CONTRIBUTIONS

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History of Ecological Sciences, Part 42: Victorian Naturalists Abroad—Hooker, Huxley, Wallace

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Hooker, Huxley, and Wallace were leading English naturalists during the Darwinian Revolution (McCalman 2009:83–362). They made substantial contributions to ecological thought in many of their publications. We have already reviewed Wallace's Amazonian experiences and observations (Egerton 2011). His Malay experiences, observations, conclusions are discussed here. However, Hooker is discussed first and then Huxley.

Joseph Dalton Hooker (1817–1911) was the son of botanist William Jackson Hooker (1785–1865), who became Director of the Royal Botanic Gardens, Kew. The son would succeed his father in that position, and both were knighted for their services. In 1839, Joseph received an M.D. degree from Glasgow University, where William taught until 1841. Joseph's bibliography is included in his first biography (Huxley 1918, II:486–506). A later Kew botanist, W. B. Turrill, compiled an anthology of Joseph Hooker's phytogeographical writings (1953), which is a valuable resource of ecological interest. Some of Hooker's writings are also reprinted at the Joseph Dalton Hooker web site.

Inspired by the travelogues of Humboldt and Darwin, Joseph had the connections to obtain a position of assistant surgeon and naturalist on a British naval expedition to the Antarctic in 1839 in *Erebus*, one of two ships under the command of an experienced polar explorer, Captain James Clark Ross (1800–1862), who would seek to map Tasmania, New Zealand, other southern islands, and part of Antarctica in September 1839–September 1843 (Bravo 2004). Hooker was as well trained for this adventure as Darwin had been for his (Huxley 1918, I:1–36, Reed 1942:129–131, Turrill 1963:1–12, Allan 1967:84–94, Desmond 1972, 1999:11–15, Bellon 2000, Endersby 2004*a*, *b*, 2008) (on Darwin's training, Egerton 2010:398–399). Hooker was appointed Assistant Surgeon and Botanist; and the Surgeon–Zoologist was Robert McCormick (1800–1890), who had been on a previous expedition. In 1839, before leaving, Hooker had walked through Trafalgar Square with a naval officer who had sailed with Darwin on the *Beagle*; they encountered Darwin, and the officer introduced them to each other (Huxley 1918, I:487).

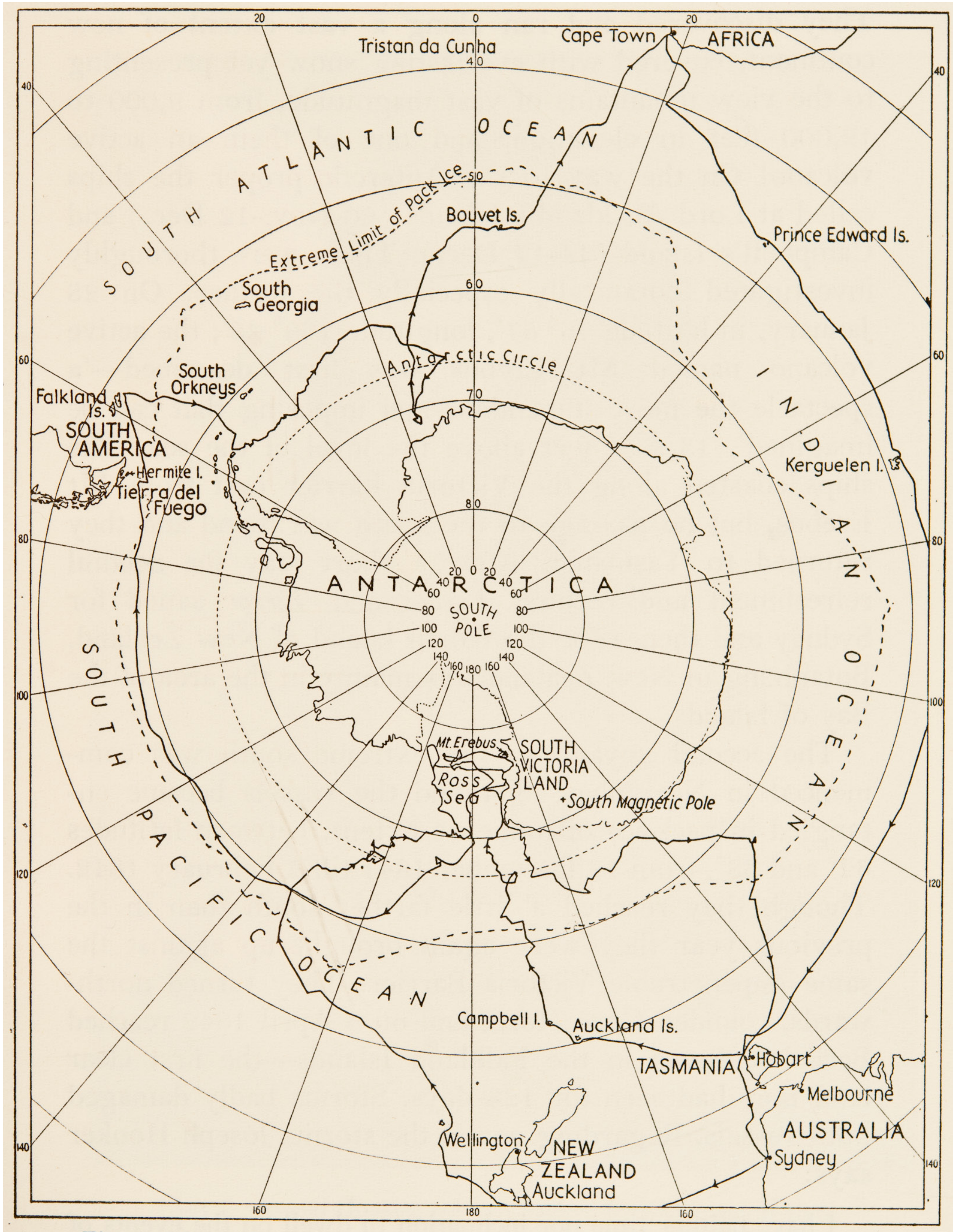

Fig. 1. Map of the Antarctic voyage of *Erebus*, 1839–1843, from Cape Town, South Africa, and back (Turrill 1963:19). A larger-scale map is in Desmond 1999: inside front cover.

Just as Darwin took a copy of Humboldt's travels on his voyage, so Hooker took Darwin's *Journal of Researches* with him on the expedition (a gift from Charles Lyell), and read it often (Raby 1996:28).

Hooker's task was simpler than Darwin's, because Darwin had collected animals, plants, and fossils, whereas Hooker mainly collected plants (his illustrations of a squid, *Loligo gahi*, and a fish, *Pagothenia phocae*, are reproduced by Desmond [1999:168–169]). He did trail plankton nets from his ship as it sailed along, and Christian Gottfried Ehrenberg (1795–1876), Humboldt's companion in Siberia, described his diatoms, but he never found anyone to study his other plankton and larger animals (Huxley 1918, I:56–60). However, Hooker was as diligent as Darwin, and after returning home, he published an account of all his plants, with collaborators only on brief articles on mosses and algae (Huxley 1918, II:487–490, Turrill 1963:24, Stafleu and Cowan 1976–1988, II:269–272, Desmond 1999:276, Short 2004:297–304). His *Botany of the Antarctic Voyage* was three works in six volumes: (1) *Flora Antarctica* (two parts, 1844–1847), (2) *Flora Nouvae-Zelandiae* (two parts, 1852–1855), (3) *Flora Tasmaniae* (two parts, 1855–1860). The titles of these works indicate the main parts of the voyage, and his main plant collections. Although Hooker did not publish a travelogue of his four-year expedition, his father published a long article based on his letters and notes (Hooker 1843), and Captain Ross did publish a narrative of the voyage (two volumes, 1847), which included six quotations from Hooker, each quotation 4–6 pages long. Hooker's first biographer, Leonard Huxley (1918, I:37–167), reconstructed a narration of the voyage from letters and other documents.

H.M.S. *Erebus* and *Terror* embarked on their four-year voyage on 30 September 1839, and reached Cape Verde islands on 13 November. Hooker was a talented artist, whose sketches of landscapes and plants were later transformed into publishable plates by Walter Hood Fitch (1817–1892), a botanical artist at Kew (Desmond 1977:224, 1999:90–91). The ships entered Porto Praya, San Jago Island, where Hooker collected 110 plant species and sketched the arid landscape. He was unable to travel 12 miles inland to the more fertile highlands (Hooker 1843:250), but he did measure a solitary baobab tree *Adansonia digitata* that was 38 feet in circumference and more than 60 feet high.

