirits and 3907 dried specimens, and he would solicit the assistance of specialists to describe and name them. He collected and edited reports of zoologists who described his vertebrate specimens in *The Zoology of the Voyage of H.M.S. Beagle* 5 parts in 3 volumes, 1838–1842). Naturalists also described his specimens of plants and animals in articles in natural history journals; Paul Barrett (in Darwin 1977, II:295–300) provides a bibliography of them. Darwin also published two other volumes on the geology of the voyage (Freeman 1965, Herbert 2005).

Darwin's *Journal of Researches* was a stimulus to later explorers in the same way that Humboldt's *Personal Narrative* was (Raby 1996). Alfred Russel Wallace wrote to his friend Henry Walter Bates on 11 April 1846 (1905, I:256)

I first read Darwin's 'Journal' three or four years ago, and have lately re-read it. As the Journal of a scientific traveler, it is second only to Humboldt's 'Personal Narrative'—as a work of general interest, perhaps superior to it.

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Acknowledgments

For their assistance, I thank John van Wyhe, Department of Biological Sciences, National University of Singapore, Professor Emeritus of Geology James H. Shea, University of Wisconsin-Parkside, and Alistair W. Sponsel, Darwin Correspondence Project, Harvard University, Cambridge, Massachusetts.