These ships next stopped at St. Paul's Rocks in the middle Atlantic, where Hooker confirmed Darwin's observation that they contained no plants, though he found seaweed offshore. As they approached South Africa, he had a chance to examine a seaweed community (letter of 17 March 1841, Huxley 1918, I:72–73)

> *Till within a few days no floating seaweeds have been seen, when they suddenly appeared whilst cruising off St. Helen's Bay about sixty miles north of the Cape, whilst we were beating to the Southward; they certainly (though only of one kind) gave a most exulted notion of a submarine forest, with its accompaniment of a parasitic vegetation; with fish for birds, corals for Lichens, and shells for insects. Whilst going six or seven knots through the water, we, stationed in the quarter boats, harpooned these weeds as we passed, and very good fun for botanizing it was; the largest brought on board had a short thick branching root from which sprang four great stems, the longest 24 feet…. It belongs to the genus* Laminaria*; the old stems are brown, with flat white corals on them, and some parasitic seaweeds; the matted roots contain numerous other seaweeds, shells, Crustacea, corals, Molluscae, Actineae and red-blooded worms. The leaves are infested with Patellas, Sertularias, and Flustrae. From one specimen I took four seaweeds and upwards of thirty animals, by carefully*

Fig. 2. Porto Praya, San Jago Island, Cape Verde, showing *Erebus* and *Terror* in the harbor. By Walter Fitch, based on Hooker's sketch. Desmond 1999: title page and 27.

pulling the root to pieces. Nor were these large seaweeds; many were seen twice as large if not larger. What extraordinary power can have torn them up by the roots I cannot conceive, for, from their length, they must grow far below low water mark.

On 3 May 1842, he wrote to his father from the Falklands that officers he had met from H.M.S. *Arrow* told him that "as the *Macrocystis* grows large, it finally weighs up the stone, which was its moorings, and then the whole plant goes off to sea, which fully explains the reason for our finding so much of it alive at sea."

Since the Antarctic Voyage circumnavigated the Antarctic, Hooker could compare the floras of widely separated Kerguelen, Auckland, and Falkland islands and found they had some plants in common (Huxley 1918, I:75). The expedition spent over two months (12 May–20 July 1840), at the Kerguelens

Fig. 3. Seaweed *Macrocystis luxurians* (top) and land plants. Hooker 1844–1847, II: Plate 171.

(Îsles de Désolation), about latitude 49°S, making magnetic measurements, and Hooker increased its known species from 18 to 150 (Turrill 1963:27–28). His discoveries there included an aquatic species that bloomed under two inches of ice (Huxley 1918, I:76). His analysis of the Kerguelen flora, in *Flora Antarctica*, indicated that its strongest similarities were to the Fuegian flora of Cape Horn (quoted

Fig. 4. Kerguelen cabbage *Pringlea antiscorbutica*. Hooker 1844–1847, II: Plates 90–91.

in Turrill 1953:190). The previously known Kerguelen cabbage (*Pringlea antiscorbutica*), as its scientific name indicates, was publicized by Captain James Cook as an antidote to scurvy. Hooker first adequately described and illustrated it, grew 50 plants from its seeds, and planted them at various places for later explorers. His expedition also left sheep at Kerguelen for the future benefit of whalers (with no thought of their impact on the island's environment).

In November 1840, the expedition reached Campbell Island, south of New Zealand. Hooker's botanical observations there were quoted in Ross' *A Voyage of Discovery and Research in the Southern and Antarctic Regions* (1847, I:158–163 and reprinted by W. B. Turrill; this is the introductory paragraph [Turrill 1953:134–135])

> *Although Campbell's Island is situated 120 miles to the southward of Lord Auckland's group, and is of much smaller extent, it probably contains fully as many native plants. This arises from its more varied outline, and from its steep precipices and contracted ravines, affording situations more congenial to the growth of grasses, mosses, and lichens. Its iron-bound coast and rocky mountains, whose summits appear to the eye bare of vegetation, give it the aspect of a very desolate and unproductive rock, and it is not until the quiet harbours are opened, that any green hue save a few grassy spots is seen. In these narrow bays the scene suddenly changes; a belt of brushwood, composed of some of the trees mentioned as inhabitants of the last-visited island, but in a very stunted state, form a verdant line close to the beach. This is succeeded by bright green slopes, so studded with the* Chrysobactron *as to give them a yellow tinge, visible a full mile from the shore. Most of the beautiful plants of Lord Auckland's group, including the elegant caulescent ferns, are equally abundant here, and from many of them growing in this higher latitude at a proportionally lower elevation, their beauty strikes every one on first landing.*

In two days he collected over 200 species and thought he could have found more if he had had more time.

On the other side of the world, on 5 January 1843, the expedition reached Cockburn Island, south of the Falkland Islands at latitude 64°12′ S (not named on the map, Fig. 1, but the expedition's route from the Falklands is indicated). The Arctic Circle is at latitude 66°30′ S, so not that far south, but some 15° in latitude south of the Kerguelens. He found on Cockburn only 19 species, all mosses, algae, and lichens. He explained their habitats and ranges (Ross 1847, II:335, quoted in Turrill 1953:137)

> *Twelve are terrestrial; three inhabit either fresh water or very moist ground; and four are confined to the surrounding Ocean. Of these nineteen plants, seven are restricted to the island in question, having been hitherto found nowhere else (besides an eighth, which is a variety of a well known species); the others grow in various parts of the globe, some being widely diffused.*

Details on individual species follow, and then this overview (Ross 1847, II:341, quoted in Turrill 1953:138–139)

> *Vegetation could not be traced above the conspicuous ledge of rocks, with which the whole island is girt, at fourteen hundred feet elevation. The* lichens *ascend the highest. The singular nature of this flora must be viewed in connection with the soil and climate; than which perhaps none can be more unfriendly to vegetable life. The form of the island admits of no shelter: its rocks are volcanic, and very hard, sometimes compact, but more frequently vesicular. A steep stony bank descends from the above-mentioned ledge to the beach; and to it the plants are almost limited. The slope itself is covered with loose fragments of rock, the débris of the cliff above, further broken up by frost, and ice-bound to a depth which there was no opportunity of ascertaining; for on the day the island was visited, the superficial masses alone were slightly loosened by the sun's rays. Thus the plants are confined to an almost incessantly frozen locality, and a particularly barren soil, liable to shift at every partial thaw. During nearly the entire year, even during the summer weeks which the Expedition spent in sight of Cockburn Island, it was constantly covered with snow….The vegetation of so low a degree of latitude might be supposed to remain torpid, except for a few days in the year; when if the warmth were genial, and a short period of growing weather took place, the plants would receive an extraordinary stimulus. But far from such being the case, the effect of the sun's rays, when they momentarily appear, is only prejudicial to vegetation. The black and porous stones quickly part with their moisture; and the* Lecanora *and* Ulva *consequently become so crisp and parched, that they crumble into fragments when an attempt is made to remove them.*

Turrill (1953:140–196) provides many quotable extracts from *Flora Antarctica*, but those above show well enough Hooker's sharp eye and ecological reasoning. What he learned during the four-year expedition became a valuable part of his cumulative knowledge of plants worldwide and their distributions. "He became the outstanding English geo-botanist of the century, and his distinction was founded upon an unrivalled basis of experience on the ground" (Raby 1996:127). A modern biogeographer, Philip Darlington, summarized Hooker's conclusions (1965:4)

> *He thought that "land communications" between the areas in question were required for the higher orders of plants, but that spore-bearing forms might have been carried long distances by the "violent and prevailing westerly winds." And he thought that cold-adapted subantarctic plants isolated on mountains on New Zealand must have dispersed while the climate was colder than now and must have been stranded on mountain tops by a change (warming) of climate.*

Darlington commented: "The land communications are very doubtful; the change of climate is certainly correct in general."

Darwin had presented his plants from his own voyage to Henslow, but as we saw (Egerton 2010:417), Henslow had only described two *Opuntia* from Galápagos and the plants from South Keeling Island. He suggested turning over the others to Hooker (who married Henslow's eldest daughter). Hooker was very busy describing his own specimens, but he found the time to describe Darwin's Galapagos species (Egerton 2010:417). They became best friends.

For four years Hooker worked on publishing his *Antarctic Flora*, and then, before finishing, obtained commissions to collect fossils for the Geological Survey and plants for the Royal Botanic Gardens. (Fossils he had collected on the Antarctic voyage got mislaid and were relocated in 2011.) <bgs.ac.uk/discoveringGeology/geology/Of Britain/archives/jdhooker/home.html> He left on 11 November 1847 for a three-year expedition to India. He reached Calcutta on 12 January 1848 (Huxley 1918, I:223, 233, Desmond 1999:96–98). This was a land expedition (Coats 1969:157–168, Desmond 1999:99–177, Short 2004:57–69), prompted to some extent by discussions with Darwin over the relationship between elevation and vegetation (Reidy 2010:28–29). Although Hooker published early impressions (1848), it was his superb *Himalayan Journals* (1854) that provided valuable information, more readily available than for his Antarctic expedition. One historian thinks this book is "one of the few and certainly one of the most accomplished examples for India of a scientific travel narrative comparable to those of Humboldt, Darwin, and Wallace" (Arnold 2005*a*:185, *b*). Hooker remained in India long enough "to profit handsomely from accumulated colonial (and even, to a degree, indigenous) knowledge."

Observations of the correlation between climate and vegetation, which he began during the Antarctic voyage continued in India (Hooker 1891:30, Turrill 1953:30)

> *Though the botany of Paras-nath proved interesting, its elevation was not accompanied by such a change from the flora of its base as I had expected. This is no doubt due to its dry climate and sterile soil; characters which it shares with the extensive elevated area of which it forms a part, and upon which I could not detect above 300 species of plants during my journey. Yet, that the atmosphere at the summit is more damp as well as cooler than at the base, is proved as well by the observations as by the vegetation; and in some respects, as the increased proportion of ferns, additional epiphytal orchidous plants,* Begonias*, and other species showed, its top supported a more tropical flora than its base.*

He occasionally suffered from Humboldtian impulses, as in the Soane Valley (Hooker 1891:26, Turrill 1953:31)

> *Finding the fresh milky juice of* Calotropis *to be only 72°, I was curious to ascertain at what depth this temperature was to be obtained in the sand of the river-bed, where the plant grew.*
>
> *Surface . . . . . 1041/2°*
> *1 inch. 102*
> *2 inches. . . 94*
> *21/2 inches . . 90*

31/2 inches. . 85 Compact.
8 inches . . . . 73 Wet.
15 inches . . . 72 Ditto.

The power this plant exercises of maintaining a low temperature of 72°, though the main portion which is subterraneous is surrounded by a soiled heat to between 90° and 104°, is very remarkable, and no doubt proximately due to the rapidity of evaporation from the foliage, and consequent activity in the circulation. Its exposed leaves maintained a temperature of 80°, nearly 25° cooler than the similarly exposed sand and alluvium. On the same night the leaves were cooled down to 54°, when the sand had cooled to 51°. Before daylight the following morning the sand had cooled to 43°, and the leaves of the Calotropis *to 451/2°. I omitted to observe the temperature of the sap at the latter time; but the sand at the same depth (15 inches) as that at which its temperature and that of the plant agreed at mid-day was 68°. And assuming this to be the heat of the plant, we find that the leaves are heated by solar radiation during the day 8°, and cooled by nocturnal radiation 221/2°.*

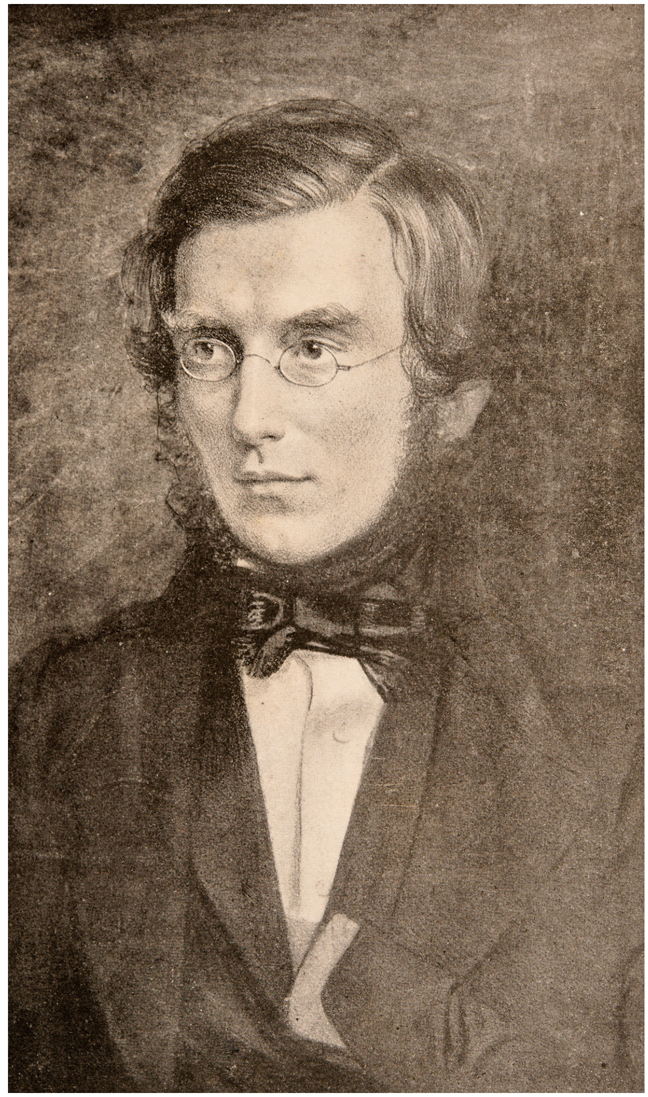

Fig. 5. Joseph Dalton Hooker, age 32, by William Tayler (1808–1892) in 1849. Huxley 1918, I: facing page 340. Tayler was Postmaster General of Bengal.

In October 1848, Hooker began a three-month expedition into the Nepal Himalayas and on into Sikkim. He wanted to enter country unknown to Europeans, which required carrying food for most of the journey, and through country that pack animals might not be able to travel. His party of 56 people included 30 porters (Hooker 1969, I:168–169). As he ascended, he drew a correlation between the plant species found and their elevation (Hooker 1891:75, Turrill 1953:31–32). Species observed at 6000 feet included both vines and trees that embraced other trees and eventually killed the host, just as explorers had found in the Amazon basin.

Continuing on to 12,000 feet elevation, he found (Hooker 1891:152–153, Turrill 1953:34)

...sloping mountains clothed for 1,000 feet with dark-green rhododendron bushes; and detached masses of rock were scattered about, and to the right and left snowy peaks towered over the surrounding mountains, while amongst the latter narrow gulleys led up to blue patches of glacial

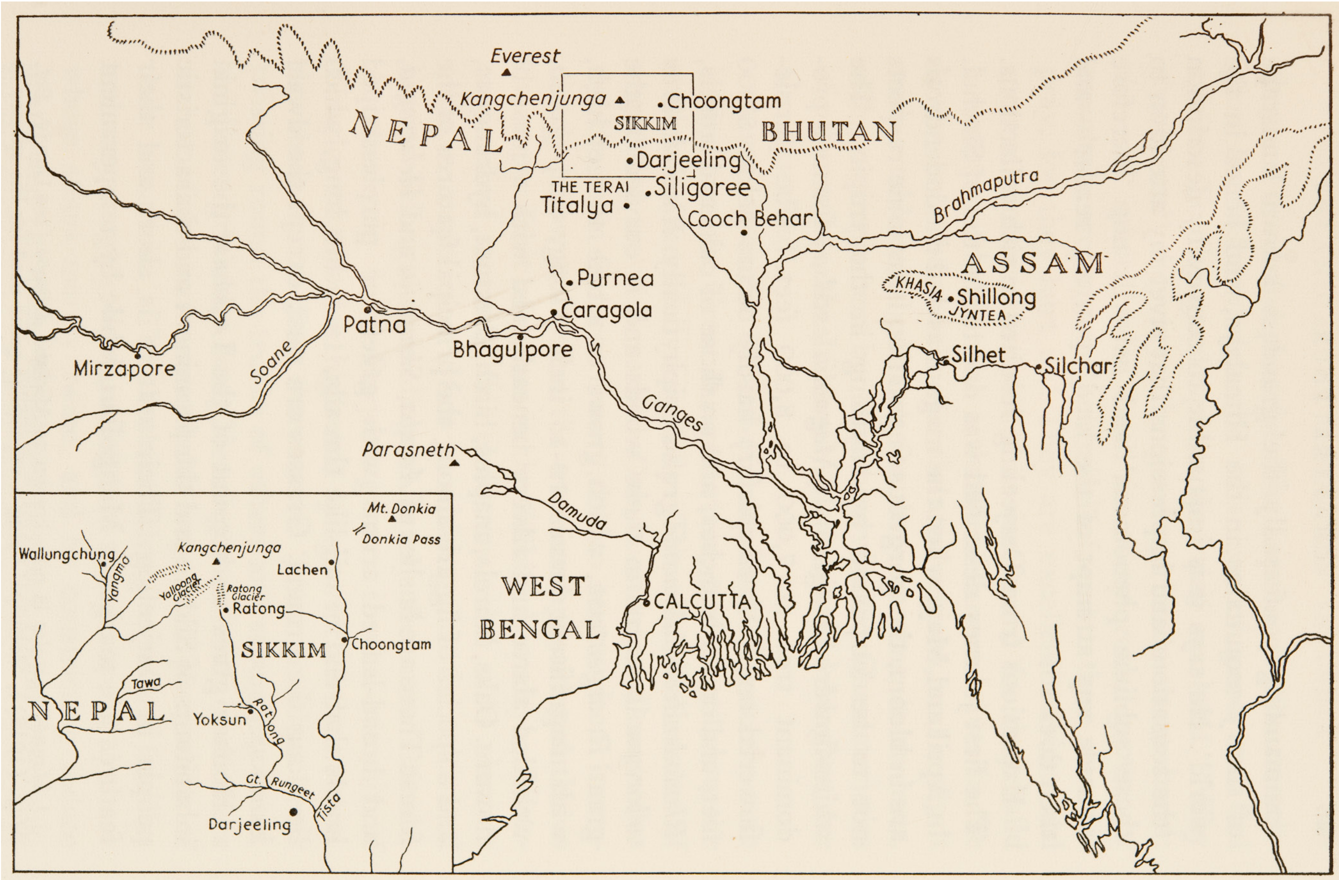

Fig. 6. Map of northeastern India and the Kangchenjunga area (inset), where Hooker mainly collected. Turrill 1963:57.

*ice, with trickling streams and shoots of stones. Dwarf rhododendrons with strongly-scented leaves (*R. anthopogon *and* setosum*), and abundance of a little* Andromeda*, exactly like ling, with woody stems and tufted branches, gave a heathery appearance to the hill-sides. The prevalence of lichens, common to this country and to Scotland (especially* L. geographicus*), which coloured the rocks, added an additional feature to the resemblance to Scotch Highland scenery.*

Hooker began publishing a book in London on the rhododendrons of the Sikkim Himalayas in 1849, while he was still in India, edited by his father, with lithographs by Walter Fitch, based on Hooker's sketches (Allan 1967:182). He also introduced many rhododendron species into British gardens. "On the climate and vegetation of the temperate and cold regions of East Nepal and the Sikkim Himalaya Mountains" (1852) was one of Hooker's most ecologically interesting writings. Although its purpose was to facilitate cultivating rhodendrons in Britain, and it appeared in a horticultural journal, it provided information on topography, climate, and which of 28 species are found at three elevations: 6000–10,000 feet, 10,000–14,000 feet, and 14,000–18,000 feet (1852:91–103). Three species were epiphytes, because in a moist climate, they found it easier to sprout on mossy limbs than in impenetrable undergrowth (Hooker 1852:72).

On 9 September 1849, Hooker reached Donkia Pass, 18,466 feet elevation, eclipsing his hero Humboldt's ascent of Chimborazo (18,096 feet). On 13 September he scaled the flanks of Donkia to 19,300 feet. However, he was not climbing mountains just because they were there (Huxley 1918, I:304–305).

I have a set of most curious new plants from between 17 and 19,000 feet—Woolly Lactuceae *and* Senecioneae *like* Culcitium, Gentians, Chrysanthemums, Saxifrages *of course,* Cyananthi*, and some very odd things. They are extremely scarce and require close hunting. Sometimes I get but one or two specimens of a kind, and poking with a headache is very disagreeable.*

...I was greatly pleased with finding my most Antarctic plant, Lecanora miniata*, at the top of the Pass, and to-day I saw stony hills at 19,000 feet stained wholly orange-red with it, exactly as the rocks of Cockburn Island were in 64° South; is not this most curious and interesting? To find the identical plant forming the only vegetation at the two extreme limits of vegetable life is always interesting; but to find it absolutely in both instances painting a landscape, so as to render its colour conspicuous in each case five miles off, is wonderful.*

Occasionally, Hooker's encyclopedic knowledge intrudes, as in this passage (1891:313–314, Turrill 1953:39).

The vegetation in the neighbourhood of Lamteng is European and North American; that is to say, it unites the boreal and temperate floras of the east and west hemispheres; presenting also a few features peculiar to Asia. This is a subject of very great importance in physical geography; as a country combining the botanical

Fig. 7. Tambur River at the lower limit of firs. By Walter Fitch based on Hooker's sketch, November 1848. Hooker 1969, I:198.

Fig. 8. *Rhododendron thomsonii*, named by Hooker for his friend Thomas Thomson. By Walter Fitch, based on Hooker's sketch. Hooker 1849–1851.

Fig. 9. “The botanist in Sikkim,” by William Tayler, 1849, perhaps modified by Fitch. Desmond 1999:138.

characters of several others, affords materials for tracing the direction in which genera and species have migrated, the causes that favour their migrations, and the laws that determine the types or forms of one region, which represent those of another. A glance at the map will show that Sikkim is, geographically, peculiarly well situated for investigations of this kind, being centrally placed, whether as regards south-eastern Asia or the Himalayan chain. Again, the Lachen valley at this spot is nearly equi-distant from the tropical forests of the Terai and the sterile mountains of Tibet, for which reason representatives both of the dry central Asiatic and Siberian, and the humid Malayan floras meet there.

The mean temperature of Lamteng (about 50°) is that of the isothermal which passes through Britain in lat. 52°, and east Europe in lat. 48°, cutting the parallel of 45° in Siberia (due north of

Lamteng itself), descending to lat. 42° on the east coast of Asia, ascending to lat. 48° on the west of America, and descending to that of New York in the United States. This mean temperature is considerably increased by descending to the bed of the Lachen at 8,000 feet, and diminished by ascending Tukcham to 14,000 feet, which gives a range of 6,000 feet of elevation, and 20° of mean temperature….the climate and vegetation becomes Arctic at 12,000 feet…

(Lamteng is not named on the map (Fig. 3) but it is in the Lachen Valley, which is named.) Hooker then illustrated the points just made with examples of genera.

On 1 May 1850, Hooker was joined by his friend from university, Thomas Thomson (1817–1878), a surgeon in the East India Company (Coats 1969:164, Desmond 1977:609–610, Endersby 2008:50–51). They explored the Khasia Mountains of Assam (Fig. 3). Hooker concluded that the Khasia flora was the richest in India, with 250 orchid species, growing on trees, rocks, in woods, and on grassy slopes. There were 150 kinds of ferns, and they collected a total of over 2500 species. But Khasia also had heavy rainfall—500 inches during their seven-month stay (Turrill 1963:71–72).

Hooker left Calcutta on 28 January 1851 and reached England on 25 March. He was not yet ready to focus entirely on India, because he had only published *Flora Antarctica* before going to India; he still had to publish *Flora Novae-Zelandiae* (1852–1855) and *Flora Tasmaniae* (1855–1859). He published the "Introductory Essay" on 6 December 1853 (pages i–xxxix; excerpts in Turrill 1953:144–156, Lomolino, Sax and Brown 2004:109–117), in which he discussed the nature of species and their distributions. He had read Darwin's 1844 essay on the origin of species, but had not been persuaded. He wanted to determine what could be clearly known. Besides his *Himalayan Journals*, he coauthored *Flora Indica* (1855) with Thomas Thomson (1817–1878), a planned multivolume work of which only the first volume appeared (Endersby 2004*c*, Woodward and Grout 2004). Hooker wrote a 280-page "Introductory Essay" to it, excerpts being reprinted by Turrill (1953:48–57). In addition to being a masterful summary of Indian botany, it is a further example of Hooker's thinking on the nature of species, with Darwin in the back of his mind. Hooker also wrote the text for *Illustrations of Himalayan Plants* (1855). In 1872, he began, with various collaborators, to publish *The Flora of British India* (seven volumes, 1872–1897). In 1904, he had a final opportunity to summarize his accumulated knowledge of Indian plants; he divided them into nine provinces and discussed each province separately, with a map (excerpted in Turrill 1953:xii [map] + 57–68).

In 1856, Darwin asked him to critique part of his own big book on species, attempting to explain the distribution of Arctic species on mountain tops (Browne 1983:131–134). Darwin hypothesized icebergs as means to transport seeds of plants from Arctic regions floating south. Hooker had first-hand experience with icebergs and had never seen one carry seeds. Furthermore, if icebergs were the means of dispersal, then the floras of mountaintops should show a random distribution similar to island floras, which was not the case.

Hooker enjoyed expeditions, but for Huxley, as for Darwin, it was a once-in-a-lifetime adventure. Thomas Henry Huxley (1825–1895) was from Ealing, a village near London (Huxley 1900, Williams 1972, Di Gregorio 1984, Desmond 1997, White 2000, 2003, 2004). He was soon apprenticed to medical practitioners, and ambition motivated him to read extensively and join the navy as assistant surgeon.

Captain Owen Stanley (1811–1850) of H.M.S. *Rattlesnake* (West 1967), a surveying ship similar to those on which Darwin and Hooker had sailed, obtained Huxley's services after consulting Sir John Richardson (Desmond 1997:40; on Richardson, see Egerton 2011). The *Rattlesnake* surveyed the waters and coast of New Guinea and eastern Australia, 1846–1850. Stanley was son of Bishop Edward Stanley (1779–1849), president of the Linnean Society of London (Prothero and Matthew 2004), and Huxley would send scientific papers to the bishop during the voyage. Before departing, Edward Forbes advised Huxley on the collecting and study of marine life. Huxley's *Rattlesnake* diary (Huxley 1935) tells what he did and with whom he interacted (he met his future wife in Sydney), but did not contain his zoological observations, as did Darwin's *Beagle Diary* (then unpublished). He kept a parallel scientific journal (two volumes manuscript), to which Julian Huxley had access when editing the diary for publication, and he summarized their contents as a chapter in *T. H. Huxley's diary on the voyage of* H.M.S. Rattlesnake (Huxley 1935:36–58). Although Huxley focused his studies on invertebrates, Julian Huxley noted that the *Rattlesnake* surveyed the Great Barrier Reef off northeast Australia, yet T. H. Huxley never studied corals. He would have known of Darwin's book on corals (1842), which might have inhibited his interest in them. Further information is in the *Narrative of the Voyage of H.M.S. Rattlesnake* (two volumes, 1852) by ornithologist John MacGillivray (1822–1867), son of William, Audubon's collaborator (Egerton 2011). Huxley provided 24 illustrations for MacGillivray's volumes, mostly landscapes and pictures of natives at places visited. MacGillivray (1852, I:21–28) described a dredge and a tow-net which he and Huxley devised to obtain zoological specimens from the bottom and top of the ocean.

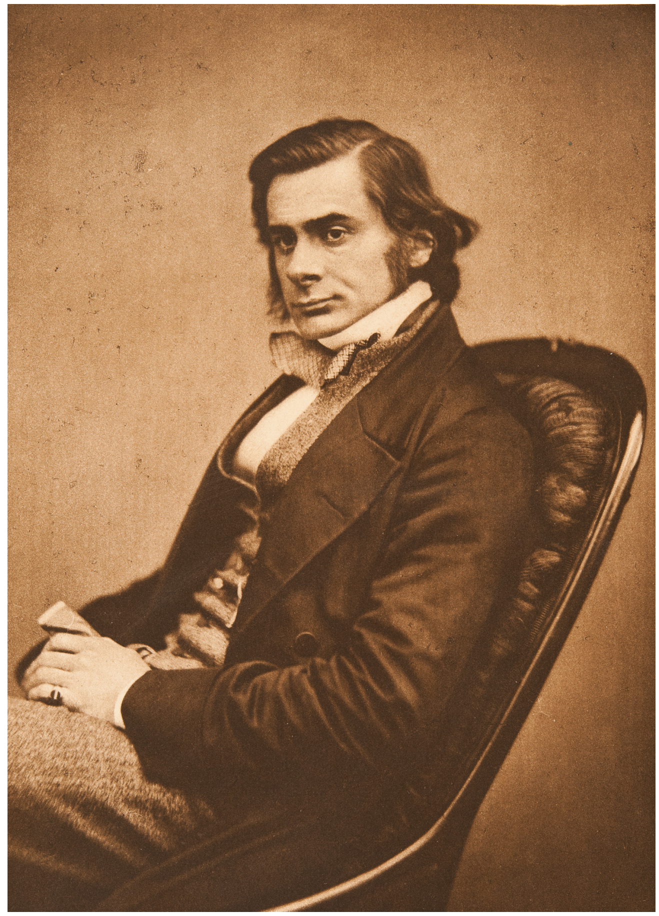

Fig. 10. Daguerreotype of Thomas Henry Huxley, 1857. Huxley 1900, I: facing 149.

Huxley's main focus was on anatomy of Coelenterata, Cephalous Mollusca, and Tunicata. In a later autobiography (Huxley 1909:6) he explained

> *…there is very little of the genuine naturalist in me. I never collected anything, and species work was always a burden to me; what I cared for was the architectural and engineering part of the business, the working out of the wonderful unity of plan in the thousands and thousands of diverse living constructions, and the modifications of similar apparatuses to serve diverse ends.*

Before leaving on the voyage he had studied the blood of *Amphioxus* (Huxley 1847, 1898:4–5). The relationship of tunicates to vertebrates remained unknown until 1870. Huxley's discoveries often

Fig. 11. Huxley's drawing of himself (center) on a brief expedition on the York Peninsula, Australia. Desmond 1997.

had implications for natural history, as in his descriptions of the digestive tract, reproductive anatomy, and oceanic distributions. Modern ecologists know they need some knowledge of the anatomy and physiology of organisms they study. On 17 January 1847, he caught a Portuguese man-of-war (*Physalia*) and thought his examination "puts in a much clearer light the true analogies of these animals" (J. Huxley 1935:17). In November 1849, he confirmed a controversial discovery by author Adelbert von Chamisso (1781–1838) that salps occur in two forms, one solitary and the other in chains. Huxley went further, pointing out that the solitary stage was asexual and the chain stage sexual (Huxley 1851, 1898, I:38–68 + 3 plates, J. Huxley 1935:43–44, Winsor 1976:64–65). In trying to determine relationships between various groups, he made good use of the archetype concept: "It is remarkable how closely Huxley's archetypal Mollusc of 1853 resembles the ancestral type of Mollusc as deduced by zoologists eighty years later" (J. Huxley 1935:48). His most significant publication while on the voyage was "On the anatomy and the affinities of the family of the *Medusae*" (Huxley 1849, 1898:9–32 + Plates II–IV), which explored the relationships between jellyfish and other groups now considered coelenerates (Marshall 1970:83–84). When he returned from his voyage, he learned that this paper had attracted favorable attention. He continued publishing on marine life collected on the voyage, culminating in *The Oceanic Hydrozoa* (1859, 12 plates; Winsor 1976:73–97, Di Gregorio 1984:4–26). He saw the connection among different kinds of colenerates in their ectoderm and endoderm layers, these terms being coined by George Allman in 1853 (Di Gregorio1984:5). It was summarized and praised in a lengthy review (Anonymous 1860).

Meanwhile, A. R. Wallace, in London, 1 October 1852–March 1854, consulted zoologists and collectors of specimens and decided to go next to the Malay Archipelago (Dajoz 1984:50–58, Shermer 2002:77–82, Slotten 2004:88–103, Smith 2004). He was probably influenced by the insect collection that Ida Laura Pfeiffer (1797–1860) made in the Malay Archipelago, 1851–1853, part of which was sold by Samuel Stevens, who continued being Wallace's agent in Malaya, as he had been when Wallace was in Brazil (Baker 1995:153–154). Wallace successfully applied to

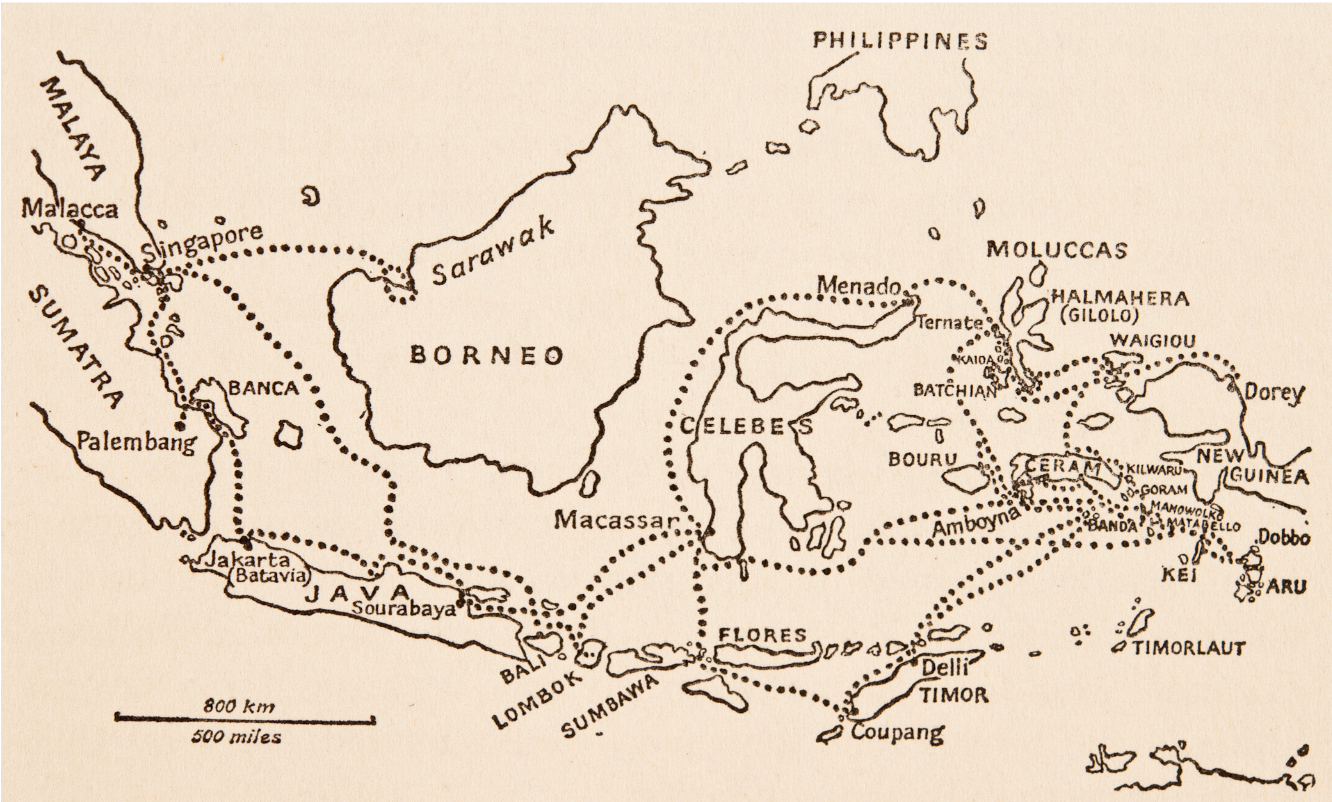

Fig. 12. Alfred Russel Wallace's travels in the Malay Archipelago, 1856–1862. George 1964:31. Wallace's own map of his travels is a fold-out (Wallace 1869: facing v, 1890: facing viii).

the Royal Geographical Society to arrange free passage for himself on government ships, and he also received letters of introduction (Raby 2001:87–88). He left England in March 1854 bound for Suez on one ship, and at the Red Sea took another to Singapore, which he reached on 20 April. Except for staying in Singapore and Malacca until 16 October, his travels were in what is now Indonesia (Fig. 12). George (1964:288–290) lists his itinerary and dates, until his return to England on 1 April 1862. It was a transformative expedition worthy of comparison to Darwin' s voyage on the *Beagle*. Two modern books retrace some of his routes, on sea (Severin 1997) and (mainly) on land (Daws and Fujita 1999).

Wallace arrived in Singapore as both an experienced collector and a dissatisfied theoretician still focused on the species question that he had not solved in Brazil. The stimulus for his writing "On the law which has regulated the introduction of new species" (1855) was reading Edward Forbes' "Presidential Address at the Geological Society," which expounded a theory of polarity (Forbes 1854:lxxvii–lxxxi, Rehbock 1983:102–113). Wallace thought it was "an ideal absurdity," when "a simple hypothesis will explain all the facts" (Wallace 1905, I:358). He tells us in his article that "It is about ten years since the idea of such a law suggested itself to the writer" (1855:185). In the article, he does not say what might have led him to his law, but his autobiography (Wallace 1905, I:256) quotes from a letter that he had written to Henry Walter Bates on 11 April 1846, in which he stated, “I first read Darwin’s *Journal* three or four years ago, and have lately re-read it.” His first reading would have been the first edition (1839), but he was likely prompted to re-read it by the appearance of a revised edition (1845).

Darwin, after discussing a large, puzzling fossil from Patagonia that Richard Owen identified as a large camel, concluded (1839:209)

> *The most important result of this discovery, is the confirmation of the law that existing animals have a close relation in form with extinct species. As the guanaco is the characteristic quadruped of Patagonia, and the vicuna of the snow-clad summits of the Cordillera, so in bygone days, this gigantic species of the same family must have been conspicuous on the southern plains.*

It is inconceivable that Wallace, such a generous man, would have intentionally “stolen” Darwin’s law. A decade or so after reading this, he remembered the thought without remembering it was Darwin’s, and not originally his own. We can now understand why Darwin, after reading Wallace’s 1855 paper at the urging of both Charles Lyell and Edward Blyth, found “nothing very new” in it (Browne 1995:537). Darwin himself had not written up this “law” as a separate article because it was part of his large book and he did not want to publicize the details of such thoughts prematurely.

Even though Wallace’s “law” was not as original as he thought it was in 1855, he wrote a very solid article that demonstrated for the first time that he was not just a collector who could write a few respectable articles: he showed he was a first-rate scientist. He pulled together four geographical and five geological “facts,” which were actually sophisticated generalizations, to support this law: “Every species has come into existence coincident both in space and time with a pre-existing closely allied species” (Wallace 1855:186). In the further elaboration of his arguments, he used examples from the Galapagos Islands, and he certainly knew he got the data, if not his arguments, from Darwin. He also drew upon a variety of other examples from other sources, which was impressive for someone on an expedition in the East.

One attraction of the Malay Archipelago was the chance to observe and collect orangutans, which were known to Europeans, but few had observed or collected them. He was pleased that he was successful in this quest, in 1865 in Borneo. He wrote three articles on his observations, published in England in 1856 (Smith 1991:476), and this information was later incorporated into Chapter 4 of *Malay Archipelago* (1869). Much of his account in Chapter 4 is about shooting specimens to sell (1869:51–74, 1890:31–48), which is unpleasant reading for anyone today concerned for their survival in the wild. Wallace did express fears about the long-term survivability of birds of paradise, but as close as he came to concern for orangutans was an expression of surprise at its range, limited to Sumatra and Borneo (Wallace 1869:72, 1890:47). Even on those islands, its habitat requirements were limiting, as he found on Borneo (Wallace 1869:68–69, 1890:44).

> *It seems at first sight very inexplicable that the Mias* [orangutans] *should be quite unknown in the Saráwak valley, while it is abundant in Sambas, on the west, and Sádong, on the east. But when we know the habits and mode of life of the animal, we see a sufficient reason for this apparent anomaly*

in the physical features of the Saráwak district. In the Sádong…Mias is only found where the country is low. Level, and swampy, and at the same time covered with a lofty virgin forest. From these swamps rise many isolated mountains, on some of which the Dyaks have settled, and covered with plantations of fruit trees. These are a great attraction to the Mias, which comes to feed on the unripe fruits, but always retires to the swamp at night. Where the country becomes slightly elevated, and the soil dry, the Mias is no longer to be found….in all the lower part of the Sádong valley it abounds, but as soon as we ascend above the limits of the tides where the country, though still flat, is high enough to be dry, it disappears.

Wallace thought that "a wide extent of unbroken and equally lofty virgin forest is necessary to the comfortable existence of these animals." They rarely descended to the ground, and natives said they only had two occasional enemies, crocodiles and pythons, and natives assured Wallace that they were strong enough to kill both.

In his Amazon *Travels*, he had discussed geography after his travelogue, but *Malay* opens with geography, and for a good reason: "Wallace's line." On 15 June 1856, he sailed from Bali to Lombok, arriving two days later (though only 15–20 miles away). Both islands have volcanoes about 8000 feet high, and one can see both volcanoes from either island. He had been on Bali only two days, but its flora and fauna seemed about the same as he had seen other islands west of it. When he reached Lombok, however, where he remained from 17 June to 30 August, he found a strikingly different flora and fauna. Bali and Lombok became for Wallace as provocative as the Galapagos Islands were for Darwin. In *Malay* (Wallace 1869:20–21 + map, 1890:7–8 + map) he showed Bali in an Indo-Malayan region and Lombok in an Austro-Malayan region. Later, when considering faunal regions of the world, he showed Bali as being in the Oriental Zoo-Graphical Region and Lombok being in the Australian Zoo-Geographical Region (Wallace 1876, I: maps facing 315, 387). Before publishing *Malay*, he found that George W. Earl had pointed out in 1845 that Sumatra, Java, and Borneo were separated from Asia by only a shallow sea, and that New Guinea and nearby islands were separated from Australia by only a shallow sea. Earl concluded that this indicated that Asia and Australia had once been connected, but because of floral and faunal differences, Wallace concluded that they had been separated for a very long time. He then put this situation within a broader context. Britain's plants and animals were very similar to those of Europe, but those of Ceylon (Sri Lanka) were more dissimilar to those of India, even though Ceylon was closer to India than Britain to Europe. By 1869, he could argue that two processes of change could account for this paradox: species change over time, and the depth of channels could increase over time. His reasoning was plausible at the time. An understanding of plate tectonics, which is now seen as essential for understanding this puzzle, was a century away (Whitmore 1981, Keast 1983, van Oosterzee 1997).

Wallace's skill at evolutionary–ecological reasoning is well illustrated in his discussion of the black cockatoo, *Microglossum aterrimum*, which has a powerful beak. He explained that this species had developed a technique for cracking hard and slippery kanary-nuts, using a leaf in its upper mandible to prevent slippage (1869:452, 1890:341–343).

Thus every detail of form and structure in the extraordinary bill of this bird seems to have its use, and we may easily conceive that the black cockatoos have maintained themselves in competition with their more active and more numerous white allies, by their power of existing on a kind of food which no other bird is able to extract from its stony shell.

Fig. 13. The line separating Oriental and Australian fauna regions according to Wallace, and as revised by later naturalists as more data became available. Mayr 1944:2.

Although he only published this observation and conclusion in 1869, they are based on his journal for March–May 1857, before he formulated his theory of evolution.

The most famous episode in Wallace's career came in 1858 when he wrote his second theoretical manuscript, "On the tendency of varieties to depart indefinitely from the original type" (1858), which

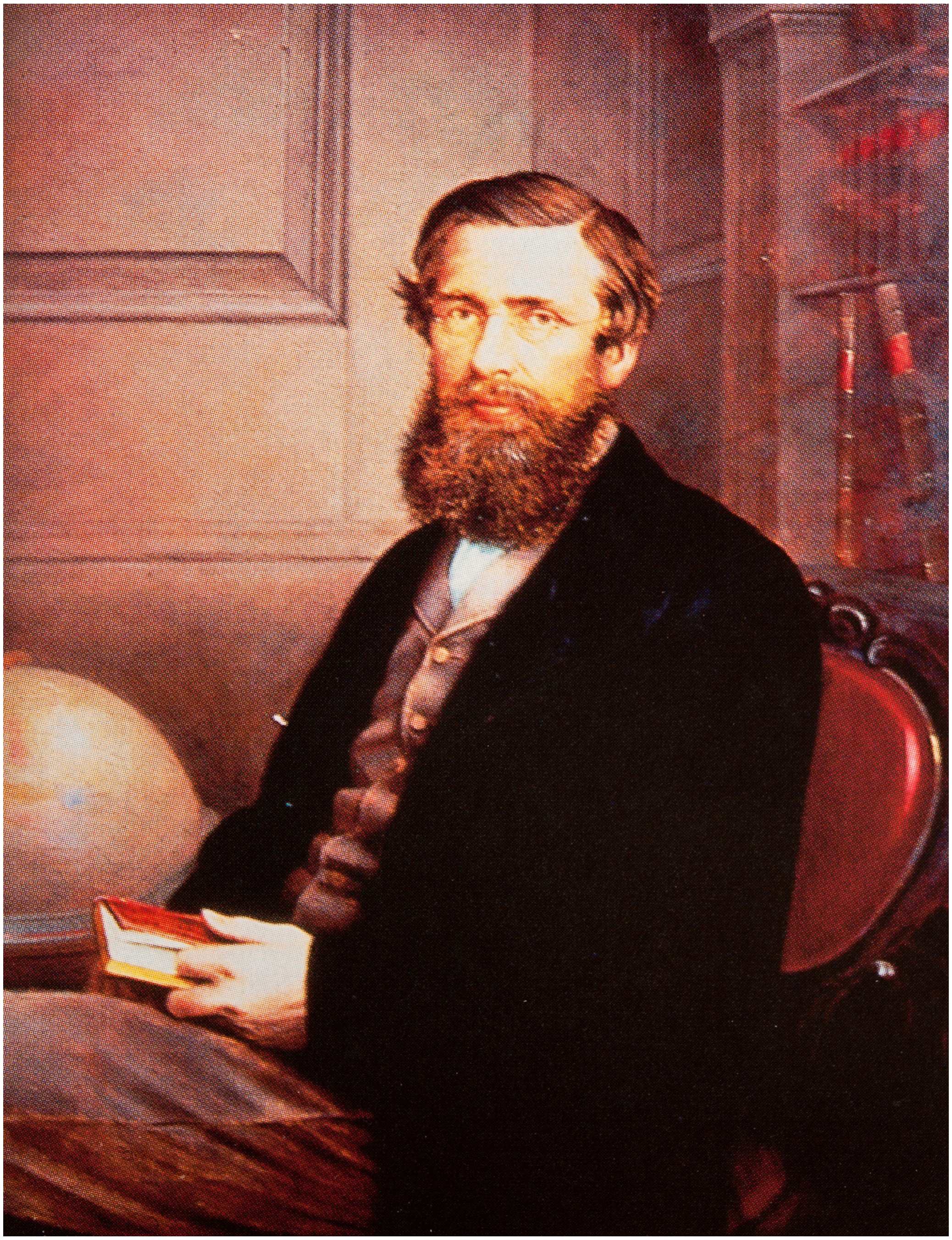

Fig. 14. Alfred Russel Wallace, age 46. A colored photograph. National Portrait Gallery, London. Severin 1997:148

he sent to Darwin. Darwin, of course, was dismayed to read Wallace's independent development of the theory of evolution by natural selection—on which Darwin was writing a lengthy treatise (Darwin 1975). How had Wallace achieved his independent discovery? In *My Life* (Wallace 1905, I:232), he says that in 1844, when living in Leicester, he used the town library and read Humboldt's *Personal Narrative* *of Travels in South America* and Malthus' *Principles of Population*. The latter

> *... I greatly admired for its masterly summary of facts and logical induction to conclusions. It was the first work I had yet read treating of any of the problems of philosophical biology, and its main principles remained with me as a permanent possession, and twenty years later gave me the long-sought clue to the effective agent in the evolution of organic species.*

It seems more than coincidental that he mentioned reading Humboldt and Malthus in the same paragraph, since Humboldt referred to "the system of Malthus" several times in his *Personal Narrative* (Egerton 1970:333–334). It seems likely that Humboldt's discussions led both Wallace and Darwin to read Malthus (Egerton 1970:359–360). Furthermore, both read and greatly admired Charles Lyell's *Principles of Geology* (three volumes, 1830–1833). Finally, Wallace seems to have read both editions of Darwin's *Journal of Researches* (1839, 1845), with their many hints about changes in species. Wallace's field observations were consistent with what he read in these works.

A journalist (Brackman 1980) and an ecologist–evolutionist (Brooks 1984) have argued that Darwin could have lifted a key idea from Wallace's manuscript without acknowledgment. However, Ospovat (1981) and Beddall (1988) have provided convincing counter-evidence, and subsequent Wallace biographers have not accepted Brackman and Brooks' arguments (Wilson 2000:177–182, Raby 2001:137–139, Shermer 2002:128–150, Fichman 2004:98–104, Slotten 2004:104–159). Darwin's correspondence with Lyell and Hooker on this dilemma of how to deal honorably with the Wallace manuscript and protect his own book-length manuscript is published in his correspondence (Darwin 1991:117–124). The large work on which Darwin had worked in 1856–1858, before receiving Wallace's manuscript in 1858, is now published (1975), showing the great detail of Darwin's work. Wallace was neither stupid nor naïve, and he always saw Darwin as a true friend and colleague (Wallace 1905, II:1–22). He dedicated *The Malay Archipelago* to Darwin, "as a token of personal esteem and friendship but also to express my deep admiration for his genius and his works."

Wallace appreciated having his 1858 essay read with some of Darwin's writings at the Linnean Society meeting on 1 July and subsequently published jointly also with Darwin's, but he was still collecting in the field and never had time to rest on his laurels. An evolutionary theory had been his main goal, and it was a gratifying achievement, but he next published his discovery of the distinction between the Oriental and Australian zoogeographical regions (Wallace 1860). It provided a working hypothesis for his further research and an organizing theme for his *Malay Archipelago*, which is organized by groups of islands, moving more or less from west to east: Indo-Malay Islands, Timor Group, Moluccas, and Papuan Group. He saw that there were two main races of people, which were comparable to the zoogeographical regions, except that the dividing line between them was farther west than the Bali-Lombok line. He attributed this geographic difference between the two lines to the Malayans being more seafaring and having a more highly organized civilization, which enabled them to either colonize islands faster than the Papuans or else push the Papuans eastward if they initially had colonized farther west than they lived in modern times (Wallace 1890:15).

However, Wallace's collecting of specimens was broad, and his interests were broader than evolution and biogeography. Of 125,660 specimens he collected, 109,700 were insects, representing at least 1250

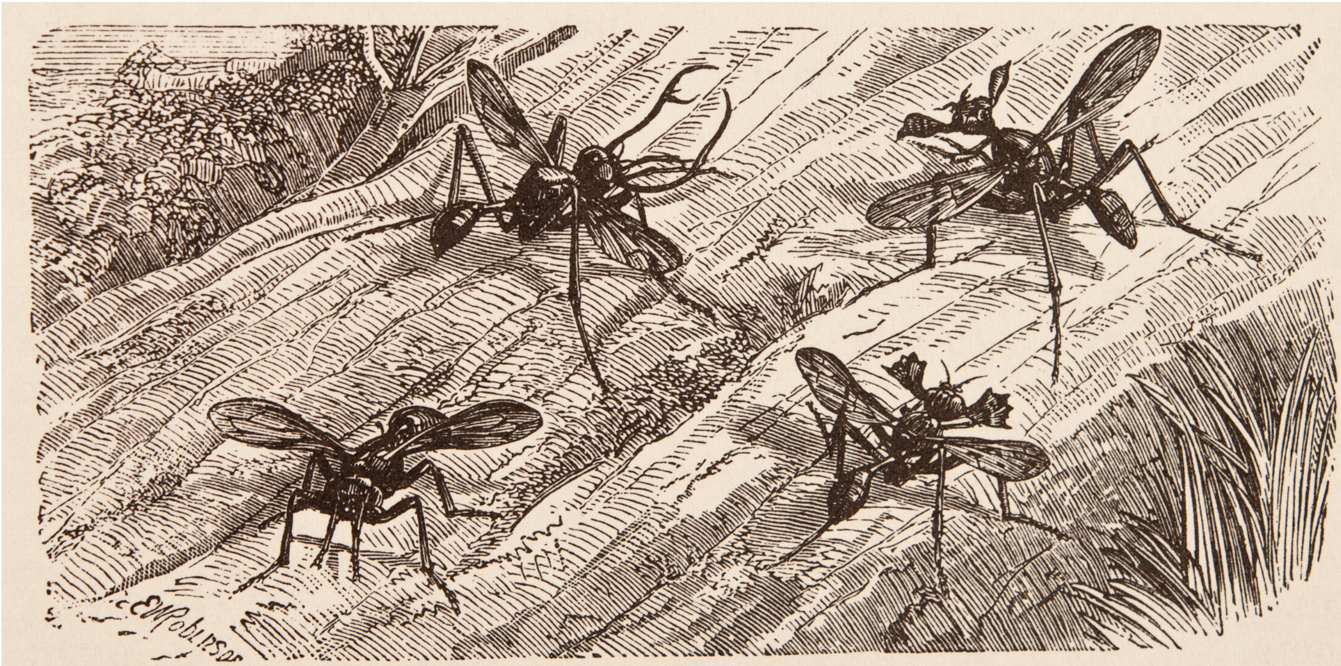

Fig. 15. Four species of horned flies from New Guinea. Wallace used Saunders' invalid *Elaphomia* genus name instead of Gerstaecher's valid *Phytalmia*. Wallace 1890:383.

new species (Mearns and Mearns 1998:319). While in New Guinea, April–July 1858, he collected 70 dipteran species, of which "the most curious and novel were a group of horned flies, of which I obtained four distinct species, settling on fallen trees and decaying trunks" (Wallace 1890:383). They were part of his next shipment to Stevens, who sold some specimens to William Wilson Saunders (1809–1879).

Saunders (1861) named and described them in the Entomological Society of London's *Transactions*. In *Malay Archipelago*, Wallace used Saunders' names for them. However, Adolf Gerstaecker (1828–1895), curator of entomology at the Museum für Naturkunde Berlin had already named the genus and two species (1860), and so his genus name, *Phytalmia*, is valid (Glaubrecht and Kotrba 2004:284). Although Wallace noted that only males have "horns," he did not speculate on their function, and in 1871 when Darwin cited this genus as an example of sexual selection, Wallace disagreed (Glaubrecht and Kotrba 2004:292).

Bates's paper on protective coloration and mimicry (1862; see Egerton 2012) was interesting to Wallace, and he read a paper to the Linnean Society on 17 March 1864, "On the phenomena of variation and geographical distribution as illustrated by the Papilionidae of the Malayan Region" (Wallace 1865). The title did not mention mimicry, but it included a discussion of Malayan *Papilios* that resembled *Danais* (Blaisdell 1992:144–156). He also wrote a more general article that appeared as an anonymous review: "Mimicry, and other protective resemblances among animals" (Wallace 1867), which was

Fig. 16. *Kallima paralekta* leaf butterflies, showing top of wings (top) while flying and bottom of wings when at rest (bottom). Drawn by T. W. Wood. Wallace 1890:101, 1962.

reprinted with additions and corrections in 1870 and reprinted again in 1891. In *Malay Archipelago* (Wallace 1869; cited in Wallace 1890:100–101), he described a different kind of mimicry: the butterfly *Kallima paralekta* resembled a dead leaf when at rest, thereby escaping detection by predators.

It was a variant of protective coloration. Predators could be confused because the upper surface of its wings was "of a rich purple, variously tinged with ash colour, and across the forewings there is a broad bar of deep orange, so that when on the wing it is very conspicuous," but that image disappeared when it landed. He thought that (Wallace 1890:102)

> *…although it is perhaps the most perfect case of protective imitation known, there are hundreds of similar resemblances in nature, and from these it is possible to deduce a general theory of the manner in which they have been slowly brought about. The principle of variation and that of "natural selection," or survival of the fittest, as elaborated by Mr. Darwin in his celebrated* Origin of Species*, offers the foundation for such a theory…*

Wallace also applied Batesian mimicry to explain why orioles resembled honeysuckers on two Molucca islands: on Bouru, the oriole *Mimeta bouruensis* resembled the honeysucker *Tropidorhynchus bouruensis*, and on Ceram *M. forsteni* resembled *T. subcornutus*. Clearly, orioles had changed, since these honeysuckers looked like other honeysuckers, but these orioles did not look like other orioles (1890:305–307). The *Tropidorhynchi* were strong with powerful claws and long, curved, sharp beaks, but orioles were weak, with small feet and claws. Small birds of prey would more likely avoid honeysuckers and catch orioles that did not resemble honeysuckers, while avoiding orioles that did look like honeysuckers. Wallace collected 8050 birds, of which 212 were new species (Mearns and Mearns 1998:319).

Malay Archipelago is a treasure trove of ecologically interesting natural histories, and more generally (Bastin 1986:vii)

> *This is the most famous of all books on the Malay Archipelago. It is the greatest travel book on the region and, in its analysis of the geographical distribution of animals, it ranks as one of the most important natural history books of the nineteenth century.*

When Wallace published *The Malay Archipelago* (London, two volumes, New York, one volume, 1869), he was far more experienced and sophisticated than he had been when he had published his Amazon *Travels* (1853), and he had stayed twice as long on his second expedition as he had on his first. He later considered that experience "the central and controlling incident of my life" (Wallace 1905, I:336), reminiscent of Darwin's claim about the impact of the voyage of the *Beagle* on him (Darwin 1959:76).

Huxley wrote "a well-reasoned paper on a limited group of birds (1868)" that also suggested modification of the world's biogeographical regions, a step toward modern boundaries of regions (Schmidt 1955:771).

Wallace's grand synthesis, *The Geographical Distribution of Animals* (two volumes, 1876) drew upon his knowledge of the Amazon Basin, the Malay Archipelago, his vast reading, museum researches, and attendance at meetings of learned societies. Both Darwin and Cambridge University ornithologist Alfred Newton had urged him to undertake the synthesis about six years earlier (Wallace 1876, I:vi). It is well organized, with 20 helpful illustrations (fig. ?) and 7 maps of zoogeographical regions. The only guide to literature Wallace provided is mention of zoologists' names and occasionally, a brief mention of titles, such as "Jerdon's Birds of India, Blyth's Catalogue, Bonaparte's Conspectus, and the Proceedings of the Zoological Society of London down to 1865" (1876, I:xiii). Wallace was probably unaware of Ludwig Schmarda's *Die geographische Verbreitung der Thiere* (1853), which accepted several centers of creation (Schmidt 1955:767–768), and Wallace omitted mention of Albert Günther, "On the Geographical Distribution of Reptiles" (1858), though he cited other Günther publications. He began (part 1) with a survey of means of dispersal and migration, then discussed "Distribution as affected by the conditions and changes of the earth's surface."

He accepted the six zoological regions of the earth (Palaearctic, Ethiopian, Oriental, Australian, Neotropical, Nearctic) that Philip L. Sclater (1858) had determined for birds (Mearns and Mearns 1992:394–397); each region had four sub-regions, this being three more than the regions August-Pyramus de Candolle had established for plants (Nelson 1983:482). Part II discussed the distribution of extinct species. Part III discussed in detail each of the six regions, and part IV was "a systematic sketch of the chief families of land animals in their geographical relations."

Darwin was quite pleased and wrote three letters: after finishing reading 184 pages, after finishing Volume I, and after finishing Volume II. Darwin expressed hope (5 June 1876) that others would publish accounts of the geography of insects, pulmonate mollusks, freshwater fishes, and plants, as Wallace had done for land vertebrates. When Darwin got to Volume II, he saw that Wallace did discuss fish and invertebrates. That Darwin included plants in his wish list shows that Alphonse de Candolle's *Géographie botanique raissonnée* (1855) had slipped his mind, though it was in his library, and both he and Hooker were favorably impressed when it appeared (Darwin 1989:419, 478, 497). That de Candolle's statistical analysis had not yielded hoped-for insights likely accounted for Darwin forgetting his treatise (Hofsten 1916:310–312, Pilet 1971, Browne 1983:310–312). More recent was Heinrich Grisebach's *Vegetation der Erde* (1871), which Darwin possibly did not know. Darwin expressed gratitude that Wallace had protested "against sinking imaginary continents in a quite reckless manner, as was started by Forbes, followed, alas, by Hooker, and caricatured by Wollaston and Murray" (Marchant 1916:235). Actually, Wallace had gone down that road with Forbes, Hooker, Wollaston, and Murray, but later backed away (Fichman 1977). A final resolution of that controversy could only come after continental drift and plate tectonics were understood in the mid-late 1900s (Nelson 1978:295–297). In his second letter (17 June 1876), Darwin praised an article by H. B. Blanford (1875) on the paleobotany of India and did not register a protest to Blanford's finding a Permian connection with South Africa (Marchant 1916:238). In his third letter (25 June 1876), Darwin lamented that Wallace had not given many references in those volumes (Marchant 1916:240). A later zoogeographer (Schmidt 1955:769) thought Wallace's treatise was ponderous, naïve in thinking there was enough knowledge available to solve certain problems (without knowledge of continental drift), yet a "necessary work to a specialist…" An even later critic thought "Wallace's overall result by today's standards is largely, if not purely, artificial" (Nelson 1983:486).

Wallace continued zoogeographical studies in *Island Life* (1880; second edition, 1895), dedicated to Hooker. He sent a copy to Darwin, requesting his comments. Darwin thought it Wallace's best book,

Fig. 17. Malayan forest on Malacca with hornbill, peacock, and gibbon. Wallace 1876, I: Plate 9, facing 340.

but enclosed seven pages of notes that Wallace could use in a second edition (Marchant 1916:251–252). Karl Schmidt thought *Island Life* represented "Wallace at his best" (1955:771). Furthermore, *Island Life* "alerted generations [of naturalists] to the dramatic possibilities islands offer for study of life," and ecologists have written more recent books on it (Carlquist 1965:8, MacArthur and Wilson 1967, Berrill and Berrill 1969, Amos 1980, Lazell 2005).

Hooker achieved as good or better knowledge of the distribution of vascular plants (Reed 1942:129–131, Turrill 1953) as Wallace's knowledge of the distribution of animals, though he did not chose to compete with de Candolle and Grisebach. Instead, he collaborated with other botanists on a *Flora of British India* (seven volumes, 1875–1897), collaborated with senior author George Bentham (1800–1884) on *Genera Plantarum* (three volumes, 1862–1883), and alone wrote other, smaller works (Huxley 1918, II:496–506, Turrill 1963:219, Stafleu and Cowan 1976–1988, II:274–283).

Hooker, Huxley, and Wallace were British biologists at the height of the British Empire in the Victorian Age. It was a time when British government and society were quite interested in sciences that cataloged and described plants and animals of interest to humanity, and there was a willingness to support scientists who went beyond the utilitarian in hopes that new uses of the biota would be discovered as knowledge increased (Brockway 1979, Baber 1996:174–176, Browne 1992, 1996, McClellan 2000, Endersby 2008). These men were glad to use their opportunities to advance their respective sciences, including evolutionary biology and biogeography, both of which became foundations for building a future science of ecology.

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